# SOKOINE UNIVERSITY OF AGRICULTURE

## PhD Thesis

# Effects of Habitat Heterogeneity on Rodent Community Ecology in West Mount Kilimanjaro, Tanzania

Suzana Mei Thomas

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# Effects of Habitat Heterogeneity on Rodent Community Ecology in West Mount Kilimanjaro, Tanzania

A thesis submitted in fulfilment of the requirements for
the degree of Doctor of Philosophy of Sokoine
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By

Suzana Mei Thomas

Supervisors

Dr. Geofrey Soka

Late Prof. Loth S. Mulungu

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# EXTENDED ABSTRACT

Mountainous regions in Sub-Saharan Africa have high diversity of rare and endemic small mammals. Mount Kilimanjaro is among the well-known biodiversity hotspots in the world. Variations in vegetation and climate along the altitudinal gradient of Mt Kilimanjaro create distinct habitats with unique conditions which support high diversity and endemism of small mammals. Rodents are widely distributed small mammals inhabiting a variety of habitats. They are considered ecosystem engineers through burrowing, pollination, and seed dispersal hence they can act as ecological indicators of ecosystem health. However, most rodents are crop pests and reservoir of zoonotic pathogens.

Studies on community ecology have reported that, rodent community is directly influenced by many factors like vertical and horizontal vegetation structure, anthropogenic activities, seasonality, predation, inter and intra specific competition, as well as disease and parasites.

Understanding rodent diversity, species composition and the ecological interaction in a community is crucial for conservation and management of target species.

Mount Kilimanjaro has high diversity of small mammals, however, climate change and increasing anthropogenic activities mainly cultivation and expansion of forest plantations particularly in west Kilimanjaro pause a challenge to conservation of small mammals. In recent decades, research on small mammals including rodents on Mt Kilimanjaro has been seriously ignored. Few existing studies were mainly based on short term surveys that provided a list of rodent species, composition and abundance. The studies did not fill in the gaps on breeding activity, population fluctuations, home range size, survival

and resource partitioning of rodents. Therefore, this study was aimed to investigate the effects of habitat heterogeneity and environmental factors like climate, soil, and topography on community ecology of rodents in West Mount Kilimanjaro, Tanzania. Specifically, it was aimed to answer four objectives; to assess rodent species diversity and community assemblage and establish habitat associations of individual species. Secondly, to evaluate the spatial-temporal variations in diet and resource partitioning of dominant rodent species. Third, to assess the breeding activity and population fluctuations of the dominant rodent species. Fourth, to determine home range size and survival probability of dominant rodent species and the influencing factors.

Data collection was conducted for two years starting from April 2020 to March 2022 covering both dry and wet seasons. Wet season occurred from October-December, and March-May and dry season was from June-September and January-February. The Capture-Mark-Recapture and Removal methods were used for trapping with the use of different traps. For Removal technique, trapping was done in seven habitats including montane forest (upper and lower), plantation forest, fallow, agricultural fields, moorland and ecotone. Sherman's live traps and snaps were placed in alternating trap stations, together with Havahart traps placed at some random points. In CMR method, a total of seven grids of 70 x 70 m were established. One replicated grid in fallow and moorland, and two replicated grids in a montane forest. Each grid had 49 Sherman's live traps in total placed 10 m apart. Different types of baits were used; peanut butter in Sherman traps, coconut in snap traps, carrots, ripe banana and roasted meat in Havarhart traps. Trapping was conducted for 3 nights consecutively in every month for two years.

For objective number one, to assess rodent species diversity and community assemblage, and establish habitat associations of individual species, data from both CMR and Removal methods were used. Vegetation characterization was conducted using nested square plots. Soil core and composite samples were collected for analysis of soil type, moisture, PH and bulk density. Fourteen species of rodents were captured. *Rhabdomys pumilio (*confirmed name *Rhabdomys dilectus)*, *Praomys delectorum* (confirmed name *Montemys delectorum*) and *Lophuromys verhageni* (confirmed name *Lophuromys aquilus)* predominated the samples and accounted for 69.35% of trapped rodents. *R. dilectus* and *L. aquilus* were found in all seven habitats except for the former whose occurrence was restricted in montane forest. Rodent species richness and abundance were positively influenced by habitat types and composition, seasonality, soil texture and bulk density. Diversity was highest in fallows followed by montane forest and lowest in plantation forest and agricultural fields. Individual species responded differently to variations in vegetation structure resulting into two distinct communities. The two distinct rodent communities identified were comprised of habitat generalists and habitat specialists, which was a result of habitat association and response of specific rodent species to vegetation structure.

Furthermore, for understanding resource partitioning and the mechanisms of coexistence, spatial and temporal variations in diets of the two dominant species *Lophuromys aquilus* and *Rhabdomys dilectus* which were found to be sympatric was determined. Gut samples of individuals that were killed by snap traps (in removal method) were analysed for food items (vegetative materials, seeds, invertebrates, roots, and hairs). Percentage occurrence, contribution, relative importance, niche breadth and overlap were compared between fallows, agricultural fields, and

moorland and between dry and wet season. The two rodent species consumed all the five food items indicating diet generalist behaviour or omnivory. Vegetative materials and seeds predominated all the diet categories (consumed in higher proportions). However, *R. dilectus* preferred the seeds whereas *L. aquilus* preferred invertebrates especially during wet season when they are abundant. Moreover, there was a significant variation in niche breadth between the species with *L. aquilus* having a broader niche breadth than *R. dilectus*. The two rodent species had a remarkable niche overlap which ranged from 0.84 to 0.98 however; this did not indicate competition but rather coexistence.

Since the two rodent species *Rhabdomys dilectus* and *Lophuromys aquilus* were found to coexist, it was important to understand their breeding activity, population fluctuations and the influencing factors across habitats and seasons. Two years CMR data was used, however comparisons were made between moorland and fallow only, because *Rhabdomys dilectus* did not occur in montane forest. Female sex ratio of both species did not differ significantly between the habitats. However, it highly fluctuated from the expected margin in the moorland habitat. The proportion of breeding individuals for both species differed significantly between the habitats but not between the seasons. In this study breeding activity was year-round in fallow and discrete or seasonal in moorland. Also, population size was significantly higher in fallow than in moorland, probably due to high vegetation cover in fallow which provides food and protection from predators.

In addition, same data set from CMR technique were analysed to determine home range and survival probability of the two species. Home range size was estimated using MCP only for individuals with at least five trap relocations. Mean home range size did not significantly differ between the species. However, *L. aquilus* had larger home range

size compared to *R. dilectus*. Results from analysis within species indicate that, home range of *Rhabdomys dilectus* significantly differed between habitats, being higher in moorland than in fallow. Similarly, home range of *Lophuromys aquilus* differed between habitats and sex. It was significantly higher in moorland than in fallow. Male *L. aquilus* had larger home range size than females. Furthermore, both survival and capture probabilities differed significantly between species. Survival probability of *L. aquilus* was significantly higher than that of *R. dilectus* suggesting that the former species is well adapted to live on Mt Kilimanjaro, whilst lower survival probability for *R.dilectus* could be due to predation, since this species prefers open grasslands. Lower capture probability of *Lophuromys* than that of *Rhabdomys* suggest that it is a trap shy species whereas *R. dilects* is a trap lover. Moreover, best models indicated that survival probability of individual species were mainly influenced by season and sex. Females of both species had higher survival probability than males, probably because females move smaller distances and spend more time inside their nest contrary to males which move longer distances searching for mates, hence increases predation risk.

The present study shows that Mt Kilimanjaro supports high diversity of rodents due to its heterogeneous habitats and complex ecosystems. It confirms with previous studies that, vegetation structure and seasonality are important factors for rodent species diversity and community assemblages. Moreover, it demonstrates that rodent’s breeding activity and population fluctuations are affected by variations in vegetation structure and seasonality. Furthermore, this study revealed that, home range size, survival and capture probability is influenced by habitat type and seasonality through resource availability. For example, during wet season there is high food availability and cover which

increase individual's survival and reproductive fitness. Understanding home range and survival of rodents is important for conservation and management. Therefore, this study has great implication in conservation and management of the rodent communities found on Mt Kilimanjaro. It provides scientific information on habitat associations, resource partitioning, breeding activity and population fluctuations of rodents which were not previously studied. Finally, this study has shed light and paves the way for further research on an endemic rodent species *Lophuromys aquilus* which has limited data in the IUCN Redlist.

# IKISIRI KUU

Maeneo ya milimani katika Afrika Kusini mwa Jangwa la Sahara yana aina nyingi za mamalia wadogo adimu na wa kawaida. Mlima Kilimanjaro ni miongoni mwa milima mirefu na maeneo yenye bayoanuwai Duniani, yenye uoto wa tabaka kando ya mwinuko wa kutoka usawa wa bahari. Tofauti hizi huunda makazi tofauti na hali ya kipekee ya tabia nchi ambayo inasaidia utofauti wa juu na wanyama wa kawaida wa mamalia wadogo. Hata hivyo, mabadiliko ya tabianchi na ongezeko la shughuli za binadamu kama vile kilimo na upanuzi wa mashamba ya miti hasa katika eneo la magharibi mwa Mlima Kilimanjaro ni changamoto na tishio kubwa kwa jamii ya mamalia wadogo wakiwemo panya.

Panya ni miongoni mwa mamalia wadogo walioenea na kuishi katika makazi mbalimbali. Wanazingatiwa kama wahandisi wa mfumo wa ikolojia kupitia kuchimba, uchavushaji na usambazaji wa mbegu kwa hivyo hutumika kama viashiria vya afya ya mfumo wa ikolojia. Ikolojia ya jamii ya panya huathiriwa na vipengele vya kibayolojia na viumbe hai kama vile muundo wa mimea, msimu, uwindaji, ushindani, magonjwa na vimelea. Kwa kuwa, panya wengi ni wanyama waharibifu wa mazao na hifadhi ya vimelea vya magonjwa yanayoambukiza kwa binadamu (*zoonotic disease),* kuelewa ikolojia ya jamii zao ni muhimu kwa uhifadhi na usimamizi bora. Kwa hivyo, utafiti huu ulilenga kuchunguza athari za kutofautiana kwa makazi na sababu za mazingira kama vile tabia nchi (msimu), udongo na muundo wa ardhi kwa jamii ya panya magharibi mwa mlima Kilimanjaro. Hasa utafiti huu ulijikita katika kuangalia aina na jamii mbali mbali za panya na kwa namna gani wamesambaa. Pia uliangalia tofauti za lishe katika nyakati na mahali tofauti miongoni mwa panya. Pamoja na kuangalia viashiria kama vile uwiano wa jinsia, kuzaliana na mabadiliko ya msomgamano na sababu zinazoathiri.

Ukusanyaji wa takwimu ulifanyika kwa kipindi cha miaka miwili kuanzia Aprili 2020 hadi mwezi Machi 2022 ikijumuisha misimu ya kiangazi na mvua. Msimu wa mvua katika vipindi viwili vya mwezi Oktoba-Disemba, na mwezi Machi-Mei. Wakati msimu wa kiangazi ukianzia mwezi Juni hadi Septemba na Januari-Februari.

Mbinu mbali mbali za kitaalamu zilitumika kukamata panya kwa kutumia aina mbalimbali za mitego. Utegaji ulifanyika katika aina mbalimbali za makazi ikiwemo, misitu ya asili (juu na chini), misitu ya kupandwa (mashamba ya miti), mashamba ya kilimo, maeneo ya wazi yasiolimwa, na kwenye uoto wa vichaka vifupi kwenye miinuko ya juu (moorland na ecotone). Mitego ya kunasa bila kuua ya Sherman na ile ya kuua iliwekwa kwa njia mbadala, pamoja na mitego ya Havahart iliyowekwa bila mpangilio maalum kwa ajili ya kunasia panya wakubwa. Katika njia ya kukamata na kurudisha yaani CMR; gridi saba za kudumu za 70 x 70 m ziliwekwa. Gridi mbili katika mashamba ya kilimo na moorland na gridi tatu katika msitu wa asili (wa juu). Kila gridi ilikuwa na jumla ya mitego 49 ya Sherman iliyowekwa umbali wa mita 10.  Mwisho kabisa mitego ya Sherman iliwekwa chambo ya siagi ya karanga, nazi kwenye mitego ya kuua na mitego ya Havarhart iliwekwa karoti na ndizi. Utegaji ulifanywa kwa usiku 3 mfululizo kila mwezi.

Ili kubainisha athari za muundo wa mimea, msimu pamoja na sifa ya udongo kwenye anuai na mikusanyiko ya jamii ya panya katika Mlima Kilimanjaro, takwimu za njia ya CMR na kuua zilitumika. Uainishaji wa mimea ulifanywa kwa kutumia viwanja vya mraba. Sampuli za udongo zilikusanywa kwa ajili ya uchambuzi wa kimaabara wa muundo wa udongo, msongamano wa wingi, PH na unyevu. Matokeo yalibainisha kuwa aina kumi na nne za panya zilikamatwa. *Rhabdomys dilectus* (iliyoitwa awali *Rhabdomys pumilio*), *Praomys delectorum* (iliyopewa jina la *Montemys*

*delectorum*) na *Lophuromys aquilus* (awali iliitwa *Lophuromys verhageni*) walikuwa spishi za panya zilizotawala zaidi zikichukua 69.35% ya jumla ya panya walionaswa. Panya aina ya *Rhabdomys dilectus* pamoja na *Lophuromys aquilus* zilipatikana kwenye makazi yote saba, isipokuwa kwa *Rhabdomys* peke yake ambaye hakupatikana kwenye misitu ya asili. Utajiri na wingi wa spishi uliathiriwa na aina za makazi, msimu, aina ya udongo na kifuniko cha majani. Maeneo yasiyolimwa na misitu ya asili ndiyo iliyokuwa tofauti (idadi kubwa) zaidi ilhali mashamba ya miti na mashamba ya kilimo yalikuwa na tofauti ndogo zaidi. Pia, panya walihusishwa na aina za makazi na muundo wa mimea (uoto) unaounda jamii mbili tofauti (wajumla wa makazi na wataalamu wa misitu).

Zaidi ya hayo, kwa kuelewa utofauti wa chakula na taratibu za kuishi pamoja, tofauti za kimaeneo na muda katika matumizi ya chakula miongoni mwa spishi mbili (*Lophuromys aquilus* na *Rhabdomys dilectus*) zilichunguzwa. Sampuli za utumbo wa panya walionaswa kutoka kwa njia ya kuondolewa na snap traps zilitumika. Asilimia ya mchango, utokeaji wa asilimia, upana wa niche na mwingiliano ulikadiriwa. Ulinganisho wa makadirio ya asilimia, mchango na umuhimu wa chakula, upana wa niche na mwingiliano ulifanywa kati ya makazi matatu (maeneo yasiyolimwa, mashamba ya kilimo na uoto wa vichaka vifupi/moorland) katika misimu ya kiangazi na ya masika/mvua. Spishi zote mbili zilitumia vyakula vyote vitano (mazao ya mimea, mbegu, Wanyama wasio na uti wa mgongo, mizizi na nywele) hali inayoashiria kuwa wao ni wataalamu wa lishe. Mazao ya mimea, na mbegu/ wanga ndivyo vyakula vilivyotawala kwa asilimia nyingi zaidi. Hata hivyo, *R. dilectus* alipendelea kula zaidi mbegu ilhali *L. aquilus* alibobea kwa wanyama wasio na uti wa mgongo na wadudu. Zaidi ya hayo, kulikuwa na tofauti kubwa katika upana wa niche kati ya spishi huku *L. aquilus* ikiwa na niche

kubwa/pana zaidi kuliko *R. dilectus*. Aina mbili za panya zilikuwa na mwingiliano uliodhihirika wa niche ambao ulikuwa kati ya 0.84 hadi 0.98 hata hivyo, hii haikuonyesha ushindani bali ni wanamuingiliano mkubwa wa kiikolojia na uwezo wa kuishi pamoja pasipokuathiri mwingine.

Kwa kuwa spishi mbili za panya *Rhabdomys dilectus* na *Lophuromys aquilus* zilipatikana kuishi Pamoja pasipo ushindani, ilikuwa muhimu kuelewa mwenendo wa shughuli ya kuzaliana, mabadiliko ya idadi au msongamano na sababu zake katika makazi na misimu. Takwimu za CMR ya miaka miwili ilitumika, hata hivyo ulinganisho ulifanywa kati ya uoto wavichaka vifupi yaani moorland na maeneo yasiyolimwa tu, kwa sababu *Rhabdomys dilectus* hakutokea katika msitu wa asili au montane forest. Uwiano wa jinsia ya kike wa spishi zote mbili haukutofautiana sana kati ya makazi. Walakini, ilibadilika sana kutoka kwa kiwango kinachotarajiwa katika makazi ya moorland. Idadi ya panya waliokuwa tayari kuzaa kwa spishi zote mbili ilitofautiana sana kati ya makazi lakini sio kati ya misimu. Katika utafiti huu mwenendo wa shughuli ya kuzaliana upo kwa mwaka mzima katika maeneo yasiyolimwa na ya kipekee au ya msimu katika moorland. Pia, msongamano kwa maana ya (uwiano wa idadi ya panya kwa eneo husika) ilikuwa ya juu zaidi katika maeneo yasiyolimwa kuliko katika moorland kutokana na uoto mnene na mfuniko wa majani ambazo zina faida kwa chakula na ulinzi dhidi ya wanyama wanaowinda.

Kwa kuongezea, takwimu za awali kutoka kwa njia ya CMR ilichanganuliwa ili kubaini anuwai ya ukubwa wa eneo la makazi na uwezekano wa kuishi wa spishi hizi mbili. Utafutaji wa eneo la makazi ulitumia njia ya MCP inayozingatia idadi ya panya mmoja mmoja waliokadiriwa kuwa na uhamishi wa nafasi za mitego angalau mara tano katka kila gridi. Tofauti katika saizi ya masafa ya makazi kati ya spishi haikuwa kubwa. Hata hivyo spishi ya

*Lophuromys aquilus* ilikuwa na anuwai kubwa ya makazi zaidi ya *Rhabdomys dilectus*. Matokeo kutoka kwa uchanganuzi na katika spishi zinaonyesha kuwa, anuwai ya makazi ya *R. dilectus* ilikuwa tofauti sana kati ya makazi, kuwa juu zaidi katika moorland ikilinganishwa na maeneo yasiyolimwa. Vile vile, anuai ya makazi ya *L. aquilus* ilikuwa ya juu zaidi katika moorland kuliko katika maeneo yasiyolimwa na tofauti kati ya jinsia ambapo, wanaume walikuwa na anuwai kubwa ya makazi kuliko wanawake. Uwezekano wa kuishi wa spishi zote mbili ulitofautiana sana. Uwezekano wa kuishi kwa *L. aquilus* ulikuwa juu zaidi ya ule wa *R. dilectus*, ikipendekeza kwamba spishi hii imezoea kuishi na inafanya vizuri zaidi kwenye mlima Kilimanjaro, ingawa hakukuwa na ushahidi wa kutosha hivyo kukosa hitimisho. Zaidi ya hayo, miundo bora zaidi ilionyesha kwamba uwezekano wa kuishi wa hizi spishi mbili uliathiriwa zaidi na jinsia na msimu. Wanawake walikuwa na uwezekano mkubwa wa kuishi kuliko wanaume japo kwa utofauti mdogo. Pengine ni kwa sababu majike hujongea umbali mdogo na kutumia muda mwingi kwenye viota vyao kuangalia watoto wao hivyo basi kupunguza hatari ya kuwindwa kinyume na wanaume.

Utafiti huu unaonyesha kuwa mlima Kilimanjaro una aina nyingi za panya, pengine kutokana na makazi yake tofauti na mifumo tata ya ikolojia. Inathibitisha kwa tafiti za awali kwamba, muundo wa mimea na msimu ni mambo muhimu zaidi yanayoathiri aina mbalimbali za panya, usambaaaji wao na mkusanyiko wa jamii. Zaidi ya hayo, inaonyesha kuwa shughuli za kuzaliana na mabadiliko ya idadi ya panya (msongamano) huathiriwa na muundo wa mimea na msimu kupitia upatikanaji wa rasilimali za chakula na ulinzi dhidi ya wanyama wanaowinda. Rasilimali za chakula zilizoboreshwa na ulinzi huongeza uwezekano wa kuishi na usawa wa uzazi wa panya mmoja mmoja. Kwa hiyo, matokeo ya utafiti huu yana maana kubwa katika uhifadhi

na usimamizi wa jamii za panya kwenye mlima Kilimanjaro na milima mingine ya kitropiki. Imetoa taarifa za kisayansi kuhusu mahusiano ya makazi, mgawanyo wa vyakula, mwenendo wa shughuli ya kuzaliana na mabadiliko ya msongamano ambayo hayakufanyiwa utafiti hapo awali. Pili, imetoa mwanga na kuweka njia kwa ajili ya utafiti zaidi juu ya panya *Lophuromys aquilus* anaepatikana katika mlima Kilimanjaro pekee ambae takwimu zake ni pungufu kwenye Umoja wa Kimataifa wa Kulinda Uasilia yaani IUCN.

# DECLARATION

**I, Suzana Mei Thomas,** do hereby declare to the Senate of Sokoine University of Agriculture that this thesis is my own origin work done within the period of registration. I declare that this work has neither been submitted nor being considered for an award in any other institution.

**Suzana Mei Thomas** **Date**

**(PhD Candidate)**

The above declaration is confirmed by:

**Dr. Geofrey E. Soka** **Date**
**(Supervisor)**

**Prof. Loth S. Mulungu** **Date**
**(Supervisor)**

# LIST OF PUBLICATIONS AND MANUSCRIPTS

Thomas, S. M., Soka, G. E., and Mulungu, L. S. (2022). Influence of vegetation structure, seasonality, and soil properties on rodent diversity and community assemblages in west Mount Kilimanjaro, Tanzania. *Ecology and Evolution*, *12*(9), e9211.

Thomas, S. M., Soka, G. E., Mulungu, L. S., and Makonda, F. (2022). Spatial-Temporal Variations in Dietary Consumption of Two Dominant Rodent Species (*Rhabdomys dilectus* and *Lophuromys aquilus*) on Mount Kilimanjaro, Tanzania. *Diversity*, *14*(8), 659.

Suzana M. Thomas[1,2,3]*, Geofrey E. Soka2, Loth S. Mulungu4, † and Rhodes H. Makundi1,4. Breeding Activity and Spatial-Temporal Population Fluctuations of the two Dominant Rodent Species (*Rhabdomys dilectus* and *Lophuromys aquilus*) on Mount Kimimanjaro. ***Submitted to the Journal of Integrative Zoology.***

Thomas, S. M., Soka, G. E., and Mulungu, L. S. Home range size and Survival probability of two major rodents (*Rhabdomys dilectus* and *Lophuromys aquilus*) on Mount Kilimanjaro. ***The manuscript is under preparation.***

# COPYRIGHT

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# DEDICATION

I dedicate this work to my supervisor, the Late Professor Loth S. Mulungu who passed away in June 2022 during the critical period when I mostly needed his supervision (May His Soul Rest in Eternal Peace). In loving memory of his life, I dedicate this work to honor his tremendous and valuable contributions in my PhD studies. I also dedicate this work to my lovely Late Mother Felister Akeyo Vitalis who died in May 2023 (May Her Soul Rest in Eternal Peace). Also, this work should be a special dedication to my lovely sons Ivan and Xavian for being patient whenever they missed me.

## TABLE OF CONTENTS

# LIST OF ABBREVIATIONS AND SYMBOLS

| | |
|---|---|
| ANOVA | Analysis of Variance |
| CMR | Capture-Mark-Recapture |
| EAM | Eastern Arc Mountains |
| df | Degrees of freedom |
| E_SURGE | A software for fitting multi event models |
| GOF | Goodness of fit |
| GLM | General Linear Model |
| H’ | Shannon Wienner Diversity Index |
| Ha | Hectare |
| IUCN | International Union for Conservation of Nature |
| Kg | Kilogram |
| Gm | Gram |
| m | Metre |
| mm | Millimetre |
| P | Capture Probability |
| Phi | Survival probability |
| PAST | Paleontological Statistics Software Package |
| $\chi^2$ | Chi square |
| % | Percentage |
| SIMPER | Similarity Percentage Analysis |
| SIMPROF | Similarity Profile Analysis |
| MNKA | Minimum Number Known Alive |
| MARK | Software for Capture-Mark-Recapture data analysis |
| MCP | Minimum Convex Polygon |
| KINAPA | Kilimanjaro National Park |
| WKFR | West Mt. Kilimanjaro Forest Reserve |
| FLW | Fallow |
| PLF | Plantation Forest |
| AGR | Agricultural fields |
| DSF | Lower montane forest (disturbed) |

| | |
|---|---|
| MFR | Higher montane forest (intact) |
| ECT | Ecotone |
| MLD | Moorland |
| U-CARE | Utilities for Capture- Recapture |

# 1.0 CHAPTER ONE

# GENERAL INTRODUCTION

## 1.1 Rodents Diversity and Distribution

Rodents are among the most successful small mammals due to their diverse body size and morphology which enable them to inhabit a range of habitats with different environmental conditions. Also, life history strategies, adaptations, and behavior of consuming almost everything such as vegetative materials, seeds and arthropods has made the rodents to be more successful. Out of 5416 World mammal species, rodents comprise about 42 % with more than 2,000 species (Monadjem *et al*., 2015). In Africa there are over 500 species of which about 17% are pests (Happold, 2013). Rodent pests cause great losses in agriculture (Mulungu *et al*., 2006) with negative impacts in public health through zoonoses (Gratz, 1997; Meerburg *et al*., 2009). Despite of the negative impacts, rodents have many ecological importance in ecosystems. They are prey to predators like reptiles and small carnivores, and are important consumers of insects and plants hence contribute greatly to maintaining food webs and chains as well as plant pollination and seed dispersal (Corlett and Hughes, 2015; Johnson *et al*., 2011). Rodents are ecosystem engineers through modification of soil structure and organic content by burrowing (Meliyo *et al*., 2014). For that case, they have great contribution to biodiversity (Linzey and Kesner, 1997) and can act as ecological indicators of habitat quality due to abrupt change in rodent community because of habitat disturbance (Avenant, 2003; Avenant and Cavallini, 2007). For that case, rodents play important roles in maintenance of ecosystem health.

Tanzania has large diversity of known rodents which are endemic and widely distributed in the Eastern Arc Mountains (Stanley *et al*., 1998; Carleton and Stanley, 2012) and the free-standing mountains such as Mount Kilimanjaro (Grimshaw *et al*., 1995; Mulungu *et al*., 2008; Stanley *et al*., 2014). These mountains are among the 25 well-known biodiversity hotspots in the world (Burges *et al*., 1998; 2007; Myers *et al*., 2000). They have diverse habitats including tropical montane forests which are home to many plants and animals (Kisingo *et al*., 2005; Gibson *et al*., 2011; Rahbek *et al*., 2019). However, increasing habitat destruction and fragmentation as a result of anthropogenic activities (specially at lower elevations) pose great threat to montane forest remnants and biodiversity (Burgess *et al*., 1998; Forestry and Bee keeping Division, 2005).

Mt. Kilimanjaro is the highest free-standing mountain in Africa, a biodiversity hotsport and a well-known heritage site in the world, thus it is very important for conservation and ecotourism activities (Newmark, 1991; Coe, 1993). It is spatially located in northeastern part of Tanzania. The mountain has varied altitudes with unique landscape and topographic characteristics comprised of heterogeneous habitats spatially located from woodlands and savanna grasslands at lower altitudes, to tropical montane forest and subalpine vegetation at mid and higher altitudes (Coe, 1993; Hemp, 2006). Heterogeneous vegetation and strong variation in temperature and rainfall (with tropical and alpine climate) creates complex and unique ecosystems for high biodiversity and endemism (Coe, 1993; Maeda and Hurskainen, 2014; Rahbek *et al*., 2019). Moreover, the mountain has high diversity of small mammals including rodents with rare and endemic species (Shore and Garbett, 1991; Grimshaw *et al*., 1991; 1995; Verheyen *et al*., 2007). For example, a rodent species *Lophuromys aquilus* and a crocidura *Myosorex zinkii* are reported to be endemic to the mountain (Verheyen *et al*., 2007; Stanley *et al*., 2005).

Heterogeneous vegetation along the altitudinal gradients serve as refuge for many rodents. For example, agricultural fields and fallows at the base of the mountain are home to opportunistic and habitat generalists like *Mastomys*, *Rhabdomys*, *Lemniscomys* and *Mus* spp (Mulungu *et al*., 2008). The mountain rain forest harbors forest specialists such as *Praomys* (recently named *Montemys delectorum*), *Graphiurus*, *Grammomys and Cricetomys*. Ecotone and moorland vegetation at higher altitudes harbors a number of habitat generalists such as *Otomys spp*, *Dendromus* and *Lophuromys*.

## 1.2 Factors Affecting Rodent Species Diversity and Community Assemblage

Rodent community is influenced by biotic and abiotic factors most importantly vegetation structure and composition, primary productivity, soil properties, climate and topography (Torre, 2004; Massawe *et al*., 2008, 2005; Currie, 2010; Meliyo *et al*., 2014).

Studies on small mammals including rodents have reported that habitat heterogeneity is an important factor affecting rodent community (Cramer and Willig, 2002; Stevens and Tello, 2011; Bantihun and Bekele, 2015). Habitat heterogeneity is the variation in vegetation structure and composition both vertically and horizontally within a habitat or habitat patches (August 1983; Cramer and Willig, 2002; Stein and Kreft, 2015). Species diversity increases when habitats are well stratified with dense vegetation and high ground cover (Ecke *et al*., 2001; Grelle, 2003). Also, when habitats become small and patchy, they provide alternative microhabitats with unique resources to some rodent species (Cramer and Willig, 2002; Stein and Kreft, 2015). Rodents are associated with different habitats and unique vegetation feautres (Cramer and Willig, 2002; Bantihun and Bekele, 2015; Admas and Yihune, 2016). Most species prefer habitats with dense vegetation for food and protection from predators. For example, *Otomys barbouri* is associated with dense vegetation in patchy grasslands and bushes (Clausnitzer *et al*., 2001). Moreover, abundance of *Rhabdomys pumulio* is associated with moderate vegetation density and grass cover as they preferably eat grass and seeds (Shore and Garbett, 1991; Clausnitzer *et al*., 2001) whereas generalists like *Mastomys natalensis* predominates agricultural fields and peridomestic habitats (Bantihun and Bekele, 2015; Admas and Yihune, 2016). Furthermore, rodent distribution and diversity is influenced by habitat modification due to anthropogenic activities like settlements, cultivation, grazing, logging and firewood collection (Mbugua, 2002; Men, *et al*., 2015; Lema and Magige, 2018).

In addition, other factors such as soil texture, climate, topography, and altitude affect rodent community in mountainous areas (Meliyo *et al*., 2014; Willig and Presley, 2016; Richard *et al*., 2022). These factors act in a number of ways that affects composition and distribution of rodents (Mortelliti and Boitani, 2006; Gitonga *et al*., 2016; Lema and Magige, 2018). Therefore, the knowledge on habitat heterogeneity and rodent community is relevant for understanding the distribution, habitat requirements of multiple species and the interactions in an environment.

## 1.3 Spatial-Temporal Variations in Rodent Diets and Resource Partitioning

Feeding ecology of rodents has been studied between sympatric species that occur together at a particular time and place (Luo and Fox, 1996; Clausnitzer *et al*., 2003; Mulungu *et al*., 2011b). Rodent’s preferences on diets varies between habitats and seasons depending on availability of the food items (Curtis and Perrin, 1979; Luo and Fox, 1996; Mulungu *et al*., 2011a,b; Soininen *et al*., 2013). The variations in dietary preference between habitats and seasons can affect the diversity of food resources, niche breadth and niche overlap between species, which could determine coexistence (Pianka, 1974; Pinotti *et al*., 2011; Sato *et al*., 2018) or competition between them (Luo and Fox, 1996; Mulungu *et al*., 2011b). During rainy season rodents specialize on the most valuable foods unlike during dry season when they maximize intake by eating varieties (Mulungu *et al*., 2011b). Food partitioning is one of the mechanisms of coexistsnce in rodent communities (Pianka, 1974). For example, Clausnitzer *et al*. (2003) reported that *Crocidura montis* and *Lophuromys flavopunctatus* overlap in both habitats and diets, however, *C. montis* consume more invertebrates while *L. flavopunctatus* prefers both invertebrates and plant materials.

Moreover, it is anticipated that rodent's diet depends on nutritional value (Clausnitzer *et al*., 2003) and distribution of resources in vicinity (Mulungu *et al*., 2011a,b). Studies on rodent diets in Africa have been mainly conducted on rodent pests such as the house mice and the multimate rat *Mastomys natalensis* (Oguge, 1995; Odhiambo *et al*., 2008a,b; Mulungu *et al*., 2011a,b; Mlyashimbi *et al*., 2018) which are common pests in households and agroecosystems respectively. Increasing crop damage (Mwanjabe, *et al*., 2002; Shiels *et al*., 2013) and zoonotics (Meerburg *et al*., 2009; Makundi and Massawe, 2011 and Julius *et al*., 2012;) caused by rodent pests has attracted more research on the subject area, however, non-pest rodents are still ignored (Luo and Fox, 1996; Clausnitzer *et al*., 2003). Studying dietary variations is importatnt for understanding pest status of a species and how it interacts with other species and its environment. For example, the role of rodents in seed dispersal and contribution to forest development in the tropics  (Brewer and Rejmánek, 1999).

### 1.4 Rodent's Population Fluctuations, Home Range and Survival

Rodent populations are influenced by density dependent and density-independent factors such as climate and survival (Torre, 2004; Currie, 2010). Rodent populations are strongly influenced by rainfall and primary productivity which initiate breeding through food availability and cover (Leirs *et al*., 1997). Most species reproduce seasonally and others throughout the year but stops only when conditions are not favorable. For example, breeding pattern of *Mastomys natalensis* is correlated with rainfall distribution (Makundi *et al*., 2007; Mulungu *et al*., 2013), it is reported that *M. natalensis* reproduce in wet season when food availability is high. This is because, food resources become of high quality and quantity during wet season (Leirs *et al*., 1994; Makundi *et al*., 2007; Mulungu *et al*., 2013). Also, high concentration of green pigments known as 6-methoxy-2-benzoxazolinone (6-MBOA) in fresh leaves during wet season triggers breeding in many rodents including *Mastomys natalensis* (Alibhai, 1986; Neal and Alibhai, 1991; Linn, 1991; Mlyashimbi *et al*., 2018). Changes in demographic parameters such as age structure, sex ratio, breeding activity, home range, survival, recruitment, immigration and emigration are major factors for rodent population fluctuations (Oli and Dobson, 1999; Getz *et al*., 2004). Moreover, movement of rodents is restricted to smaller distances within a small home range, which is highly influenced by changes in microhabitats and vegetation features at smaller scales (Stirnemann *et al*., 2015). Also, sex ratio differs in a population due to variations in behavior and sex roles between males and females. Changes in sex ratio affect mating and breeding activity of rodents hence can results into population fluctuations (Delany, 1972; Smith and Avenant, 2004; Shireleyo *et al*., 2020). Also, age structure changes temporarily due to recruitment, breeding seasonality and survival (Delany, 1972). As a result of short life span, rodents have high reproductive potential and rapid population growth which results into population fluctuations over time (Kay and Hoekstra, 2008). High population size limits growth rate and survival through increased mortality (Ostfeld, 1985; Ostfeld *et al*., 1985). Therefore, understanding the demographic parameters such as age structure, sex ratio and breeding activity is crucial for studying rodent populations (Lima *et al*., 2001a,b; 2003; Benthem *et al*., 2017). It could help answering many questions like; how many juveniles, sub-adults and adults are there in a population? How many males and females? How many individuals are sexually active/breeding? When/what month and season do they normally breed? What is the population size? What factors influence the changes in population size over space and time?

## 1.5 Problem Statement and Justification of the Study

Land use changes and rapid expansion of human population put much pressure on dependence of forest resources like firewood, livestock grazing areas, medicinal plants and forest clearing for agriculture and forest plantations (Mbonile *et al*., 2003; Kasangaki *et al*., 2005; Gibson *et al*., 2011; Kideghesho, 2015). Moreover, intensification of anthropogenic activities (especially at lower elevations) results into destruction and fragmentation of montane forest remnants hence poses great threat to biodiversity (Burgess *et al*., 1998; Forestry and Bee keeping Division, 2005). Habitat destruction and fragmentation result into habitat simplification and reduced food resources which might cause species decline and extinction (Kisingo *et al*., 2005).

Studies in East-Africa Africa have demonstrated on the impacts of human activities on the diversity, composition and distribution of small mammals including rodents through alterations of habitats and its features (Caro, 2001; Byrom *et al.*, 2015; Lema and Magige, 2018). Anthropogenic disturbance may impact environmental factors such as vegetation structure and composition, rainfall distribution and soil that influences rodent community. For example, increasing expansion of forest plantations is at alarming rate in mountainous areas including Mount Kilimanjaro and EAC Mountains, this has resulted into higher deforestation rates of natural forest remnants (Kasangaki *et al.*, 2005; Lema and Magige, 2018). Deforestation affects the abundance and survival of forest natives which have specific habitat requirements (Happold, 2013; Bryja *et al.*, 2014; Monadjem *et al.*, 2015; Cassola, 2016; Ademola *et al.*, 2021). For example, forest specialists like *Praomys* and *Graphiurus* which requires moist conditions are said to be highly threatened by deforestation. Deforestation may also affect spatial-temporal distribution of rodents, their community structure, diets and demographic parameters such as sex ratio, breeding activity, population fluctuations and home range size through reduced food availability and cover (Oguge, 1995; Mulungu *et al.*, 2011a,b; Mlyashimbi *et al.*, 2018). Therefore, understanding the diversity, distribution, habitat associations and the interactions of rodent communities is important for conservation and management (Lambert *et al.*, 2006).

In addition, increasing climate change (Thompson *et al.*, 2002; Chazal and Rounsevell, 2009; Mulangu and Kraybill, 2013) in mountainous areas including Mt Kilimanjaro pose major threats to biodiversity conservation. For example, climate change in tropical mountains has resulted into elevation range shift of plants (Zu *et al.*, 2021) and animals (Moritz *et al.*, 2008; Rogora *et al.*, 2018). Recently, the effects of climate change and global warming have been of great concern to conservation of small mammals including rodents due to elevation range shift towards higher altitudes

(Moritz *et al*., 2008; Rowe *et al*., 2009; Craig *et al*., 2020; Elsen *et al*., 2020; Gebrezgiher *et al*., 2022). Also, climate change influences rodent population outbreaks (Stenseth *et al*., 2006) which is hazardous to the agricultural sector through increased crop damage (Mulungu, 2017; Leirs *et al.,* 2010). Population outbreaks is also hazardous to the public health sector through increased prevalence of zoonotic diseases such as plague, bartonellosis and leptospirosis because of human-rodent interactions (Makundi *et al*., 2003; Meerburg *et al*., 2009).

Mount Kilimanjaro has markedly beautiful topographic landscapes with unique climate and heterogeneous habitats which harbors high diversity and endemism (Shore and Garbett, 1991; Grimshaw *et al*., 1991; 1995; Hemp, 2006; Verheyen *et al.*, 2007). The complex ecosystems could make it of greater concern for high diversity of small mammals yet to be discovered. For that case, Mt Kilimanjaro has been of high interest for conservation and research (Newmark, 1991; Coe, 1993), however, most research on Mt Kilimanjaro have been mainly focused on plants (Hemp, 2006) and large mammals (Grimshaw and Foley, 1991; Grimshaw *et al*., 1995). For the past two decades research on small mammals and rodents on Mt Kilimanjaro have been poorly ignored compared to other mountains (Stanley *et al*., 1998; Clausnitzer *et al*., 2001; 2003; Stanley and Hutterer, 2007; Makundi *et al*., 2007; Yihune and Bekele, 2012; Lema and Magige, 2018; Chidodo *et al*., 2020; Ademola *et al*., 2021). Recently, only few studies have documented on the diversity and distribution of rodents in associations with altitude (Mulungu *et al*., 2008; Stanley *et al*., 2014). The existing studies were mainly based on short term surveys along the mountain (Shore and Garbet, 1991; Grimshaw *et al*., 1995). Few of the studies used systematic methods of rodent sampling along a transect line (Mulungu *et al*., 2008; Stanley *et al*., 2014), however, none of them had employed intensive methods of sampling like Capture Mark Recapture (CMR). CMR is a systematic method involving intensive sampling of rodents over a long period of time hence provides detailed information on population ecology which has not been previously studied. Therefore, these studies, have provided limited information on rodent species check list (Shore and Garbett, 1991; Grimshaw *et al*., 1995), diversity, composition and distribution in association with altitudinal gradient (Mulungu *et al*., 2008; Stanley *et al*., 2014). Apparently, there is no published data on influence of habitat heterogeneity (variations in vegetation structure, season and soil properties) on rodent species richness and abundance. Also, information on rodent community assemblages and habitat associations (response of individual species to habitats) is scarce. Such information is crucial for management of rodent communities considering habitat destruction in unprotected areas of west Kilimanjaro.

In addition, there is no documentation on dietary variations and resource partitioning among the existing rodents on Mt Kilimanjaro. In East-Africa, most research on diets is focused on rodent pest including the multimammate mouse and mole rats (Mlyashimbi *et al*., 2018). Information on rodent diets is crucial for understanding reproduction and survival of rodents, the ecological roles played and the mechanisms of coexistence in a community.

Moreover, breeding activity, population fluctuations, home range size and survival probability of rodents have not been previously studied on Mt. Kilimanjaro. Such information is essential for understanding the factors affecting rodent populations and survival for management and conservation of the rodent populations (Sato *et al*., 2018). Therefore, this study will fill in the gaps and provide scientific information for understanding rodent-habitat relationships. Also, it will generate knowledge for a broader understanding of rodent foraging behaviour and resource partitioning, as well as population fluctuations for effective control and management actions. The study will provide scientific information to the ecologists and Park managers for informed decisions on conservation and management planning. Last but not least, the study will add knowledge on non-pest rodent species for enhanced conservation and management, since most studies in Sub-Saharan Africa have been mainly focused on rodent pests (Swanepoel *et al*., 2017).

## 1.6 Objectives

### 1.6.1 Overall objective

The general objective of this study was to investigatet the effects of habitat heterogeneity and environmental factors on community ecology of rodents in West Mount Kilimanjaro, Tanzania, with the aim of improving knowledge on abundance, diversity, distribution, and demography of rodent species in the area.

### 1.6.2 Specific objectives

The specific objectives of this study were:

1. To determine the effects of vegetation structure, season and soil properties on rodent diversity and community assemblage in west Mt Kilimanjaro.
2. To evaluate variations in diet and resource partitioning of dominant rodent species at spatial-temporal scales as a mechanism of coexistence.
3. To assess breeding activity and population fluctuations of the dominant rodent species across habitats and seasons.
4. To determine home range size and survival probability of dominant rodent species and the factors influencing them.

# 2.0 CHAPTER TWO

## Influence of Vegetation structure, Seasonality and Soil Properties on Rodent Diversity and Community assemblages in West Mount Kilimanjaro, Tanzania

Suzana M. Thomas1,2,3 | Geofrey E. Soka2 | Loth S. Mulungu4,†

[1]The African Centre of Excellence for Innovative Rodent Pest Management and Biosensor Technology Development

Project, Sokoine University of Agriculture, Morogoro, Tanzania

[2]Department of Wildlife Management, Sokoine University of Agriculture, Morogoro, Tanzania

[3]Department of Biology, University of Dodoma, Dodoma, Tanzania

[4]Institute of Pest Management, Sokoine University of Agriculture, Morogoro, Tanzania

Corresponding Author: Email: meydancan@gmail.com

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**KEYWORDS**
community assemblage, Mount Kilimanjaro, rodent diversity, vegetation structure

**TAXONOMY CLASSIFICATION**
Community ecology

## 1 | INTRODUCTION

Rodents are among the most diverse and widely distributed mammals on earth. This is due to their ability to inhabit natural and seminatural habitats and consume almost everything (Kay & Hoekstra, 2008).They play a great role in ecological systems such as pollination and seed dispersal (Johnson et al., 2011). Rodents have low movement patterns and small home ranges (Saanya et al., 2021), which make them sensitive to changes in vegetation structure at smaller scales (Malcolm & Ray, 2000; Stirnemann et al., 2015); hence, they serve as ecological indicators of the environment (Avenant, 2003, 2011). The influence of habitat types, vegetation structure, and composition on rodent diversity and community assemblages is underlined by the habitat heterogeneity hypothesis (Stevens & Tello, 2011). The habitat heterogeneity hypothesis explains that heterogeneous habitats support high species diversity due to increased microhabitats that provide more niches for coexisting species (August, 1983; Stein & Kreft, 2015). Heterogeneous habitats or habitat patches affect rodent diversity, abundance, and community assemblages through the provision of alternative microhabitats that serve as refuges and provide limiting resources to habitat generalists (Cramer & Willig, 2002; Mayamba et al., 2019, 2020; Stein & Kreft, 2015). The influence of vegetation structure has been a central focus in the community ecology of small mammals including rodents (Cramer & Willig, 2002). Vegetation structure is among the most determinant factors of rodent species diversity, composition, and abundance (Admas & Yihune, 2016; Bantihun & Bekele, 2015; Chidodo et al., 2020; Cramer & Willig, 2002; Grelle, 2003; Sullivan et al., 2000; Torre Corominas, 2004). Generally, the influence of vegetation structure on rodent community is determined through habitat associations (Admas & Yihune, 2016; Bantihun & Bekele, 2015; Chidodo et al., 2020; Cramer & Willig, 2002).

In addition, rodent diversity and community assemblage are influenced by many factors such as food availability, competition, predation, diseases and parasites, soil properties, climate, and altitude (Torre Corominas, 2004). For example, seasonal variations in rainfall distribution affect food quantity and quality which influences rodent's diet (Mulungu et al., 2011) and breeding patterns (Leirs et al., 1994, 1997; Makundi et al., 2005, 2007; Mulungu et al., 2013). Physical properties of soil such as soil type/texture, bulk density and soil moisture influences the distribution, population size and survival of rodents due to burrowing for nests and cover (Massawe et al., 2008; Mlyashimbi et al., 2019). Furthermore, elevation range influences rodent species composition and distribution through vegetation zoning. Also, climate variability and anthropogenic activities in low altitudes affect vegetation zoning and rodent species distribution (Hemp, 2006; Lema & Magige, 2018; Mbugua, 2002).

Mount Kilimanjaro is the highest mountain in Africa (roof of Africa) and the world's famous heritage site and tourist attraction, with high diversity of rare and endemic small mammals including rodents (Grimshaw et al., 1995; Shore & Garbett, 1991; Verheyen et al., 2007). Despite that, research on community ecology of rodents on Mt Kilimanjaro has received relatively little scientific attention than high mountains of East and Central Africa, including Mount Elgon in Kenya and Uganda (Clausnitzer et al., 2003; Clausnitzer & Kityo, 2001), Mount Gecoche in Ethiopia (Bantihun & Bekele, 2015; Yihune & Bekele, 2012), and the Eastern Arc Mountains (Ademola et al., 2021; Chidodo et al., 2020; Makundi et al., 2007: Stanley et al., 1998; Stanley & Hutterer, 2007). Most studies on these mountains including Mt Kilimanjaro have been focused on diversity and distribution of rodents along the altitudinal gradients. Previous studies along the Marangu, Mweka, and Shira routes of Mt. Kilimanjaro provided checklists and the distribution of rodent species in association with altitude (Grimshaw et al., 1995; Grimshaw & Foley, 1991; Mulungu et al., 2008; Stanley et al., 2014). However, none of these studies investigated the influence of vegetation structure, seasonality, and soil properties on rodent community assemblages. Such knowledge is relevant to park managers for understanding species–habitat relationships for management and conservation purposes. Therefore, we aimed to determine the influence of vegetation structure, seasonality, and soil properties on rodent species richness and abundance in west Mt. Kilimanjaro. Second, we aimed to determine community assemblages and habitat association of individual rodent species. We hypothesized that: (H1) Variations in vegetation structure, seasonality, and soil properties affect rodent species richness and abundance. We predict high rodent species richness and abundance in heterogeneous habitats. Heterogeneous habitats have high primary productivity and ground cover which improves food availability and reduce predation risk (Cramer & Willig, 2002). (H2) Rodent community assemblage is influenced by structural complexity and heterogeneity of a habitat in association with other environmental variables. We predict that, community assemblage would vary remarkably across the habitats with respect to variations in vegetation structure and soil properties (Hernández et al., 2005). Moreover, heterogeneous habitats of Mt Kilimanjaro would support higher diversity and strong interactions of rodent communities due to complex ecosystems as compared with simple habitats (Mulungu et al., 2008).

## 2 | MATERIAL AND METHODS

### 2.1 | Study site description

The study was conducted on Mount Kilimanjaro which is located in northeastern Tanzania. The study area lies between 3°07S and 37°35E on the western slopes of Mt Kilimanjaro in Siha district, covering a total area of 1668 km$^2$ and reaching a maximum altitude of 5895 m a.s.l. (Figure 1). According to Mulangu and Kraybill (2013) the Mountain is characterized by a tropical montane climate with two rainy and two dry seasons. Rainy season 1 is a long and major season from March to May, and rainy season 2 is a short and minor one from October to December. Also, there is dry season 1 which is the shortest and driest one from January to February, as well as dry season 2 which is long and less dry from June to September. Frosts are also common from June to August during the nights (Thompson et al., 2002). The estimated mean annual rainfall ranges from 700 mm in the lowlands to around 2200 mm in highlands. The general range of temperatures is between −6°C in the highlands and 29°C in the lowlands. The parent material for most soils in the area is volcanic ash and pumice which are typically well-drained. The soils are highly fertile and predominantly dark grayish, dark brown, and dark yellowish-brown with sandy and clay loams (Nanzyo et al., 1993).

Generally, the mountain is covered with a zonation of habitat types along the altitudinal gradient (Hemp, 2006; Mulungu et al., 2008). Habitat types were classified as plantation forest and cultivated zone, montane rain forest, alpine heath, and moorland. Plantation forest and cultivated zones range from 1500 to 2400 m a.s.l. covering a total area of 7630 ha. It occupies a transition zone between human settlements with an estimated human population of 2500 people (Mbonile et al., 2003; National Bureau of Statistics, 2012). This zone includes agricultural fields and farms, fallows, and plantation forests. The latter habitat is comprised of extensive tree stands of *Pinus patula*, *Grevillea robusta*, *Eucalyptus* spp, *Cupressus lusitanica*, and *Acrocarpus fraxinifolius*. Also, within young plantations, there are cultivated agricultural fields under the taungya system, a free space between newly planted trees accommodating seasonal crops mainly carrots (*Daucus carota*), cabbage (*Brassera oleracea*), green peas (*Pisum sativum*), and Irish potatoes (*Solanum tuberosum*).

The montane rain forest zone is found in both WKFR (West Mt. Kilimanjaro Forest Reserve) as a remaining natural forest from human disturbance named lower montane forest (DSF) and largely in Mt. Kilimanjaro National Park KINAPA named higher montane forest (MFR). The montane forests has indigenous tree species such as *Podocarpus latifolius*, *Olea europea*, *Ficus thonningii*, and *Cassipourea*

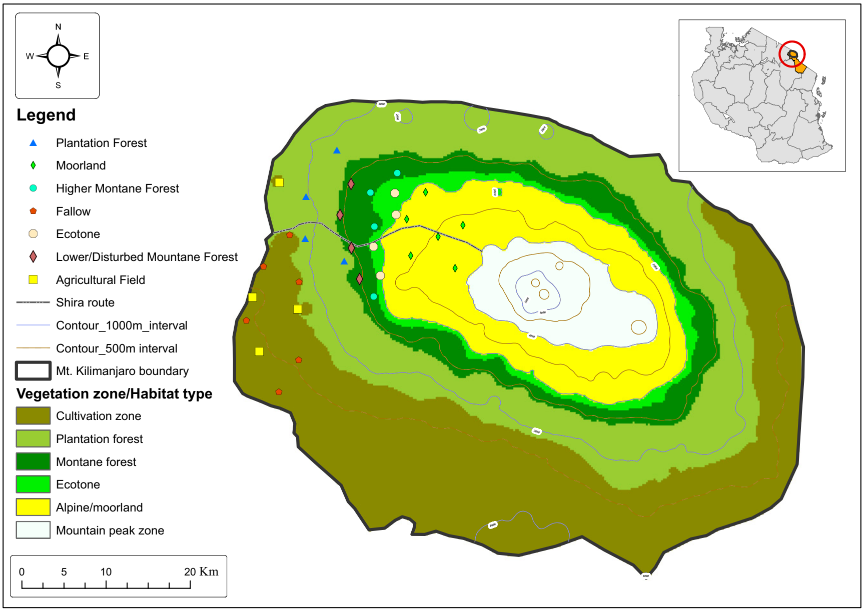

FIGURE 1 Map of Mt Kilimanjaro showing study sites in the selected habitats along the Shira route (in West Kilimanjaro).

*molasana*. Others are *Schefflera* spp, *Juniperus procera*, *Hagenia abyssinica*, and *Cussonia spicata*. It is an evergreen rainforest dominating from 1800 m a.s.l. up to 2800 m a.s.l., and the wettest part receiving up to 2300 mm of annual rain fall. Alpine heath or ecotone was another habitat type observed from 2800 to 3200 m a.s.l. transitioning to moorland. In this zone, there is sparser and drier vegetation than in the montane rain forest dominated by *Erica excelsa* and *Philippia trimera* shrubs. The heath/ecotone also includes bearded lichen which hangs from the *Erica excelsa* and other trees mostly *Hagenia abyssinica* and *Podocarpus* spp. The annual rainfall is around 1300 mm and such grasses as *Agrostis producta*, *Festuca convoluta*, and *Koeleria gracilis* dominate this area. Lastly, a subalpine zone with a moorland habitat type was evident from 3200 m a.s.l. dominated by Erica bush and changing to *Helichrysum* spp. up to 4500 m a.s.l. as well as rocky and bare land (Hemp, 2006). *Protea kilimandscharica*, *Kniphofia thomsonii*, and *Lobelia deckenii* are also prevalent. It is the coldest with day and night temperatures ranging from 10 to 21 and −1 to 10°C respectively.

## 2.2 | Study design and sampling procedures

The study was purposively conducted in seven habitat types: agricultural fields AGR, fallows FLW, plantation forest PLF, lower DSF and higher MFR montane forests, ecotone/alpine heath ECT, and moorland MLD between April 2020 and March 2021. To maximize capture and diversity of rodents two methods, capture–mark–recapture/release (CMR) and removal techniques were employed for rodent trapping with a combination of different traps as conducted by Welegerima et al. (2020) and Shilereyo et al. (2020).

In capture–mark–recapture (CMR) method, permanent experimental grids of 70 m × 70 m (with a 10 m buffer from the edges) were established in both fallows, higher montane forest, and moorland. Two replicate grids at a minimum distance of 500 m were established in each of the fallow and moorland habitats and three replicate grids in higher montane forest, making a total of seven grids. For each grid, medium-sized Sherman's live traps (23 × 9.5 × 8 cm H.B. Sherman's Traps, Inc.) were arranged in seven lines with seven trapping stations 10 m apart making a total of 49 traps. Traps were baited with peanut butter mixed with maize flour and left for three consecutive nights. Trapping was conducted every month at a 4-week interval. Traps were inspected every morning before 10:00 am to avoid death and suffocation from harsh weather conditions. Trapped individuals were toe clipped and coded following animal health and safety marking procedures (Borremans et al., 2015). Animals were weighed, sexed, and their reproductive conditions examined. Finally, trapped animals were released at a capture station, and the traps were re-baited for the next trapping night.

In the removal method, trapping was conducted in all seven habitat types using a combination of traps following procedures described in Shilereyo et al. (2020) and Welegerima et al. (2020). For each habitat type, at least four plots were randomly selected. Five transect lines 50 m long and 10 m apart were established in each plot. Sherman and snap traps (1.0 × 8.5 × 16.5 cm) were alternately placed in 10 trapping stations spaced 5 m apart. In addition, four wire cages/Havahart traps (60 × 15 × 170 cm) were randomly placed in the plot specifically for trapping larger species such as *Cricetomys* and squirrels (Shilereyo et al., 2020; Welegerima et al., 2020). In total, 54 traps (twenty-five Sherman, twenty-five snaps and four Havaharts) were employed in each of the plot. Sherman traps were baited with peanut butter mixed with maize flour. Snap traps were baited with coconut and Havahart traps with either bananas, carrots, or roasted meat. The traps were left for three consecutive nights at an interval of 4 weeks. Some of the trapped animals from Sherman traps were euthanized (killed humanly) using Halothene solution soaked in cotton wool so as to remove tissue samples such as muscles, liver, and kidney for further research. The animals were weighed, sexed, and morphometric measurements such as head-body, tail, and hind leg lengths were recorded. The rest were released at capture site. Larger animals from Havahart traps were anesthetized, had their ears pierced, and released at the capture site. Whereas, animals from snap traps were dissected, and their stomachs preserved in 70% ethanol for further research.

Animals caught using both methods (CMR and removal) were identified to species level following Happold (2013) and Monadjem et al. (2015). Toe clip tissue samples were preserved in 99% ethanol for further molecular identifications. Some species (from the removal method) were collected as voucher specimens that are deposited in the museum at the Institute of Pest Management of Sokoine University of Agriculture, Tanzania.

## 2.3 | Habitat characterization

In each of the seven habitats, two main sample plots each measuring 50 m × 20 m were established on the existing plots/grids used for rodent trapping resulting in a total of 14 plots. A nested quadrant approach which is a modified Whittaker method was employed as narrated by Stohlgren et al. (1995). The plots were used for recording trees encountered within and identified to species level. Tree diameter at breast height (DBH) was measured using a caliper, and tree height was estimated by a Suunto hypsometer. For shrubs, two nested plots of 2.0 m × 2.0 m in each of the 50 m × 20 m main plots were used resulting in 28 subplots. All the shrubs were identified to species level, and their numbers were recorded. For grasses and herbs, 56 nested plots each of size 1.0 m × 1.0 m were established, four within each of the 50 m × 20 m main plots. All grasses and herbs were identified and enumerated. Percentage cover was used as an indirect measure of the performance of the species found within the plot using a scale of 0%–100%. Therefore, a single species covering the entire plot was given a score of 100%. Ground cover was estimated as the total percentage cover of grasses in proportion to bare soil using a scale of 0%–100%. Canopy cover was estimated as the percent of a forest area occupied by the vertical projections of tree crowns following procedures described by Avsar and Ayyildiz (2010). In addition, soil composite samples (250 g) and soil cores at 30 cm depth were collected and preserved in zipper bags for laboratory analysis of soil physical properties such as soil type, pH, bulk density, and soil moisture (Gee & Bauder, 1986).

Disturbance levels were assigned subject to observations in the field and were ranged from 1 to 3. Disturbance levels were based on the presence–absence of human activities such as logging, cultivation, and entrepreneurial facilities (restaurants). History of fire occurrences and disturbance from wild animals were also used. In addition, disturbance levels were based on location of the habitat whether inside or outside the park. For example, agricultural fields and plantation forests were assigned disturbance level 3 (highly disturbed) because they were located outside the national park and were predominated by human activities. Lower montane forest and fallow were assigned disturbance level 2 (moderately disturbed) because they had minimal human intervention despite of being located outside the park. Higher montane forest, ecotone, and moorland were located inside the national park hence were assigned disturbance level 1 (less disturbed only by wild animals).

## 2.4 | Data analysis

Trapped animals from both the CMR and removal methods were combined. However, to standardize the sample size, recaptured individuals in the CMR method were not considered for estimating rodent abundance. Following methods by Chidodo et al. (2020), Shilereyo et al. (2020) and Welegerima et al. (2020) rodent abundance was treated as total counts of new captures only. Vegan package 2.4–1 (https://CRAN.R-project.org/package) in R 3.6.2 (R Core Team, 2013) was used to estimate the abundance of rodents in each habitat. Also, species richness and the Shannon–Wiener diversity index of both rodents and plants were estimated (Oksanen et al., 2013). $H' = -\sum pilnpi$ was used to calculate the Shannon–Wiener diversity index (H′).Where H′ denotes the diversity index and Pi denotes the proportion of individuals found in the ith species (Shannon & Weaver, 1949). Chi-square test $\chi^2$ was used to compare the variation in rodent species composition across habitats and seasons. However, following a modified technique by Chidodo et al. (2020), three species such as *Arvicanthis niloticus*, *Pelomys fallax*, and *Aethomys kaiseri* were excluded from the analysis due to their low representation (Table 1). In addition to that, soil samples were processed and analyzed in the laboratory following procedures explained in Gee and Bauder (1986) and FAO (2006).

General linear models (GLM) were fitted to determine the influence of explanatory variables on species richness and abundance of rodents (Smith & Warren, 2019). Independent variables were both categorical and numerical. The numerical independent variables were soil pH, bulk density, soil moisture, ground cover, canopy cover, tree DBH, plant species richness and diversity. Categorical independent variables were habitat types, soil types, and seasonality. Data were pooled and analyzed into two major seasons (dry and wet). Because other seasons were very short, for

**TABLE 1** Species composition of rodents in percentages (number in parentheses) across habitats. The codes correspond to abbreviations of scientific names and habitats types

| | Habitats | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Species** | **AGR** | **DSF** | **ECT** | **FLW** | **MFR** | **MLD** | **PLF** | **Total** |
| Arv | 0 (0) | 0 (0) | 0 (0) | 1 (0.19) | 0 (0) | 0 (0) | 0 (0) | 1 (0.07) |
| Crtmy | 0 (0) | 10 (10.53) | 0 (0) | 0 (0) | 3 (0.78) | 0 (0) | 0 (0) | 13 (0.93) |
| Dn | 0 (0) | 0 (0) | 1 (1.61) | 34 (6.42) | 17 (4.42) | 22 (12.09) | 1 (2.5) | 75 (5.38) |
| Eith | 0 (0) | 0 (0) | 0 (0) | 2 (0.38) | 0 (0) | 0 (0) | 0 (0) | 2 (0.14) |
| Grm | 0 (0) | 7 (7.37) | 4 (6.45) | 35 (6.6) | 10 (2.6) | 0 (0) | 1 (2.5) | 57 (4.09) |
| Gr | 0 (0) | 3 (3.16) | 2 (3.23) | 2 (0.38) | 27 (7.01) | 0 (0) | 0 (0) | 34 (2.44) |
| LmZ | 0 (0) | 4 (4.21) | 0 (0) | 26 (4.91) | 0 (0) | 0 (0) | 0 (0) | 30 (2.15) |
| Lph | 11 (11.11) | 14 (14.74) | 23 (37.1) | 92 (17.36) | 76 (19.74) | 28 (15.38) | 16 (40) | 260 (18.66) |
| MnN | 41 (41.41) | 0 (0) | 0 (0) | 45 (8.49) | 0 (0) | 0 (0) | 1 (2.5) | 87 (6.25) |
| Mus | 0 (0) | 1 (1.05) | 0 (0) | 54 (10.19) | 34 (8.83) | 0 (0) | 3 (7.5) | 92 (6.6) |
| Ot | 0 (0) | 0 (0) | 0 (0) | 22 (4.15) | 5 (1.3) | 4 (2.2) | 0 (0) | 31 (2.23) |
| Plf | 0 (0) | 0 (0) | 0 (0) | 5 (0.94) | 0 (0) | 0 (0) | 0 (0) | 5 (0.36) |
| Pr | 1 (1.01) | 54 (56.84) | 10 (16.13) | 24 (4.53) | 213 (55.32) | 0 (0) | 15 (37.5) | 317 (22.76) |
| Rbd | 46 (46.46) | 2 (2.11) | 22 (35.48) | 188 (35.47) | 0 (0) | 128 (70.33) | 3 (7.5) | 389 (27.93) |
| Total | 99 | 95 | 62 | 530 | 385 | 182 | 40 | 1393 |

Abbreviations: Arv, *Arvicanthis niloticus*; Crtmy, *Cricetomys ansorgei*; Dn, *Dendromus* spp; Eith, *Aethomys kaiseri* (Noack, 1887); Grm, *Grammomys dolichurus* (smuts, 1832); Gr, *Graphiurus murinus* (Desmarest, 1822); LmZ, *Lemniscomys striatus*; Lph, *Lophuromys verhegeni* (Verheyen et al., 2007); MnN, *Mastomys natalensis* (Smith, 1834); Mus, *Mus musculoides* (Temminck, 1853); Ot, *Otomys spp*; Plf, *Pelomys fallax* (peters, 1852); Pr, *Praomys delectorum* (Thomas, 1910); Rbd, *Rhabdomys pumilio* (Spamnan, 1784); AGR, agricultural fields; DSF, lower montane forest; ECT, ecotone; FLW, fallow; MFR, higher montane forest; MLD, moorland; PLF, plantation forest.

example, dry season 1 had only 2 months (January and February). Pearson's pairwise correlation analysis in R was conducted for multicollinearity of the independent variables at $r \geq .5$ (Appendix A). Correlated variables were excluded from the same model (Smith & Warren, 2019). Before statistical analyses, assumptions of general linear models such as normality (using Shapiro test and Q-Q plots), independence of variance, and heterogeneity were checked (Smith & Warren, 2019; Zuur & Ieno, 2016). Unlike the data for species richness, rodent abundance did not follow the normal distribution and the data were over dispersed. Due to that, negative binomial distribution models (with log link function) were fitted for rodent abundance. We ran different models in which rodent species richness and abundance were allowed to differ between habitat types, seasonality, and soil types. Also, they were allowed to vary with ground cover, herbs density, soil bulk density, and the interactions between them (Appendix B and C). Akaike information criterion (AIC) was used for model selection whereby the one with the lowest AIC was selected as best model that better describe our data (Burnham & Anderson, 2004). An *F*-test was used for goodness of fit of the model and $R^2$ for the explained variation in rodent species richness. Moreover, two-way ANOVA ($p \leq .05$) was used to compare estimates of rodent abundance and species richness across habitats and seasons.

For community assemblages and habitat association of rodents, cluster analysis of rodent samples was performed in the PRIMER v6 program (Clarke & Warwick, 2001). Bray–Curtis similarity matrix with a distance measure was used to cluster the samples (Bray & Curtis, 1957). Previously, the data were square-root transformed to reduce the influence of dominant species (Clarke & Warwick, 2001). The similarity profile test (SIMPROF) was performed to determine genuine clustering and structuring of rodent samples and statistically test the difference between and within the clusters (Clarke & Warwick, 2001). Analysis of similarity (ANOSIM) test was performed for similarity of rodent community assemblages or clusters between pairs of habitats. Analysis was based on 999 times permutations with the sample statistic Global R (0–1) and the significance level of sample statistic (pi) $p \leq .05$ (Clarke & Warwick, 2001). Furthermore, canonical correspondence analysis (CCA) was performed in PAST Paleontological Statistics software (Hammer et al., 2002) at the correlation coefficient ($r \geq .5$). An ordination plot showing the association between individual species and habitat attributes was produced (Hammer et al., 2002; McCune et al., 2002).

### 2.5 | Ethical considerations

Our research was approved by the Sokoine University of Agriculture SUA postgraduate committee, Tanzania (Ref no: SUA/DPRTC/PFC/D/2019/0002/13). Registered, approved, and provided a research permit (No: 2020-163-NA-2020-127) to conduct research on rodents by the Tanzania Commission for Science and Technology (COSTECH) in collaboration with Tanzania Wildlife Research Institute (TAWIRI). An entry permit into Mount Kilimanjaro National Park was granted by Tanzania National Parks (TANAPA). Moreover, the research was conducted following guidelines by the American Society of Mammologists (ASM) for appropriate methods of research on wild animals.

## 3 | RESULTS

### 3.1 | Rodent species composition

A total of 1393 individuals from 14 species of rodents were trapped on 25,956 trap nights. *Rhabdomys pumilio*, *Praomys delectorum*, and *Lophuromys verhegeni* were the most dominant species contributing to 69.35% of the total captures. *P. delectorum* predominated both higher and lower montane forests with 55.32% and 56.84%, respectively (Table 1). Whereas, *Rhabdomys pumilio* predominated the moorland and agricultural fields with 70.33% and 46.46%, respectively. *R.pumilio* was restricted from occurring in montane forests. However, two individuals were unexpectedly trapped in the lower montane forest. On the contrary, *Lophuromys verhegeni* occurred across all habitats and seasons predominantly in ecotone. *Mastomys natalensis* was the fourth dominant species occurring predominantly in agricultural fields. Other species such as *Aethomys kaiseri*, *Arvicanthis niloticus*, and *Pelomys fallax* had the lowest percentage composition of total captures; with 0.14%, 0.07%, and 0.36%, respectively. Moreover, most species occurred across both habitats and seasons (Tables 1 and 2); however, Chi-square test indicated that percentage composition (occurrence) of only three species varied significantly across habitats and seasons (Table 3). For example, *P. delectorum* ($\chi^2$ = 200.38, df = 5, $p < .001$), *L.verhegeni* ($\chi^2$ = 15.03, df = 6, $p$ = .02), and *R. pumilio* ($\chi^2$ = 377.72, df = 5, $p < .001$). The percentage composition of other species did not statistically differ across habitats and seasons (Table 3).

### 3.2 | Rodent species richness and diversity

Rodent species diversity H (Shannon Wiener diversity Index) was highest in fallow FLW habitat (H = 1.92), followed by lower montane forest DSF (H = 1.64), and lowest in agricultural fields AGR (H = 1.06).

From GLM models, rodent species richness was influenced by both habitat types, seasonality, ground cover, and soil type as they were included in the best model ($F_{11,1396} = 95.78$, $p = .001$, $R^2 = .43$). However, the influence of seasonality was not significant ($p = .632$), and species richness did not significantly differ between dry and wet seasons. Species richness differed significantly between habitats. Whereby, it was highest in fallow but not significant (13 species) followed by both montane forests (higher MFR and lower DSF) (each with eight species) and significantly lower in both moorland and agricultural fields (each with four species, $p < .001$). It was significantly highest in clay soil CLY (0.839 ± 0.165, $p < .001$) and lowest in clay loam soil CLYLM (−1.458 ± 0.205, $p < .001$). Moreover, species

**TABLE 2** Abundance and species composition of rodents in percentages (number in parentheses) across the two seasons

| | Season | | |
|---|---|---|---|
| **Species** | **Dry** | **Wet** | **Total** |
| *Arvicanthis niloticus* | 0 (00) | 1 (0.15) | 1 (0.07) |
| *Cricetomys ansorgei* | 8 (1.1) | 5 (0.75) | 13 (0.93) |
| *Dendromus* spp | 43 (5.93) | 32 (4.79) | 75 (5.38) |
| *Aethomys kaiseri* (Noack, 1887) | 2 (0.28) | 0 (0) | 2 (0.14) |
| *Grammomys dolichurus* (Smuts, 1832) | 30 (4.14) | 27 (4.04) | 57 (4.09) |
| *Graphiurus murinus* (Desmarest, 1822) | 17 (2.34) | 17 (2.54) | 34 (2.44) |
| Lemniscomys striatus (Linnaeus, 1758) | 16 (2.21) | 14 (2.1) | 30 (2.15) |
| *Lophuromys verhegeni* | 139 (19.17) | 121 (18.11) | 260 (18.66) |
| *Mastomys natalensis* (Smith, 1834) | 54 (7.45) | 33 (4.94) | 87 (6.25) |
| *Mus musculoides* (Temminck, 1853) | 56 (7.72) | 36 (5.39) | 92 (6.60) |
| *Otomys* spp | 22 (3.03) | 8 (1.2) | 30 (2.15) |
| *Pelomys fallax* (Peters, 1852) | 3 (0.4) | 2 (0.3) | 5 (0.36) |
| *Praomys delectorum* (Thomas, 1910) | 133 (18.34) | 185 (27.69) | 318 (22.83) |
| *Rhabdomys pumilio* (Spamnan, 1784) | 202 (27.86) | 187 (27.99) | 389 (27.93) |
| Total | 725 | 668 | 1393 (100) |

**TABLE 3** Results from Chi-square test on rodent distribution across both habitats and seasons

| **Species** | $\chi^2$ | **df** | ***p*** | **Critical value** |
|---|---|---|---|---|
| *Arvicanthis niloticus* | 3 | 3 | .39 | 7.81 |
| *Cricetomys ansorgei* | 1.31 | 1 | .25 | 3.84 |
| *Dendromus* spp | 2.61 | 4 | .63 | 9.49 |
| *Aethomys kaiseri* (Noack, 1887) | 6 | 3 | .11 | 12.59 |
| *Grammomys dolichurus* (Smuts, 1832) | 5.11 | 4 | .28 | 9.49 |
| *Graphiurus murinus* (Desmarest, 1822) | 4.68 | 3 | .2 | 7.81 |
| *Lemniscomys striatus* | 1.49 | 1 | .22 | 3.84 |
| *Lophuromys verhegeni* | 15.03 | 6 | **.02** | 12.59 |
| *Mastomys natalensis* (Smith, 1834) | 3.75 | 2 | .15 | 5.99 |
| *Mus musculoides* (Temminck, 1853) | 3.23 | 3 | .36 | 7.82 |
| *Otomys* spp | 0.19 | 6 | 1 | 12.59 |
| *Pelomys fallax* (Peters, 1852) | 4 | 0 | NA | 5.99 |
| *Praomys delectorum* (Thomas, 1910) | 200.38 | 5 | **<.001** | 11.07 |
| *Rhabdomys pumilio* (Spamnan, 1784) | 377.72 | 5 | **<.001** | 11.07 |

Abbreviations: $\chi^2$, Chi-square test statistic; df, degrees of freedom.
Bold indicated: < .001 = significant at 0***.

richness was positively correlated and increased with increasing ground cover (0.051 ± 0.003, $p < .001$) (Table 4).

## 3.3 | Rodent abundance

The GLM model indicated that, rodent abundance was influenced by the variations in habitat type ($p = .001$), seasonality ($p = .01$), soil type ($p < .001$), ground cover ($p < .001$), and soil bulk density; however, the effect of soil bulk density was not significant ($p = .06$). Rodent abundance differed across habitats and seasons. Abundance (Estimate ± SE, *p*-value) was highest in fallow FLW but not significant (0.151 ± 0.183, $p = .408$) followed by higher montane forest MFR (−0.031 ± 0.206, $p = .879$) and was significantly lowest in plantation forest PLF (−1.475 ± 0.151, $p < .001$). Moreover, rodent abundance differed between seasons whereby it was significantly higher in the dry season (1.222 ± 0.258, $p < .001$) than in wet season (−0.157 ± 0.067, $p = .019$). Moreover, rodent abundance differed between soil types whereby it was significantly highest in clay soil CLY (1.222 ± 0.258, $p < .001$) and lowest in clay loam soil CLYLM (−1.183 ± 0.172, $p < .001$) than in other soil types. In addition, rodent abundance had a significantly linear relationship with ground cover (0.024 ± 0.002, $p < .001$) and a linear relationship with bulk density (Table 5).

**TABLE 4** Summary of best GLM model (from linear regression) that better describes the influence of independent variables (parameters) on rodent species richness representing estimate, standard error, *Z*-value and *p*-value

| Parameters | Estimate | Std. error | *Z*-value | *p*-value |
|---|---|---|---|---|
| (Intercept) | 0.839 | 0.165 | 5.092 | 4.03e-07*** |
| Habitat:Lower montane forest | −1.425 | 0.227 | −6.266 | 4.92e-10*** |
| Habitat: Ecotone | −1.582 | 0.207 | −7.656 | 3.58e-14*** |
| Habitat: Fallow | 0.35 | 0.221 | −1.585 | .113 |
| Habitat: Higher montane forest | −0.348 | 0.261 | −1.333 | .183 |
| Habitat: Moorland | −1.546 | 0.191 | −8.075 | 1.45e-16*** |
| Habitat: Plantation forest | −1.32 | 0.181 | −7.312 | 4.42e-13*** |
| Season: Wet | −0.046 | 0.083 | −0.56. | .576 |
| GCv | 0.051 | 0.003 | 17.601 | <2e-16*** |
| Soil: Clay loam | −1.458 | 0.205 | −7.108 | 1.87e-12*** |
| Soil: Sandy clay loam | −0.447 | 0.136 | −3.28 | .001** |
| Soil: Sandy loam | −0.835 | 0.15 | −5.575 | 2.97e-8*** |

*Note*: Significant codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1.

Abbreviation: GCv, ground cover.

**TABLE 5** Summary of best GLM model (negative binomial) that better describes the influence of independent variables (parameters) on rodent abundance representing estimate, standard error, *Z*-value and *p*-value

| Parameters | Estimate | Std. error | *Z*-value | *p*-value |
|---|---|---|---|---|
| (Intercept) | 1.222 | 0.258 | 4.735 | 2.19e-06*** |
| Habitat:Lower montane forest | −0.705 | 0.183 | −3.85 | .000*** |
| Habitat: Ecotone | −1.119 | 0.167 | −6.694 | 2.17e-11*** |
| Habitat: Fallow | 0.151 | 0.183 | 0.827 | .408 |
| Habitat: Higher montane forest | −0.031 | 0.206 | −0.152 | .879 |
| Habitat: Moorland | −0.521 | 0.152 | −3.419 | .001*** |
| Habitat: Plantation forest | −1.475 | 0.151 | −9.795 | <2e-16*** |
| Season: Wet | −0.157 | 0.067 | −2.345 | .019* |
| GCv | 0.024 | 0.002 | 10.01 | <2e-16*** |
| Soil: Clay loam | −1.183 | 0.172 | −6.861 | 6.85e-12*** |
| Soil: Sandy clay loam | −0.39 | 0.132 | −2.949 | .003** |
| Soil: Sandy loam | −1.176 | 0.134 | −1.312 | .19 |
| BD | 0.423 | 0.214 | 1.975 | .058 |

*Note*: Significant codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1.

Abbreviations: GCv, ground cover; BD, bulk density.

### 3.4 | Community assemblages and habitat association

From cluster analysis based on the Bray–Curtis dissimilarity index, there was evidence of genuine structuring of rodent samples forming two major community assemblages/clusters at 99% efficiency (Figure 2). Community assemblage one (C1) predominated in forested habitats mainly in ecotone, montane (higher and lower), and plantation forests. Whereas, the second community assemblage (C2) predominated in the moorland, fallow, and agricultural fields (Figure 2). The SIMPROF test showed a statistically significant difference between and within the two clusters with sample statistic (pi) of 2.483, $p$ = .002 at 999 permutations. Furthermore, the ANOSIM test showed statistically significant differences in community assemblages between pairs of habitats at sample statistic (Global R) = .05, $p$ = .01 at 999 permutations (Table 6). For example, agricultural fields AGR were completely distant and significantly different from both lower DSF and higher MFR montane forests (Global-*R* statistic = 1, $p$ = .029) and not significantly different from fallow FLW (Global-*R* statistic = .218, $p$ = .119). Moorland MLD was significantly different from both lower and higher montane forests (Global-*R* statistic = .833, $p$ = .005) (Table 6).

In addition, CCA canonical correspondence analysis explained about 80% of the variations in two axes (Figure 3). Axis 1 (CCA 1) explained 59.4% of the variation. *Praomys delectorum*, *Graphiurus murinus*, and *Cricetomys ansorgei* loaded positively to canopy cover, leaf litter, tree and herbs density, higher (MFR) and lower (DSF) montane forests. While *R. pumilio* and moorland habitat (MLD) loaded negatively. Indicating that, *P. delectorum*, *G. murinus*, and *C.ansorgei* are more associated with montane forests and their abundance increased with increasing tree and herb density, leaf litter, and canopy cover. While *R. pumilio* was more associated with moorland habitat.

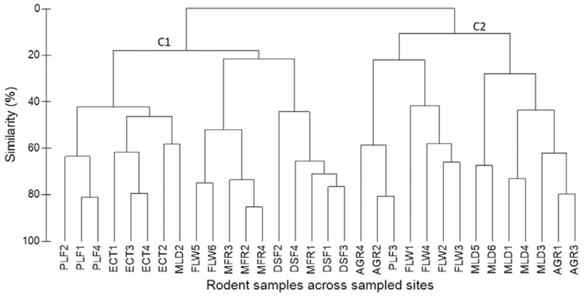

**FIGURE 2** Dendrogram based on Bray–Curtis similarity distance measure showing two broad clusters of rodent communities among the rodent samples across the study area. There was a significant structuring between and within the two major clusters (community assemblages). AGR1-4, PLF 1-4, FLW 1-6, MLD 1-6, ECT 1-4, MFR1-4 and DSF 1-4 refers to replicated sites in agricultural fields, plantation forest, fallow, moorland, ecotone, higher montane forest, and lower montane forest, respectively.

**TABLE 6** Results from analysis of similarity test ANOSIM on rodent community assemblages at 999 permutations

| Pairwise tests | | | | | |
|---|---|---|---|---|---|
| **Groups** | ***R* statistic** | **Significance level %** | **Possible permutations** | **Actual permutations** | **Number >=Observed** |
| AGR, DSF | 1 | 2.9 | 35 | 35 | 1 |
| AGR, ECT | .698 | 2.9 | 35 | 35 | 1 |
| AGR, FLW | .218 | 11.9 | 210 | 210 | 25 |
| AGR, MFR | 1 | 2.9 | 35 | 35 | 1 |
| AGR, MLD | .333 | 4.8 | 210 | 210 | 10 |
| AGR, PLF | .625 | 5.7 | 35 | 35 | 2 |
| DSF, ECT | .698 | 2.9 | 35 | 35 | 1 |
| DSF, FLW | .349 | 5.2 | 210 | 210 | 11 |
| DSF, MFR | .51 | 8.6 | 35 | 35 | 3 |
| DSF, MLD | .833 | 0.5 | 210 | 210 | 1 |
| DSF, PLF | .37 | 8.6 | 35 | 35 | 3 |
| ECT, FLW | .262 | 8.6 | 210 | 210 | 18 |
| ECT, MFR | .792 | 2.9 | 35 | 35 | 1 |
| ECT, MLD | .143 | 18.6 | 210 | 210 | 39 |
| ECT, PLF | .188 | 14.3 | 35 | 35 | 5 |
| FLW, MFR | .508 | 1.9 | 210 | 210 | 4 |
| FLW, MLD | .435 | 1.5 | 462 | 462 | 7 |
| FLW, PLF | .361 | 7.1 | 210 | 210 | 15 |
| MFR, MLD | .833 | 0.5 | 210 | 210 | 1 |
| MFR, PLF | .49 | 2.9 | 35 | 35 | 1 |

*Note*: There were significant differences in rodent community assemblages between pairs of habitats. Sample statistic (global *R*) = .5, significance level statistic *p* = .001.

Abbreviations: AGR, agricultural fields; DSF, disturbed/lower montane forest; ECT, ecotone; FLW, fallow; MFR, higher montane forest; MLD, moorland; PLF, plantation forest.

Axis 2 (CCA 2) explained 20.47% of the variations with *Dendromus* spp, soil moisture and shrub density loading negatively. While *M. natalensis* loaded positively to disturbance level and agricultural fields. Indicating that, *Dendromus* was more associated with shrub density and soil moisture and their abundance increased with increasing shrub density. Whereas, *M. natalensis* was more associated with agricultural fields and disturbance (Figure 3).

## 4 | DISCUSSION

### 4.1 | Species composition, community assemblages, and habitat association

Results indicated that, 14 species of rodents were recorded across habitats and seasons. Out of the captured species, two major community assemblages with different composition were formed. Community assemblage one mainly comprised of forest-adapted species such as *Praomys delectorum*, *Graphiurus murinus*, and *Cricetomys ansorgei*. Whereas, the second community assemblage was mainly comprised of habitat generalists such as *Rhabdomys pumilio*, *Lophuromys verhageni*, *Mastomys natalensis*, *Mus musculoides*, and *Dendromus* spp. The observed community assemblages were probably a result of the variations in vegetation structure across the habitats. Montane forests were characterized by dense and homogenous vegetation which favors forest specialists. Fallow and ecotone were dense and heterogeneous supporting habitat generalists. Whereas, agricultural fields and moorland were homogeneous with sparse vegetation favoring opportunistic species. It is reported that community assemblage of rodents is determined by the coexistence of species which depends on species-specific traits such as nesting, food availability, and predation risk (Cramer & Willig, 2002). Consistently, in this study, rodents were associated not only with distinct habitat types but also with vegetation attributes. For example, in community assemblage one, *Praomys delectorum* and *Graphiurus murinus* were more dominant in montane forests than in plantation forest. The species were positively associated with tree and herb density, leaf litter, and canopy cover probably because they are habitat specialists and typical forest-adapted species that prefer areas with dense canopy and vegetation cover. Dense herbs and leaf litter provide enough food, protection from predators, and nesting grounds for the species. Canopy cover maintains humidity and soil moisture which creates suitable microclimate for *P. delectorum* (Bantihun & Bekele, 2015). Similarly, *P. delectorum* has been reported a closed forest dweller that forages on deep leaf litter (Happold, 2013) and builds its nest from litter and other vegetative materials (Monadjem et al., 2015). Moreover, *P. delectorum* has been previously reported as the dominant species in montane forests of Mt Kilimanjaro (Mulungu et al., 2008; Stanley et al., 2014), Mt Elgon in Kenya and Uganda (Clausnitzer et al., 2001) and other mountains including the Eastern Arc Mountains (Ademola et al., 2021; Chidodo et al., 2020; Makundi et al., 2007; Stanley et al., 1998). In addition, *P. delectorum* is reported to inhabit both intact and disturbed forests (Ademola et al., 2021; Gitonga et al., 2016; Monadjem et al., 2015; Mulungu et al., 2008) as well as edges between forest and ecotone (Mulungu et al., 2008). On the contrary, low percentage composition of *P. delectorum* in plantation forest (despite it is a forest-adapted species) was probably due to high levels of disturbance from anthropogenic activities including cultivation, logging, and firewood collection. These activities result into habitat destruction and fragmentation which adversely affects the survival of native species.

*Rhabdomys pumilio*, *L. verhageni*, *M. natalensis*, and *Dendromus* spp were the most abundant species in the second community assemblage. *R. pumilio* predominated in the moorland and agricultural fields and was moderately associated with ground cover, probably because it is most important and preferred food is grass and seeds hence commonly named the grass rat (Clausnitzer et al., 2001; Shore & Garbett, 1991; Happold, 2013). Moreover, *R. pumilio* occurred in all habitats except in montane forests (however, we unexpectedly caught two individuals in the lower montane forest). This was probably because, *R. pumilio* prefers areas with dry conditions while montane forests of Mt. Kilimanjaro remains wet throughout the year. Consistently, Clausnitzer et al. (2001) reported that *R. pumilio* prefers drier areas with sparse vegetation and bare soil which creates suitable microclimate. Clausnitzer et al. (2001) added that, the species is adapted to cold weathers in the moorland habitat (which gets

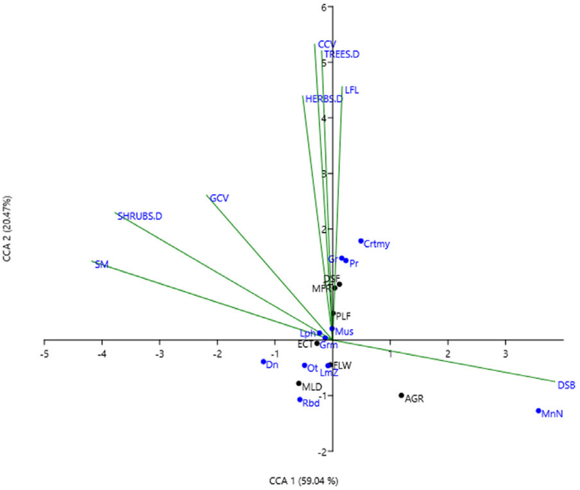

**FIGURE 3** Habitat association of rodents in West Mt Kilimanjaro. Canonical correspondence CCA1explained 59.4% of the variations, while canonical correspondence CCA2 explained 20.47% of the variations. AGR, agricultural fields; DSF, lower montane forest; ECT, ecotone; FLW, fallows; MFR, higher montane forest; MLD, moorland and PLF, plantation forest; LFL, leaf litter; CCV, canopy cover; GCV, ground cover; SM, soil moisture; DSB, disturbance level; Pr, *Praomys delectorum*; MnN, *Mastomys natalensis*; Rbd, *Rhabdomys pumilio*; Ot, *Otomys spp*; Dn, *Dendromus spp*; Gr, *Graphiurus murinus*; Grm, *Grammomys dolichurus*; Mus, *Mus musculoides*; Lph, *Lophuromys verhageni*; LmZ, *Lemniscomys striatus*; Crtmy, *Cricetomys ansorgei*. SHRUBS.D, TREES.D and HERBS.D = shrub, tree and herb density, respectively.

harsh during the night) by being active during the day. In contrast, Grimshaw et al. (1995) and Stanley et al. (2014) revealed that *R. pumilio* is rarely found in higher montane forests near human habitations with Stanley et al. (2014) trapping few individuals near Horombo tourist huts along the Marangu route of Mt. Kilimanjaro.

Among the captured rodents in this study, *Lophuromys verhageni* was the only endemic species in west Mt Kilimanjaro (Verheyen et al., 2007). It occurred across all habitats and seasons hence termed a habitat generalist. Similarly, species of the same genus have been reported to occur in moist places of montane forests (from 500 m s.a.l in lowland forests) and highland habitats up to 4500 m a.s.l in the Afro-alpine zone (Bantihun & Bekele, 2015; Happold, 2013). They are widely distributed in bushlands, fallows, plantation forests, montane forests, heath lands, and alpine zones in East, Central, and South Africa (Bantihun & Bekele, 2015; Clausnitzer et al., 2001, 2003; Happold, 2013; Mulungu et al., 2008; Ssuuna et al., 2020; Stanley et al., 1998, 2014; Stanley & Kihaule, 2016).

*Mastomys natalensis* predominated in the agricultural fields (mostly maize, potato, and carrot farms) and was positively associated with disturbance. It was more abundant in the dry season than in wet season. This observation coincides with crop harvest in Kilimanjaro region which is mostly conducted in dry season. Crop remains from harvesting provide supplementary food to *M. natalensis* and other rodents inhabiting the agricultural fields. Similarly, *M. natalensis* is reported as the most common crop pest predominating in agro ecosystems (Mulungu et al., 2013, 2014; Mulungu, 2017). As a habitat generalist and opportunist, *M. natalensis* takes advantage of human disturbance due to the available food resources from cultivation (Happold, 2013; Lema & Magige, 2018; Mulungu et al., 2013, 2014). *Mastomys natalesnsis* together with *Mus musculoides* and *Arvicanthis niloticus* have been reported to prefer agricultural fields and fallows close to human habitation (Admas & Yihune, 2016; Bantihun & Bekele, 2015; Makundi et al., 2010; Mulungu et al., 2006).

*Dendromus* spp were associated with fallow and moorland habitats and positively correlated with shrub density and soil moisture. More individuals of *Dendromus spp* were trapped in dense patches of Erica bushes. Similarly, Happold (2013) reported that *Dendromus* spp is among the species occurring in high abundance above the tree line preferably in dense shrubs and moist places. On the contrary, species such as *Aethomys kaiseri*, *Arvicanthis niloticus*, and *Pelomys fallax* were underrepresented across both habitats and seasons. This observation could be attributed to trapping in higher altitudes from 1500 a m.s.l and above while the species are said to be widely distributed in low-elevation grasslands and bushes (Grimshaw et al., 1995; Stanley et al., 1998).

Generally, most of the trapped species in this study have been previously captured on both sides of Mt. Kilimanjaro and their distribution and conservation status are well known (Grimshaw et al., 1995; Mulungu et al., 2008; Stanley et al., 2014). However, *Pelomys fallax* has never been previously reported along the Shira route, and therefore, its distribution and conservation status is poorly known. The smaller number of individuals trapped in the current study ($n = 5$) is consistent with Happold (2013) who suggested that *Pelomys fallax* is neither a rare nor an abundant species. Similarly, Mlyashimbi et al. (2019) reported smaller number of *Pellomys fallax* in semiarid areas of Tanzania. However, our results are contrary to Admas and Yihune (2016) who reported similar species of genus Pelomys (*Pelomys harringtoni*) among the most abundant species across habitats of east Gojjam, Ethiopia. Furthermore, in this study, most species have been captured in higher numbers compared with previous studies by Mulungu et al. (2008) and Stanley et al. (2014) in the same study area. This was probably because our study had an extensive sampling period throughout the year covering a relatively large area with a combination of methods and traps.

### 4.2 | Influence of vegetation structure, seasonality, and soil type on species richness and abundance

Fallow was the most diverse habitat probably due to high ground cover and shrub density which provide niches for many species (Cramer & Willig, 2002). Fallows are intermediates between agricultural fields and montane forests that serve as refuge to other rodents providing alternative food resources and protection from predators (Cramer & Willig, 2002; Makundi et al., 2010). Montane forests (both higher MFR and lower DSF) were the next diverse habitats with high rodent species richness and abundance. This was probably due to high canopy and ground cover, high vegetation density, and plant species diversity (particularly in the higher montane) forest which provides food and protection to rodents. Lower montane forest on the other hand, had high species diversity and abundance despite the fact that it was less dense than higher montane forest. This was due to moderate disturbance which provided microhabitats to habitat generalists such as *L. verhegeni*, *G. dolichurus* and *Mus musculoides* (Ademola et al., 2021; Mulungu et al., 2008). Similarly, a study by Mulungu et al. (2008) reported maximum rodent abundance in montane forests that decreased above the tree line forming a hump-shaped distribution, due to maximum rainfall at mid-elevation (Hemp, 2006). Montane forests receive maximum amount of rainfall which increases primary productivity hence improves vegetation structure and food availability (Clausnitzer & Kityo, 2001). Similar patterns of rodent abundance in montane forests have been reported in the Mabira central forest reserve in Uganda and the Ukaguru Mountains of Tanzania (Ademola et al., 2021; Ssuuna et al., 2020). On the contrary, agricultural fields, plantation forest, and moorland were the least diverse among the seven habitats with lower species richness and abundance. This observation was linked to high disturbance from anthropogenic activities in the agricultural fields and plantation forest which affect the integrity of habitats and reduce diversity of most rodents (Bennett, 1990). In addition, poor vegetation structure and adverse environmental conditions in the moorland affect the survival and distribution of Afro-alpine rodents (Clausnitzer et al., 2001). Afro alpine environments are characterized by extreme cold weather which restricts movement and activity pattern of rodents forcing them to take cover inside burrows and grasses.

In addition to habitat type and ground cover, seasonality influenced rodent species richness and abundance. However, the influence of seasonality on rodent species richness was not significant probably because most species occurred across both dry and wet seasons. Rodent abundance was relatively higher in the dry season than in wet season. This was probably due to that most species start breeding 1 month after the long rains until the end of wet season. During this period, there is high cover and green foliage which triggers breeding in most rodents (Mlyashimbi et al., 2018). Therefore, rodent population tends to peak 2–4 months later (Mulungu et al., 2013). Similarly, it is reported that the variation in rainfall distribution influence rodents' diet (Mulungu et al., 2011) and breeding patterns (Leirs et al., 1994; Mlyashimbi et al., 2018; Mulungu et al., 2014) through resource availability which in turn affect population abundance (Leirs et al., 1997; Makundi et al., 2007). Moreover, the observed high abundance in dry season could be a result of crop remains in agricultural fields which ensures continuous food supply to rodents inhabiting them.

Furthermore, soil type and microclimate have been reported to influence the distribution, population abundance, and survival of rodents elsewhere (Massawe et al., 2008; Meliyo et al., 2014; Mlyashimbi et al., 2019). In this study, clay soil had higher rodent species richness and abundance than other soils probably because of its good texture. Clay soil hardens during the rainy season allowing the survival of rodents (Meliyo et al., 2014). While other volcanic ash soils of Mt. Kilimanjaro have low bulk density and poor structure that can easily collapse or shrink during rainy season making them unsuitable for most rodents (Nanzyo et al., 1993). However, our results are contrary to those by Mlyashimbi et al. (2019) and Massawe et al. (2008) who reported low abundance and survival of *Mastomys natalensis* and other rodents in clay soils.

## 5 | CONCLUSION AND RECOMMENDATION

Results from this study indicated that rodent species richness and abundance in west Mt. Kilimanjaro were a result of several factors including habitat types in synergy with vegetation structure, seasonality, and soil physical properties. Rodent community assemblages reflected the variation in habitat types, vegetation structure, and disturbance level along the altitudinal gradient. Moreover, Mt. Kilimanjaro has heterogeneous habitats that support high diversity of rodents with fallows and montane forests being the most diverse habitats supporting complex communities. However, increasing cultivation and forest plantation in unprotected areas of Mt Kilimanjaro results in habitat destruction and fragmentation. Habitat destruction and fragmentation simplifies vegetation structure favoring the abundance and survival of the habitat generalists and opportunists at the expense of forest-adapted species. Therefore, the development of ecologically sound strategies is crucial for management and conservation of the rodent communities in Mt Kilimanjaro.

## AUTHOR CONTRIBUTIONS

**Suzana M. Thomas:** Conceptualization (equal); data curation (lead); formal analysis (equal); funding acquisition (lead); investigation (equal); methodology (equal); project administration (lead); resources (equal); software (equal); supervision (supporting); validation (equal); visualization (equal); writing – original draft (lead); writing – review and editing (equal). **Geofrey E. Soka:** Conceptualization (equal); data curation (supporting); formal analysis (equal); funding acquisition (supporting); investigation (equal); methodology (equal); project administration (supporting); resources (equal); software (equal); supervision (lead); validation (equal); visualization (equal); writing – original draft (supporting); writing – review and editing (equal). **Loth S. Mulungu:** Conceptualization (equal); data curation (supporting); formal analysis (equal); funding acquisition (supporting); investigation (equal); methodology (equal); project administration (supporting); resources (equal); software (equal); supervision (lead); validation (equal); visualization (equal); writing – original draft (supporting); writing – review and editing (equal).

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## CONFLICT OF INTEREST

Authors declare no conflict of interest among themselves.

## DATA AVAILABILITY STATEMENT

Authors agree to deposit the data associated with this study in an Institutional repository of Sokoine University of Agriculture SUA and make it publicly available, once the manuscript is accepted for publication under the Journal of Ecology and Evolution. https://www.suaire.sua.ac.tz/handle/123456789/4206.

## ORCID

*Suzana M. Thomas* https://orcid.org/0000-0002-2450-7610

## ENDNOTES

Abbreviations: GCv, ground cover; BD, bulk density; Herbs.D, herb density, Shrubs.D, shrub density; Trees.D, tree density.

*Note*: Model with the lowest AIC (shown in bold) is the one that better describes and fits our data. For every model; the number of parameters (df), AIC and delta ΔAIC are given. ΔAIC is the difference in AIC between the current model and the best model.

Abbreviations: GCv, ground cover; BD, bulk density; Herbs, herb density.

## REFERENCES

Ademola, O. J., Vanden Broecke, B., Leirs, H., Massawe, A. W., Mulungu, L. S., & Makundi, R. H. (2021). Effects of forest disturbance on the fitness of an endemic rodent in a biodiversity hotspot. *Ecology and Evolution*, *11*(5), 2391–2401.

Admas, A., & Yihune, M. (2016). Species composition, relative abundance and habitat association of rodents in Yekoche Forest, east Gojjam, Ethiopia. *International Journal of Biodiversity and Conservation*, *8*(9), 216–223.

August, P. V. (1983). The role of habitat complexity and heterogeneity in structuring tropical mammal communities. *Ecology*, *64*(6), 1495–1507.

Avenant, N. (2011). The potential utility of rodents and other small mammals as indicators of ecosystem 'integrity' of south African grasslands. *Wildlife Research*, *38*(7), 626–639.

Avenant, N. L. (2003). The use of small mammal community characteristics as an indicator of ecological disturbance in the Korannaberg conservancy. In G. R. Singleton, L. A. Hinds, C. J. Krebs, & D. M. Spratt (Eds.), *Rats, mice and people: Rodent biology and management. ACIAR Monograph No. 96, 564 Pp.* (pp. 95–98).

Avsar, M. D., & Ayyildiz, V. (2010). Estimation of stand canopy cover by different methods oncrown projections: Sample of Lebanon cedar stands of the Yavsan Mountain, Kahramanmaras, Turkey. *Journal of Applied Sciences*, *10*(1), 1326–1330.

Bantihun, G., & Bekele, A. (2015). Diversity and habitat association of small mammals in Aridtsy forest, Awi zone, Ethiopia. *Zoological Research*, *36*(2), 88–94.

Bennett, A. F. (1990). Habitat corridors and the conservation of small mammals in a fragmented forest environment. *Landscape Ecology*, *4*(2), 109–122.

Borremans, B., Sluydts, V., Makundi, R. H., & Leirs, H. (2015). Evaluation of short-, mid- and long-term effects of toe clipping on a wild rodent. *Wildlife Research*, *42*, 143–148.

Bray, J. R., & Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, *27*(4), 326–349.

Burnham, K. P., & Anderson, D. R. (2004). Model selection and multimodel inference. In K. P. Burnham & D. R. Anderson (Eds.), *Model selection and multimodel inference*. Springer New York. https://doi.org/10.1007/b97636

Chidodo, S., Kilawe, C. J., Mnyone, L. L., Vanden Croecke, B., & Mulungu, L. S. (2020). Factors affecting the composition of rodent assemblages in north Uluguru Mountains, Tanzania. *Journal of Vertebrate Biology*, *69*(2), 20047.1–20047.10. https://doi.org/10.25225/jvb.20047

Clarke, K. R., & Warwick, R. M. (2001). *Change in marine communities. An approach to statistical analysis and interpretation* (Vol. 2, pp. 1–168). PRIMER-E, Ltd., Plymouth Marine Laboratory.

Clausnitzer, V., Churchfield, S., & Hutterer, R. (2003). Habitat occurrence and feeding ecology of *Crocidura montis* and *Lophuromys flavopunctatus* on Mt. Elgon, Uganda. *African Journal of Ecology*, *41*(1), 1–8.

Clausnitzer, V., Denys, C., Granjon, L., & Poulet, A. (2001). Rodents of the afro-alpine zone of Mt. Elgon. *African Small Mammals*, 427–443.

Clausnitzer, V., & Kityo, R. (2001). Altitudinal distribution of rodents (Muridae and Gliridae) on Mt Elgon, Uganda. *Tropical Zoology*, *14*(1), 95–118.

Cramer, M. J., & Willig, M. R. (2002). Habitat heterogeneity, habitat associations and rodent species diversity in a sand-shinnery-oak landscape. *Journal of Mammalia*, *83*, 743–753.

FAO. (2006). *Guidelines for soil description* (4th ed., p. 30). Food and Agriculture Organization of the United Nations.

Gee, G. W., & Bauder, J. W. (1986). Particle size analysis. In A. Klute (Ed.), *Methods of soil analysis. Physical and mineralogical methods* (pp. 383–409). American Society of Agronomy.

Gitonga, J., Simbauni, J., & Oguge, N. (2016). Effect of habitat fragmentation on some aspects of reproduction among Praomys delectorum sub-populations in the Taita and Kyulu hills, Kenya. *International Journal of Advanced Research in Biological Sciences*, *3*(4), 143–151.

Grelle, C. E. V. (2003). Forest structure and vertical stratification of small mammals in a secondary Atlantic forest, southeastern Brazil. *Studies on Neotropical Fauna and Environment*, *38*(2), 81–85.

Grimshaw, J. M., Cordeiro, N. J., & Foley, C. A. H. (1995). The mammals of Kilimanjaro. *Journal of East African Natural History*, *84*(2), 105–139.

Grimshaw, I. M., & Foley, C. A. H. (1991). *Kilimanjaro Elephant Project 1990 – Final Report*. Friends of Conservation.

Hammer, Ø., Harper, D. A. T., & Ryan, P. D. (2002). Past: Paleontological statistics software package for education and data analysis. *Paleontological Electronica*, *4*, 9.

Happold, D. (2013). *Mammals of Africa. Volume III, rodents, hares and rabbits* (p. 784). Bloomsbury Publishing.

Hemp, A. (2006). Continuum or zonation? Altitudinal gradients in the forest vegetation of Mt. Kilimanjaro. *Plant Ecology*, *184*(1), 27–42.

Hernández, L., Romero, A. G., Laundré, J. W., Lightfoot, D., Aragón, E., & Portillo, J. L. (2005). Changes in rodent community structure in the Chihuahuan Desert Mexico: Comparisons between two habitats. *Journal of Arid Environments*, *60*(2), 239–257.

Johnson, S. D., Burgoyne, P. M., Harder, L. D., & Dötterl, S. (2011). Mammal pollinators lured by the scent of a parasitic plant. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1716), 2303–2310.

Kay, E. H., & Hoekstra, H. E. (2008). Rodents. *Current Biology*, *18*(10), R406–R410.

Leirs, H., Stenseth, N., Nichols, J. D., Hines, J. E., Verhagen, R., & Verheyen, W. (1997). Stochastic seasonality and non-linear dependent factors regulate population size in an African rodent. *Nature*, *389*, 176–180.

Leirs, H., Verhagen, R., & Verheyen, W. (1994). The basis of reproductive seasonally in *Mastomys* rats (Rodentia: Muridae) in Tanzania. *Journal of Tropical Ecology*, *10*(1), 55–66.

Lema, R., & Magige, F. J. (2018). The influence of agricultural activities on the diversity of rodents in Kindoroko forest reserve and surrounding areas, north Pare Mountains, Tanzania. *Tanzania Journal of Science*, *44*(1), 97–106.

Makundi, R., Massawe, A., & Mulungu, L. (2005). Rodent population fluctuations in three ecologically heterogeneous locations in northeast, central and Southwest Tanzania. *Belgium Journal of Zoology*, *135*, 159–165.

Makundi, R. H., Massawe, A. W., & Mulungu, L. S. (2007). Breeding seasonality and population dynamics of three rodent species in the Magamba Forest reserve, Western Usambara Mountains, north-East Tanzania. *African Journal of Ecology*, *45*(1), 17–21.

Makundi, R. H., Massawe, A. W., Mulungu, L. S., & Katakweba, A. (2010). Species diversity and population dynamics of rodents in a farm-fallow field mosaic system in Central Tanzania. *African Journal of Ecology*, *48*, 313–320.

Malcolm, J. R., & Ray, J. C. (2000). Influence of timber extraction routes on central African small-mammal communities, forest structure, and tree diversity. *Conservation Biology*, *14*(6), 1623–1638.

Massawe, A. W., Rwamugira, W., Leirs, H., Makundi, R. H., Mulungu, L., Ngowo, V., & Machang'u, R. (2008). Soil type limits population abundance of rodents in crop fields: Case study of the multimammate rat Mastomys natalensis Smith, 1834 in Tanzania. *Integrative Zoology*, *3*(1), 27–30.

Mayamba, A. R., Modest, R., Kimaro, D. N., Moses, I., Kifumba, D., Nakiyemba, A., Leirs, H., Mdangi, M. E., Isabirye, B. E., & Mulungu, L. S. (2020). Factors influencing the distribution and abundance of small rodent pest species in agricultural landscapes in eastern Uganda. *Journal of Vertebrate Biology*, *69*(2), 20002.1–20002.17. https://doi.org/10.25225/jvb.20002

Mayamba, A., Byamungu, R. M., Makundi, R. H., Kimaro, D. N., Isabirye, M., Massawe, A. W., Kifumba, D., Nakiyemba, A., Leirs, H., Mdangi, M. E., Isabirye, B. E., & Mulungu, L. S. (2019). Species composition and community structure of small Pest rodents (Muridae) in cultivated and fallow fields in maize growing areas in eastern Uganda. *Ecology and Evolution*, *9*(13), 7849–7860.

Mbonile, M. J., Misana, S., & Sokoni, C. (2003). Land use change patterns and root causes of land use change on the southern slopes of Mount Kilimanjaro, Tanzania. LUCID Working Paper.

Mbugua, S. M. (2002). Influence of land use patterns on diversity, distribution and abundance of small mammals in Gachoka dvision of Mbeere District, Kenya. LUCID Working Paper.

McCune, B., Grace, J. B., & Urban, D. L. (2002). *Analysis of ecological communities* (Vol. *28*). MjM Software Design.

Meliyo, J. L., Massawe, B. H. J., Msanya, B. M., Kimaro, D. N., Hieronimo, P., Mulungu, L. S., Kihupi, N. I., Deckers, J. A., Gulinck, H., & Leirs, H. (2014). Landform and surface attributes for prediction of rodent burrows in the west Usambara Mountains, Tanzania. *Tanzania Journal of Health Research*, *16*(3), 182–193. https://doi.org/10.4314/thrb.v16i3.5

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 & Agriculture*, *4*(1), 1–13.

Mlyashimbi, E. C. M., Vanden Broecke, B., Mariën, J., Kimaro, D. N., Tarimo, A. J. P., Machang'u, R. S., Isabirye, M., Makundi, R. H., Massawe, A. W., Hieronimo, P., Kifumba, D., Leirs, H., Mdangi, M. E., Belmain, S. R., & Mulungu, L. S. (2019). Influences of soil types on the population dynamics and survival of multimammate rat (*Mastomys natalensis*, Smith 1832) in semi-arid areas in Tanzania. *Crop Protection*, *124*, 104829. https://doi.org/10.1016/j.cropro.2019.05.023

Monadjem, A., Taylor, P. J., Denys, C., & Cotterill, F. P. (2015). *Rodents of sub-Saharan Africa: A biogeographic and taxonomic synthesis*. Walter de Gruyter GmbH & Co KG.

Mulangu, F., & Kraybill, D. (2013). Climate change and the future of mountain farming on mt. Kilimanjaro. In *The future of mountain agriculture* (pp. 73–88). Springer.

Mulungu, L. S. (2017). Control of rodent pests in maize cultivation: The case of Africa. In D. Watson (Ed.), *Achieving sustainable maize cultivation* (Vol. *2*, pp. 318–337). Francis Dodds, Burleigh Dodds Science Publishing. https://doi.org/10.199103/AS.2016.0002.18

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.

Mulungu, L. S., Makundi, R. H., & Massawe, A. W. (2006). Characteristics of rodent damage to major crops in Tanzania and crop loss assessment techniques. In R. H. Makundi (Ed.), *Management of selected crop pests in Tanzania* (pp. 248–267) Tanzania Publishing House Limited. (ISBN 9976 1 0210 0), 476 pp.

Mulungu, L. S., Makundi, R. H., Massawe, A. W., Machang'u, R. S., & Mbije, N. E. (2008). Diversity and distribution of rodent and shrew species associated with variations in altitude on Mount Kilimanjaro, Tanzania. *Journal of Mammalia*, *72*(3), 178–185.

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* (Smith 1834) in irrigated rice field in eastern Tanzania. *International Journal of Pest Management*, *60*(1), 1–8.

Mulungu, L. S., Ngowo, V., Mdangi, M., Katakweba, A. S., Tesha, P., Mrosso, F. P., Mchomvu, M., Sheyo, P. M., & Kilonzo, B. S. (2013). Population dynamics and breeding patterns of multi-mammate mouse, *Mastomys natalensis* (Smith 1834) in irrigated rice field in eastern Tanzania. *Pest Management Science*, *69*(3), 371–377.

Nanzyo, M., Shoji, S., & Dahlgren, R. (1993). Physical characteristics of volcanic ash soils. In *Developments in soil science* (Vol. *21*, pp. 189–207). Elsevier.

National Bureau of Statistics (2012). Population Projections for the Period of 2013 to 2035 at National Level

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., & Oksanen, M. J. (2013). Package 'vegan'. Community Ecology Package, Version *2*(9), 1–295. https://cran.r-project.org

R Core Team. (2013). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org/

Saanya, A., Makundi, R., Mulungu, L., & Massawe, A. (2021). Abundance, relative home range and species-habitat association of small mammal species in Nyerere National Park, Tanzania. *Authorea*. https://doi.org/10.22541/au.163251327.71229630/v1

Shannon, C., & Weaver, W. (1949). *The mathematical theory of communication* (1st ed.). The University of Illinois Press.

Shilereyo, M., Magige, F. J., Ogutu, J. O., & Røskaft, E. (2020). Small mammal community demography and reproductive seasonality under protection, pastoralism and agriculture in the Serengeti ecosystem, Tanzania. *International Journal of Biodiversity and Conservation*, *12*(4), 253–269.

Shore, R. F., & Garbett, S. D. (1991). Notes on the small mammals of the Shira plateau, Mt. Kilimanjaro. *Mammalia*, *55*(4), 601–608.

Smith, C., & Warren, M. (2019). *GLMs in R for ecology*.

Ssuuna, J., Makundi, R. H., Isabirye, M., Sabuni, C. A., Babyesiza, W. S., & Mulungu, L. S. (2020). Rodent species composition, relative abundance, and habitat association in the Mabira central Forest reserve, Uganda. *Journal of Vertebrate Biology*, *69*(2), 20021.1–20021.15. https://doi.org/10.25225/jvb.20021

Stanley, W. T., & Hutterer, R. (2007). Differences in abundance and species richness between shrews and rodents along an elevational gradient in the Udzungwa Mountains, Tanzania. *Acta Theriologica*, *52*(3), 261–275.

Stanley, W. T., & Kihaule, P. M. (2016). Elevational distribution and ecology of small mammals on Tanzania's second highest mountain. *PLoS One*, *11*(9), e016200.

Stanley, W. T., Kihaule, P. M., Howell, K. M., & Hutterer, R. (1998). Small mammals of the eastern Arc Mountains, Tanzania. *Journal of East African Natural History*, *87*(1), 91–1001.

Stanley, W. T., Rogers, M. A., Kihaule, P. M., & Munissi, M. J. (2014). Elevational distribution and ecology of small mammals on Africa's highest mountain. *PLoS One*, *9*(11), 1–13.

Stein, A., & Kreft, H. (2015). Terminology and quantification of environmental heterogeneity in species-richness research. *Biological Reviews*, *90*(3), 815–836.

Stevens, R. D., & Tello, J. S. (2011). Diversity begets diversity: Relative roles of structural and resource heterogeneity in determining rodent community structure. *Journal of Mammalogy*, *92*(2), 387–395.

Stirnemann, I., Mortelliti, A., Gibbons, P., & Lindenmayer, D. B. (2015). Fine-scale habitat heterogeneity influences occupancy in terrestrial mammals in a temperate region of Australia. *PLoS One*, *10*(10), e0140802.

Stohlgren, T. J., Falkner, M. B., & Schell, L. D. (1995). A modified-Whittaker nested vegetation sampling method. *Vegetation*, *113*, 113–121.

Sullivan, T. P., Sullivan, D. S., & Lindgren, P. M. F. (2000). Small mammals and stand structure in young pine, seed-tree, and old-growth forest, Southwest Canada. *Ecological Applications*, *10*(5), 1367–1383.

Thompson, L., Mikhalenko, V., Mosley-Thompson, E., Davis, M., Brecher, H., Lin, P., Hardy, D., & Zagorodnov, V. (2002). Kilimanjaro ice core records: Evidence of Holocene climate change in tropical Africa. *Science*, *298*, 589–593.

Torre Corominas, I. (2004). Distribution, population dynamics and habitat selection of small mammals in Mediterranean environments: The role of climate, vegetation structure, and predation risk (pp. 178). A PhD thesis submitted at the department of animal biology, Universitat de Barcelona, Spain.

Verheyen, W. N., Hulselmans Jan, L. J., Dierckx, T., Mulungu, L., Leirs, H., Corti, M., & Verheyen, E. (2007). The characterization of the Kilimanjaro Lophuromys aquilus true 1892 population and description of five new Lophuromys species (Rodentia, Muridae). *Bulletin L'Insitut Royal des Sciences Naturalles de Belgique, Biologie*, *77*, 23–75.

Welegerima, K., Meheretu, Y., Haileselassie, T. H., Gebre, B., Kidane, D., Massawe, A. W., & Makundi, R. H. (2020). Abundance and microhabitat use of rodent species in crop fields and bushland in Ethiopia. *Journal of Vertebrate Biology*, *69*(2), 1–12.

Yihune, M., & Bekele, A. (2012). Diversity, distribution and abundance of rodent community in the afro-alpine habitats of the Simien Mountains National Park, Ethiopia. *International Journal of Zoological Research*, *8*(4), 137–149.

Zuur, A. F., & Ieno, E. N. (2016). A protocol for conducting and presenting results of regression-type analyses. *Methods in Ecology and Evolution*, *7*(6), 636–645.

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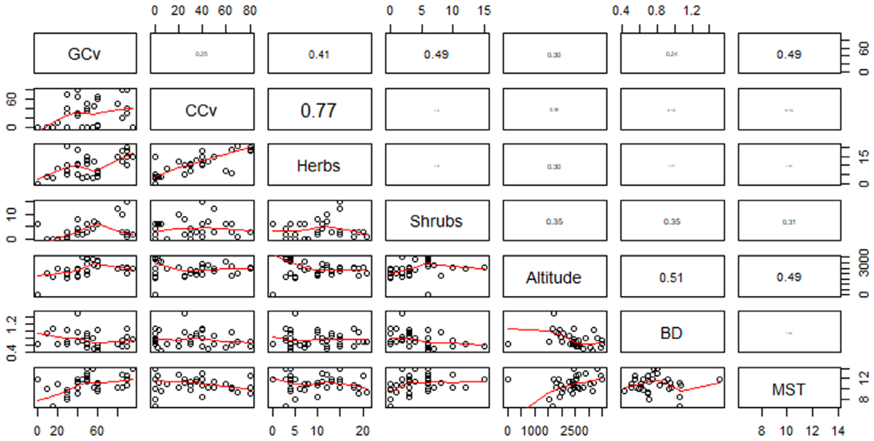
## APPENDIX A

### Pearson's correlation matrix indicating correlation coefficients ($r \geq .5$) for independent variables

Canopy cover CCv was highly correlated with herbs density. Altitude was correlated with BD bulk density and MST soil moisture. Ground cover GCv was correlated with shrubs density and MST soil moisture. Multiple correlated variables such as canopy cover, soil moisture and altitude were not included in the models.



## APPENDIX B

**Model selection results of the 15 models based on the AIC**

| Model | Details | df | AIC | ΔAIC |
|---|---|---|---|---|
| 1 | Richness ~ 1 | 2 | 6029.05 | 769.73 |
| 2 | Richness ~ Soil type | 5 | 6029.51 | 770.19 |
| 3 | Richness ~ Habitat | 8 | 5549.76 | 290.44 |
| 4 | Richness ~ Season | 3 | 6030.88 | 771.57 |
| 5 | Richness ~ GCv | 3 | 5501.59 | 242.28 |
| 6 | Richness ~ Habitat + Season | 9 | 5551.53 | 292.21 |
| 7 | Richness ~ Habitat + GCv | 9 | 5312.27 | 52.95 |
| 8 | Richness ~ GCv + Herbs | 4 | 5489.96 | 230.64 |
| 9 | Richness ~ Habitat + Season + GCv | 10 | 5313.95 | 54.64 |
| **10** | **Richness ~ Habitat + Season + GCv + Soil type** | **13** | **5259.31** | **0.00** |
| 11 | Richness ~ Habitat +Season + GCv + Soil type + BD | 14 | 5260.42 | 1.11 |
| 12 | Richness ~ Habitat + Season + GCv + Soil type + BD + Herbs | 14 | 5260.73 | 1.42 |
| 13 | Richness ~ Habitat + Season + Habitat*Season + GCv + Soil type | 19 | 5263.10 | 3.79 |
| 14 | Richness ~ Habitat + Season + Habitat*Season + GCv + Soil type + BD + Herbs | 20 | 5264.22 | 4.91 |
| 15 | Richness~ Habitat + Season + Habitat*Season + GCv | 16 | 5318.19 | 58.87 |

Abbreviations: GCv, ground cover; BD, bulk density; Herbs, herb density.

Bold indicates: significant at 0***.

## APPENDIX C

**Model selection results of the 15 models based on the AIC**

| Model | Details | df | AIC | Δ AIC |
|---|---|---|---|---|
| 1 | Abundance ~ 1 | 2 | 9201.28 | 538.04 |
| 2 | Abundance ~ Soil type | 5 | 9201.83 | 538.58 |
| 3 | Abundance ~ Habitat | 8 | 8804.52 | 141.28 |
| 4 | Abundance ~ Season | 3 | 9201.79 | 538.55 |
| 5 | Abundance ~ GCv | 3 | 8869.89 | 206.65 |
| 6 | Abundance ~ Habitat + Season | 9 | 8800.75 | 137.51 |
| 7 | Abundance ~ Habitat + GCv | 9 | 8716.94 | 53.69 |
| 8 | Abundance ~ GCv + Herbs | 4 | 8865.80 | 202.56 |
| 9 | Abundance~ Habitat + Season + GCv | 10 | 8714.52 | 51.27 |
| 10 | Abundance ~ Habitat + Season + GCv + Soil type | 13 | 8664.87 | 1.63 |
| **11** | **Abundance ~ Habitat + Season + GCv + Soil type + BD** | **14** | **8663.24** | **0.00** |
| 12 | Abundance ~ Habitat + Season + GCv + Soil type + BD + Herbs | 14 | 8667.82 | 4.58 |
| 13 | Abundance ~ Habitat + Season + Habitat*Season + GCv + Soil type | 19 | 8669.38 | 6.14 |
| 14 | Abundance ~ Habitat + Season + Habitat*Season + GCv + Soil type + BD + Herbs | 20 | 8669.05 | 5.81 |
| 15 | Abundance ~ Habitat + Season + Habitat*Season + GCv | 16 | 8717.81 | 54.57 |

*Note*: Model with the lowest AIC (shown in bold) is the one that better describes and fits our data. For every model; the number of parameters (df), AIC and delta ΔAIC are given. ΔAIC is the difference in AIC between the current model and the best model.

Abbreviations: GCv, ground cover; BD, bulk density; Herbs, herb density.

Bold indicates: significant at 0***.

# 3.0 CHAPTER THREE

## Spatial-Temporal Variations in Dietary Consumption of two Dominant Rodent Species (*Rhabdomys Dilectus* and *Lophuromys Acquilus*) on Mount Kilimanjaro, Tanzania

[1] The African Centre of Excellence for Innovative Rodent
Pest Management and Biosensor Technology

Development Project, Sokoine University of Agriculture,
Morogoro P.O. Box 3110, Tanzania

[2] Department of Wildlife Management, Sokoine University of
Agriculture, Morogoro P.O. Box 3073, Tanzania

[3] Department of Biology, University of Dodoma, Dodoma
P.O. Box 338, Tanzania

[4] Institute of Pest Management, Sokoine University of
Agriculture, Morogoro P.O. Box 3110, Tanzania

[5] Department of Forest Technology and Wood Sciences,
Sokoine University of Agriculture,

Morogoro P.O. Box 3073, Tanzania

*Corresponding Author: meydancan@gmail.com

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*Article*

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

**Suzana M. Thomas [1,2,3,*], Geofrey E. Soka [2], Loth S. Mulungu [4,†] and Fortunatus B. S. Makonda [5]**

[1] The African Centre of Excellence for Innovative Rodent Pest Management and Biosensor Technology Development Project, Sokoine University of Agriculture, Morogoro P.O. Box 3110, Tanzania
[2] Department of Wildlife Management, Sokoine University of Agriculture, Morogoro P.O. Box 3073, Tanzania
[3] Department of Biology, University of Dodoma, Dodoma P.O. Box 338, Tanzania
[4] Institute of Pest Management, Sokoine University of Agriculture, Morogoro P.O. Box 3110, Tanzania
[5] Department of Forest Technology and Wood Sciences, Sokoine University of Agriculture, Morogoro P.O. Box 3073, Tanzania
* Correspondence: meydancan@gmail.com; Tel.: +255-763817556
† Deceased.

**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].

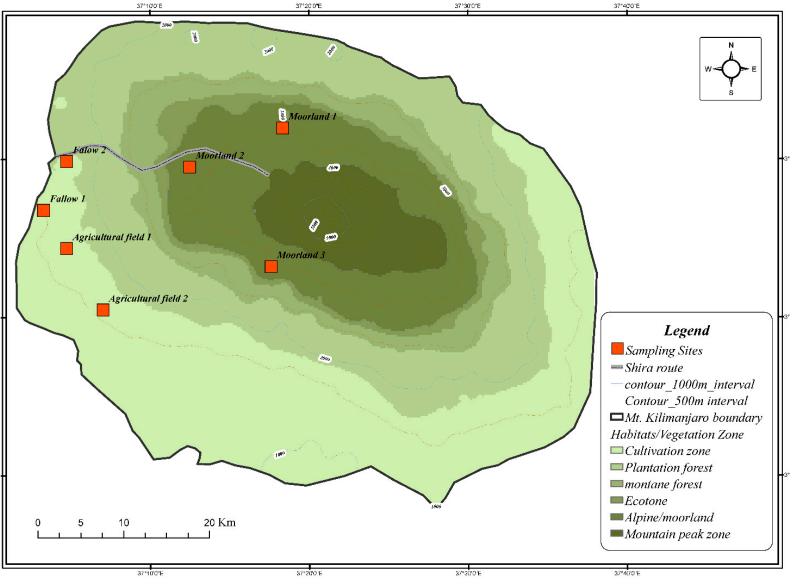


**Figure 1.** A map of Mount Kilimanjaro showing study sites in the selected three habitats along the Shira route.

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:

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

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:

$$\mathrm{B_s} = (\mathrm{B} - 1/\mathrm{n} - 1).$$

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]

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

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, $p = 0.871$).

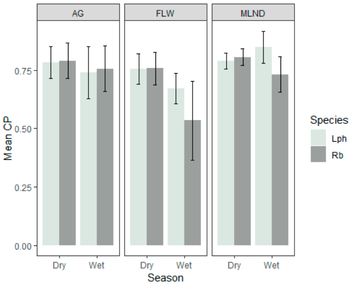
Among the food categories, vegetative materials and seeds/starch predominated in the diets of both species. The percentage occurrence of vegetative materials did not significantly differ between the two species ($F_{1,172} = 0.025$, $p = 0.87$). However, *R. dilectus* had a relatively higher proportion 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%).

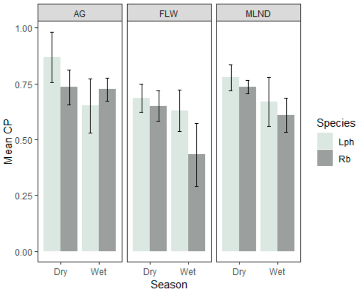
The Percentage occurrence of invertebrates was significantly different between species ($F_{1,171} = 32.38$, $p = 0.000$). In addition, it significantly differed across seasons ($F_{1,171} = 5.79$, $p = 0.02$) and the interaction between species and seasons ($F_{1,171} = 10.04$, $p = 0.001$). Invertebrates 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).

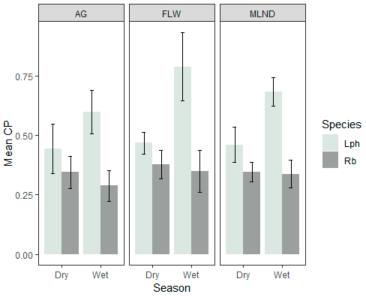


(**a**)

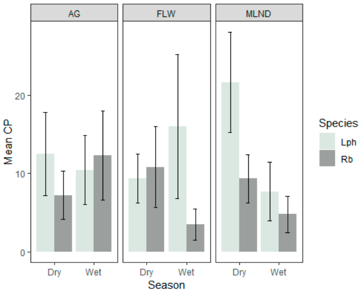


(**b**)

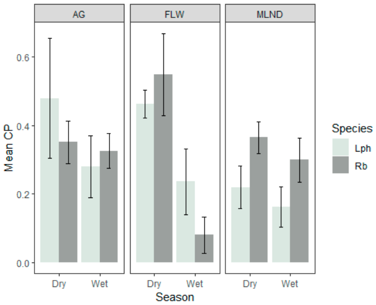
**Figure 2.** *Cont.*



(**c**)



(**d**)



(**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).

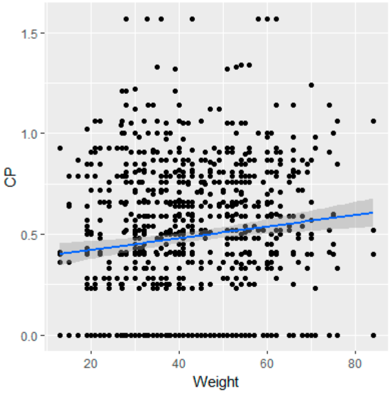
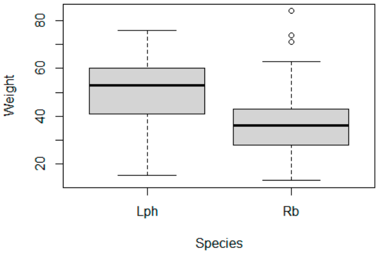
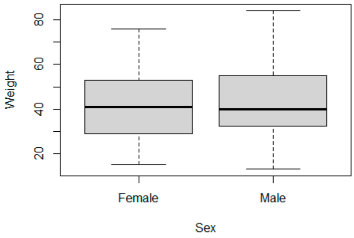


**Figure 3.** Relationship between the overall percentage occurrence of food items (CP) and weight of speciesPercentage occurrence was moderately positively correlated with weight of rodents as indicated by the blue line.

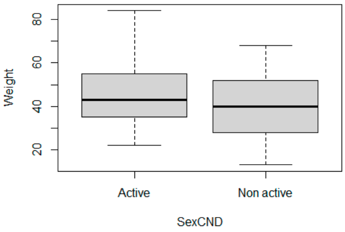


(**a**)

**Figure 4.** *Cont.*



(**b**)



(**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 Hanney [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.

**Author Contributions:** Conceptualization: S.M.T., L.S.M., G.E.S. and F.B.S.M., designed the ideas; Methodology, S.M.T., L.S.M., G.E.S. and F.B.S.M.; software, S.M.T.; Data curation S.M.T. (conducted both field and laboratory work). Formal analysis; S.M.T. and F.B.S.M. All authors contributed to

writing—review and editing the manuscript. Funding acquisition; S.M.T.; Supervision; L.S.M. and G.E.S. All authors have read and agreed to the published version of the manuscript.

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**Institutional Review Board Statement:** The research proposal was approved by Sokoine University of Agriculture (SUA) (Ref no: SUA/DPRTC/PFC/D/2019/0002/1) and provided with ethical clearance for use of animals. Registered, approved, and provided with a research permit (2020-163-NA-2020-127) by the Tanzania Commission for Science and Technology COSTECH in collaboration with Tanzania Wildlife Research Institute (TAWIRI). An entry and a research permit inside Mount Kilimanjaro National Park was provided by Tanzania National Parks TANAPA (BE.161/376/01). Moreover, this research was conducted following guidelines by the American Society of Mammologists (ASM) for appropriate methods of doing research on wild animals.

**Informed Consent Statement:** Not applicable.

**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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## References

1. Datiko, D.; Bekele, A.; Belay, G. Feeding ecology of pest rodents from Arbaminch forest and farmlands, Ethiopia. *SINET Ethiop. J. Sci.* **2008**, *30*, 127–134. [CrossRef]
2. Pianka, E.R. Niche Overlap and Diffuse Competition. *Proc. Natl. Acad. Sci. USA* **1974**, *71*, 2141–2145. [CrossRef] [PubMed]
3. Sassi, P.L.; Borghi, C.E.; Dacar, M.A.; Bozinovic, F. Geographic and seasonal variability in feeding behaviour of a small herbivorous rodent. *Acta Thériol.* **2010**, *56*, 35–43. [CrossRef]
4. Finke, D.L.; Snyder, W.E. Niche Partitioning Increases Resource Exploitation by Diverse Communities. *Science* **2008**, *321*, 1488–1490. [CrossRef]
5. Curtis, B.; Perrin, M. Food preferences of the vlei rat (*Otomys Irroratus*) and the four-striped mouse (*Rhabdomys pumilio*). *S. Afr. J. Zool.* **1979**, *14*, 224–229. [CrossRef]
6. Luo, J.; Fox, B.J. Seasonal and successional dietary shifts of two sympatric rodents in coastal heathland: A possible mechanism for coexistence. *Austral Ecol.* **1996**, *21*, 121–132. [CrossRef]
7. Mulungu, L.S.; Massawe, A.W.; Kennis, J.; Crauwels, D.; Eiseb, S.; Mahlaba, T.A.; Monadjem, A.; Makundi, R.H.; Katakweba, A.A.; Leirs, H.; et al. Differences in diet between two rodent species, Mastomys natalensisandGerbilliscus vicinus, in fallow land habitats in central Tanzania. *Afr. Zool.* **2011**, *46*, 387–392. [CrossRef]
8. Soininen, E.M.; Ravolainen, V.T.; Bråthen, K.A.; Yoccoz, N.G.; Gielly, L.; Ims, R.A. Arctic Small Rodents Have Diverse Diets and Flexible Food Selection. *PLoS ONE* **2013**, *8*, e68128. [CrossRef]
9. Clausnitzer, V.; Churchfield, S.; Hutterer, R. Habitat occurrence and feeding ecology of Crocidura montis and Lophuromys flavopunctatus on Mt. Elgon, Uganda. *Afr. J. Ecol.* **2003**, *41*, 1–8. [CrossRef]
10. 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.; et al. Dietary differences of the multimammate mouse, Mastomys natalensis (Smith, 1834), across different habitats and seasons in Tanzania and Swaziland. *Wildl. Res.* **2011**, *38*, 640–646. [CrossRef]
11. Odhiambo, R.O.; Makundi, R.H.; Leirs, H.; Verhagen, R. Dietary selection in Mastomys natalensis (Rodentia: Muridae) in the maize agro-ecosystems of central and southwestern Tanzania. *Mammalia* **2008**, *72*. [CrossRef]
12. Mulungu, L.; Mlyashimbi, E.; Ngowo, V.; Mdangi, M.; Katakweba, A.; Tesha, P.; Mrosso, F.; Mchomvu, M.; Kilonzo, B.; Belmain, S. Food preferences of the multi-mammate mouse, Mastomys natalensis, in irrigated rice habitats in Tanzania. *Int. J. Pest Manag.* **2014**, *60*, 1–8. [CrossRef]

13. Bomford, M. Food and reproduction of wild house mice. 2. A field experiment to examine the effect of food availability and food quality on breeding in spring. *Wildl. Res.* **1987**, *14*, 197–206. [CrossRef]
14. Bomford, M. Food and reproduction of wild house mice. 1. Diet and breeding seasons in various habitats on irrigated cereal farms in New South Wales. *Wildl. Res.* **1987**, *14*, 183–196. [CrossRef]
15. Tann, C.; Singleton, G.; Coman, B. Diet of the House Mouse, Mus domesticus, in the Mallee Wheatlands of North-Western Victoria. *Wildl. Res.* **1991**, *18*, 1–12. [CrossRef]
16. Htwe, N.M.; Singleton, G.R. Is quantity or quality of food influencing the reproduction of rice-field rats in the Philippines? *Wildl. Res.* **2014**, *41*, 56–63. [CrossRef]
17. Brettschneider, H.; Julius, R.S.; Bastos, A.D.; Chimimba, C.T. Dynamics of Rodent-Borne Zoonotic Diseases and Their Reservoir Hosts: Invasive Rattus in South Africa. *Proc. Vertebr. Pest Conf.* **2012**, *25*. [CrossRef]
18. Meerburg, B.G.; Singleton, G.; Kijlstra, A. Rodent-borne diseases and their risks for public health. *Crit. Rev. Microbiol.* **2009**, *35*, 221–270. [CrossRef]
19. Davies, M.; Béné, C.; Arnall, A.; Tanner, T.; Newsham, A.; Coirolo, C. Promoting resilient livelihoods through adaptive social protection: Lessons from 124 programmes in South Asia. *Dev. Policy Rev.* **2013**, *31*, 27–58. [CrossRef]
20. Makundi, R.H.; Massawe, A.W. Ecologically based rodent management in Africa: Potential and challenges. *Wildl. Res.* **2011**, *38*, 588–595. [CrossRef]
21. Ralaizafisoloarivony, N.A.; Kimaro, D.N.; Kihupi, N.I.; Mulungu, L.S.; Leirs, H.; Msanya, B.M.; Deckers, J.A.; Gulinck, H. Vegetation habitats and small mammals in a plague endemic area in Western Usambara Mountains, Tanzania. *Tanzan. J. Health Res.* **2014**, *16*, 194–205. [CrossRef] [PubMed]
22. Oguge, N.O. Diet, seasonal abundance and microhabitats of Praomys (Mastomys) natalensis (Rodentia: Muridae) and other small rodents in a Kenyan sub-humid grassland community. *Afr. J. Ecol.* **1995**, *33*, 211–223. [CrossRef]
23. Leirs, H.; Verhagen, R.; Verheyen, W.; Mwanjabe, P.; Mbise, T. Forecasting Rodent Outbreaks in Africa: An Ecological Basis for Mastomys Control in Tanzania. *J. Appl. Ecol.* **1996**, *33*, 937. [CrossRef]
24. Mwanjabe, P.S.; Sirima, F.B.; Lusingu, J. Crop losses due to outbreaks of Mastomys natalensis (Smith, 1834) Muridae, Rodentia, in the Lindi Region of Tanzania. *Int. Biodeterior. Biodegrad.* **2002**, *49*, 133–137. [CrossRef]
25. Shiels, A.B.; Flores, C.A.; Khamsing, A.; Krushelnycky, P.D.; Mosher, S.M.; Drake, D.R. Dietary niche differentiation among three species of invasive rodents (Rattus rattus, R. exulans, Mus musculus). *Biol. Invasions* **2012**, *15*, 1037–1048. [CrossRef]
26. Corti, M.; Castiglia, R.; Verheyen, W. A note on three new cytotypes of *Lophuromys flavopunctatus* sensu lato (Rodentia, Muridae) from Tanzania. *Mammalia* **2004**, *68*, 69–74. [CrossRef]
27. Mulungu, L.S.; Makundi, R.H.; Massawe, A.W.; Machang'U, R.S.; Mbije, N.E. Diversity and distribution of rodent and shrew species associated with variations in altitude on Mount Kilimanjaro, Tanzania. *Mammalia* **2008**, *72*. [CrossRef]
28. Stanley, W.T.; Rogers, M.A.; Kihaule, P.M.; Munissi, M.J. Elevational Distribution and Ecology of Small Mammals on Africa's Highest Mountain. *PLoS ONE* **2014**, *9*, e109904. [CrossRef]
29. Gebrezgiher, G.B.; Makundi, R.H.; Meheretu, Y.; Mulungu, L.S.; Katakweba, A.A.S. A Decade-Long Change in the Elevational Distribution of Non-Volant Small Mammals on Mount Meru, Tanzania. *Diversity* **2022**, *14*, 454. [CrossRef]
30. Hanney, P. The Harsh-Furred Rat in Nyasaland. *J. Mammal.* **1964**, *45*, 345–358. [CrossRef]
31. Bekele, A.; Corti, M. Multivariate morphometries of the Ethiopian populations of harsh-furred rat (Lophuromys: Mammalia, Rodentia). *J. Zool.* **1994**, *232*, 675–689. [CrossRef]
32. Ademola, O.J.; Massawe, A.W.; Mulungu, L.S.; Makundi, R.H. Dietary composition of rodents across different habitats in the Ukaguru Mountains, Tanzania. *Afr. J. Ecol.* **2022**. [CrossRef]
33. Krug, C.B. Reproduction of Rhabdomys pumilio in the Namib Desert: Pattern and possible control. *Basic Appl. Dryland Res.* **2007**, *1*, 67–85. [CrossRef]
34. Perrin, M.; Kotler, B. A test of five mechanisms of species coexistence between rodents in a southern African savanna. *Afr. Zool.* **2005**, *40*, 55–61. [CrossRef]
35. Henke, Z.; Sahd, L.; Matthee, S.; Kotzé, S.H. Morphometric analysis of the gastrointestinal tract of four African muroid rodent species (*Rhabdomys dilectus, Rhabdomys pumilio, Aethomys chrysophilus,* and *Lemniscomys rosalia*). *J. Morphol.* **2018**, *279*, 1282–1289. [CrossRef]
36. Mulungu, L.S.; Ngowo, V.; Mdangi, M.; Katakweba, A.S.; Tesha, P.; Mrosso, F.P.; Mchomvu, M.; Sheyo, P.M.; Kilonzo, B.S. Population dynamics and breeding patterns of multimammate mouse, *Mastomys natalensis* (Smith 1834), in irrigated rice fields in Eastern Tanzania. *Pest Manag. Sci.* **2012**, *69*, 371–377. [CrossRef]
37. Field, A.C. Seasonal changes in reproduction, diet and body composition of two equatorial rodents. *Afr. J. Ecol.* **1975**, *13*, 221–235. [CrossRef]
38. Leirs, H.; Verhagen, R.; Verheyen, W. The basis of reproductive seasonally in *Mastomys* rats (Rodentia: Muridae) in Tanzania. *J. Trop. Ecol.* **1994**, *10*, 55–66. [CrossRef]
39. Thomas, S.; Mulungu, L.; Soka, G. Influence of Vegetation Structure, Seasonality, and Soil Physical Properties on Rodent Species Diversity and Community Assemblages on West Mount Kilimanjaro, Tanzania. *Authorea Prepr.* **2021**. [CrossRef]
40. Monadjem, A. Stomach contents of 19 species of small mammals from Swaziland. *S. Afr. J. Zool.* **1997**, *32*, 23–26. [CrossRef]
41. Mulangu, F.; Kraybill, D. Climate Change and the Future of Mountain Farming on Mt. Kilimanjaro. In *The Future of Mountain Agriculture*; Springer: Berlin/Heidelberg, Germany, 2012; pp. 73–88. [CrossRef]

42. Hemp, A. Continuum or zonation? Altitudinal gradients in the forest vegetation of Mt. Kilimanjaro. *Plant Ecol.* **2005**, *184*, 27–42. [CrossRef]
43. Monica, S.; Flora, J.M.; Joseph, O.O.; Eivin, R. Small mammal community demography and reproductive seasonality under protection, pastoralism and agriculture in the Serengeti Ecosystem, Tanzania. *Int. J. Biodivers. Conserv.* **2020**, *12*, 253–269. [CrossRef]
44. Welegerima, K.; Meheretu, Y.; Haileselassie, T.H.; Gebre, B.; Kidane, D.; Massawe, A.W.; Mbije, N.E.; Makundi, R.H. Abundance and microhabitat use of rodent species in crop fields and bushland in Ethiopia. *J. Vertebr. Biol.* **2020**, *69*, 1–12. [CrossRef]
45. Shorrocks, B. Mammals of Africa Volume 1. Introductory Chapters and Afrotheria Jonathan Kingdon, David Happold, Michael Hoffman Thomas Butynski, Meredith Happold and Jan Kalina. Bloomsbury Publishing, London (2013) 351 pp. ISBN 978-1-4081-2251-8. *Afr. J. Ecol.* **2013**, *52*, 254–255. [CrossRef]
46. Sikes, R.S. The Animal Care and Use Committee of the American Society of Mammalogists 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *J. Mammal.* **2016**, *97*, 663–688. [CrossRef]
47. 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.; et al. Relationships between seasonal changes in diet of Multimammate rat (*Mastomys natalensis*) and its breeding patterns in semi-arid areas in Tanzania. *Cogent Food Agric.* **2018**, *4*, 1507509. [CrossRef]
48. Smith, V.; Avenant, N.; Chown, S. The diet and impact of house mice on a sub-Antarctic island. *Polar Biol.* **2002**, *25*, 703–715. [CrossRef]
49. Cooper, R.; Skinner, J. Importance of Termites in the diet of the Aardwolf Proteles Cristatus in South Africa. *S. Afr. J. Zool.* **1979**, *14*, 5–8. [CrossRef]
50. Levins, R. *Evolution in Changing Environment*; Princeton University Press: Princeton, NJ, USA, 1968.
51. MacArthur, R.H.; Pianka, E.R. On Optimal Use of a Patchy Environment. *Am. Nat.* **1966**, *100*, 603–609. [CrossRef]
52. Winemiller, K.; Pianka, E.R. Organization in Natural Assemblages of Desert Lizards and Tropical Fishes. *Ecol. Monogr.* **1990**, *60*, 27–55. [CrossRef]
53. R Core Team. *R. A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2013. Available online: https://cran.r-project.org/bin/windows/base/old/3.6.2 (accessed on 19 March 2022).
54. Schradin, C.; Pillay, N. Female striped mice (Rhabdomys pumilio) change their home ranges in response to seasonal variation in food availability. *Behav. Ecol.* **2006**, *17*, 452–458. [CrossRef]
55. Clausnitzer, V.; Denys, C.; Granjon, L.; Poulet, A. Rodents of the afro-alpine zone of Mt. Elgon. *Afr. Small Mamm.* **2001**, 427–443.
56. Clausnitzer, V.; Kityo, R. Altitudinal distribution of rodents (Muridae and Gliridae) on Mt Elgon, Uganda. *Trop. Zool.* **2001**, *14*, 95–118. [CrossRef]
57. Krug, C.B. Survival in the Namib: Adaptations of the striped mouse to an arid environment. *Trans. R. Soc. S. Afr.* **2004**, *59*, 93–98. [CrossRef]
58. Taylor, K.D.; Green, M.G. The influence of rainfall on diet and reproduction in four African rodent species. *J. Zool.* **1976**, *180*, 367–389. [CrossRef] [PubMed]
59. Makundi, R.H.; Massawe, A.W.; Mulungu, L.S. Breeding seasonality and population dynamics of three rodent species in the Magamba Forest Reserve, Western Usambara Mountains, north-east Tanzania. *Afr. J. Ecol.* **2007**, *45*, 17–21. [CrossRef]
60. Wells, K.; Corlett, R.T.; Lakim, M.B.; Kalko, E.K.V.; Pfeiffer, M. Seed consumption by small mammals from Borneo. *J. Trop. Ecol.* **2009**, *25*, 555–558. [CrossRef]
61. Massawe, A.W.; Mrosso, F.P.; Makundi, R.H.; Mulungu, L. Breeding patterns of *Arvicanthis neumanni* in central Tanzania. *Afr. J. Ecol.* **2008**, *46*, 320–324. [CrossRef]
62. Massawe, A.W.; Makundi, R.H.; Mulungu, L.S.; Katakweba, A.; Shayo, T.N. Breeding Dynamics of Rodent Species Inhabiting Farm—Fallow Mosaic Fields in Central Tanzania†. *Afr. Zool.* **2012**, *47*, 128–137. [CrossRef]
63. Kitessa, H.; Tsegaye, G.; Hundera, K.; Gadisa, T. The reproductive and feeding ecology of rodents in Sekoru district, Southwest Ethiopia. *J. Ecol. Nat. Environ.* **2015**, *7*, 188–195. [CrossRef]
64. Cole, L.R. Foods and foraging places of rats (Rodentia: Muridae) in the lowland evergreen forest of Ghana. *J. Zool.* **1975**, *175*, 453–471. [CrossRef]
65. Brown, J.S. Desert Rodent Community Structure: A Test of Four Mechanisms of Coexistence. *Ecol. Monogr.* **1989**, *59*, 1–20. [CrossRef]
66. Lema, R.; Magige, F.J. The influence of agricultural activities on the diversity of rodents in Kindoroko forest reserve and surrounding areas, North Pare Mountains, Tanzania. *Tanzan. J. Sci.* **2018**, *44*, 97–106.
67. Petraitis, P.S. Likelihood Measures of Niche Breadth and Overlap. *Ecology* **1979**, *60*, 703–710. [CrossRef]
68. May, R.M.; Mac Arthur, R.H. Niche Overlap as a Function of Environmental Variability. *Proc. Natl. Acad. Sci. USA* **1972**, *69*, 1109–1113. [CrossRef]
69. Christian, D.P. Diurnal Activity of the Four-Striped Mouse, Rhabdomys Pumilio. *Zool. Afr.* **1977**, *12*, 238–239. [CrossRef]

# 4.0 CHAPTER FOUR

## Breeding Activity and Spatial-Temporal Population Fluctuations of the two Dominant Rodent Species (*Rhabdomys dilectus* and *Lophuromys aquilus*) on Mount Kimimanjaro

Suzana M. Thomas[1, 2, 3,*], Geofrey E. Soka[2],
Loth S. Mulungu[4, †] and Rhodes H. Makundi[1,4]

[1] The African Centre of Excellence for Innovative Rodent Pest Management and Biosensor Technology Development, Sokoine University of Agriculture, Morogoro, Tanzania.

[2]Department of Wildlife Management, Sokoine University of Agriculture,

Morogoro, Tanzania.

[3]Department of Biology, University of Dodoma, Dodoma, Tanzania.

[4]Institute of Pest Management, Sokoine University of Agriculture, Morogoro, Tanzania.

*Corresponding Author: meydancan@gmail.com

† Deceased

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## Abstract

The African four-striped grass rat *Rhabdomys* and the African brush-furred rat *Lophuromys* are among the complex rodent taxa in Africa. Distribution range of the two genera is well known, however, there is limited information on population ecology. Moreover, two species from the afore mentioned genera; *Rhabdomys dilectus* and *Lophuromys aquilus* are among the most dominant rodents in west Mt Kilimanjaro, however, their population ecology has not been studied. This study was aimed to investigate on sex ratio, breeding activity and population fluctuations of the two species across habitats and seasons. Data collection was conducted for two years from April 2020 to March, 2022. Capture-mark-recapture technique using Sherman's live traps was employed for rodent trapping. Two grids at a distance of 500 m apart were established in each of the moorland and fallow habitat. The trapping was conducted for three nights consecutively after every month. Sex ratio of *R. dilectus* and *L. aquilus* did not significantly differ between habitats and months. Sex ratio of both species fluctuated more from the expected margins in moorland habitat. Number of sexually active females of both species differed significantly between habitats but no temporal or seasonal differences were observed. Sexually active females occurred almost throughout the year in fallow and intermittently in moorland. Interestingly there were no sexually active females of both species around October in the moorland, this was probably due to less and delayed rainfall which is important for rodent breeding. Results indicate that, breeding activity of the two species was continuous or year-round in fallow and seasonal in moorland probably due to year-round availability of food resources in fallow. Moreover, population size (in MNKA) of both species significantly differed between habitats. It was significantly higher in fallow than in moorland. Also, comparison between seasons revealed higher population size of both species in dry season than in wet season (significant for *R. dilectus*). Conclusively, the findings indicate that, seasonality and habitat type have major influence on breeding activity and population fluctuations of the two dominant rodent species. Most certainly the effects were attributed to variations in food resources and cover. Also, distinct climate variability on Mt Kilimanjaro could have contributed to the significant differences in breeding activity and population fluctuations of the two species between habitats. Further long-term research should be undertaken for understanding the effects of climate change on rodent population ecology.

**Key words:** sex ratio, breeding activity, season, habitat, population fluctuations.

## 4.1 Introduction

In tropical Africa rodents have rapid population growth associated with fluctuations over space and time (Leis *et al*., 2007; Massawe *et al*.,2012; 2011). The rapid population fluctuations are a result of short maturation period and high reproductive potential which causes rapid increase in population size (Kay and Hoekstra, 2008). Many rodents are capable of rapid population increase during wet season due to favorable conditions for growth and survival of juveniles (Wolff and Sherman, 2007; Makundi *et al*., 2007; 2010).

Moreover, reproductive seasonality in small mammals is associated with variations in food availability (Mulungu *et al*., 2011a) and demographic parameters like sex ratio and age structure (Oli and Dobson, 1999; Shereliyo *et al*., 2020). Sex ratio is balanced in some populations but not (biased) in others (Bantihun and Bekele, 2015; Mulungu *et al*., 2013). A biased sex ratio causes male-male competition for mates and breeding stress for females which have a direct impact on population size (Olenev and Grigorkina, 2011; Schärer *et al*., 2012; Fritzsche *et al*., 2016). Furthermore, breeding seasonality is caused by rainfall distribution which determine the availability of resources over space and time (Leirs *et al*., 1994; 1997; Madsen and Shine, 1999; Odhiambo *et al*., 2008b). Rainfall influences reproductive phenology and trigger the onset of breeding in small mammals including rodents through provision of food and cover (Odhiambo *et al*., 2008b). Sprouting of fresh vegetation during wet season ensures abundant and high-quality food for rodents (Bai *et al*., 2015; Lima *et al*., 2003; Makundi *et al*., 2007). Breeding of some rodents in Tropical Africa occurs throughout the year reaching the peak during wet season, but numbers decline towards the end of dry season when food is limited (Afework and Leirs, 1997) and of low quality (Francisco *et al*., 1995; Wube, 2005). Recruitment of juveniles occur in the population throughout the year (Bantihun and Bekele, 2015) but peaks at the end of rain season (Gebresilassie *et al*., 2006). Therefore, breeding seasonality in most rodents is due to seasonal variation in resources, which could be an adaptive mechanism to maximize reproductive fitness.

*Lophuromys* and *Rhabdomys* are among the complex rodent taxa in Africa. The African four-striped mouse, *Rhabdomys* is distributed across varied geographical regions (Meynard and Pillay, 2012; Ganem *et al*., 2020). Recently genus *Rhabdomys* has been discovered to show distinct morphological polymorphism with fragmented or disjoint populations. There are two commonly known groups of *Rhabdomys* with markedly different geographical distributions; the mesic and semi-arid groups which includes *Rhabdomys pumilio* and *Rhabdomys dilectus* respectively (Rambau *et al*., 2003; du Toit *et al*., 2012). The two groups prefer different habitats and microhabitats (Dufour *et al*., 2015) with distinct behavioral adaptations (Schradin and Pillay, 2006). Also, the African hash-furred rat *Lophuromys* is a cryptic genus with radiation of species that are widely distributed across West, Central and East Africa (Bekele and Corti, 1994; Verheyen *et al*., 2002; Corti *et al*., 2004; Verheyen *et al*., 2007). *Lophuromys* is distributed cross a wide range of habitats and altitudes and is mainly associated with vegetation cover. Distribution range of the two genera is well known, however, information on population ecology is limited. Fewer studies in Africa have investigated the influence of rainfall on demography of rodent species from genus *Rhabdomys* (Jackson and Bernad, 2006) and *Lophuromys* (Makundi *et al*., 2005; Makundi *et al*., 2007). In addition, previous studies on Mt Kilimanjaro revealed that, two species from the afore mentioned genera; *Lophuromys aquilus* and *Rhabdomys dilectus* are sympatric (Mulungu *et al*., 2008; Stanley *et al*., 2014; Thomas *et al*., 2022a). This observation made it more interesting to investigate further on their ecological interactions. Generally, the species are well documented in interms of distribution and abundance on Mt Kilimanjaro and elsewhere (Stanley *et al*., 2014; Gebrezgiher *et al*., 2022; Thomas *et al*., 2022a). However, population ecology of the species has not been documented and there is scanty information on demographic characteristics like sex ratio, breeding activity and population fluctuations (Makundi *et al*., 2007; Jackson and Bernad, 2006; Krug, 2007). Investigating demographic characteristics is vital for management and control of populations. Therefore, the current study analyzes spatial-temporal variations in demographic characteristics of the the two dominant rodents on Mt Kilimanjaro. Specifically, it assessed the variations in sex ratio, number of actively breeding individuals and population size (in MNKA) across habitats and seasons/ months.

## 4.2 Materials and Methods

### 4.2.1 Study site description

The study area is located on west Mt Kilimanjaro, in Siha district of Kilimanjaro region located in northeast Tanzania between 3°07'S and 37°35'E. Trapping was conducted along an altitudinal gradient ranging from 1500 up to 3500 a.m.s.l (in Shira plateau). The study area has two distinct seasons: dry and wet season. Moreover, there are two wet seasons: from October to December and from March to May. Similarly, there are two dry seasons from January to February and June to September (Mulangu and Kraybill, 2013). Mean annual rainfall is 700 mm in lower altitudes and 300 mm in higher altitudes which decrease after wards. Daily mean temperatures range from 21 to 29 °C in lowlands and -6 to -29 °C in highlands (Mulangu and Kraybill, 2013). This study was conducted in two habitats: fallow and moorland as previously described in Thomas *et al*. (2022b). Fallow ranges from 1,500 to 2,400 m.a.s.l. It was defined as uncultivated land that is left out either for crop rotation or other land uses. Moorland was located in the subalpine zone ranging from 3,200 to 4,500 m.a.s.l. The habitat is commonly dominated by shrubs/ Erica bush and herbs (Hemp, 2006). Moorland was characterized by the coldest weather in night with temperatures ranging from -1 to 10 °C, while day temperatures range from 10 to 21 °C (Figure 4.1).

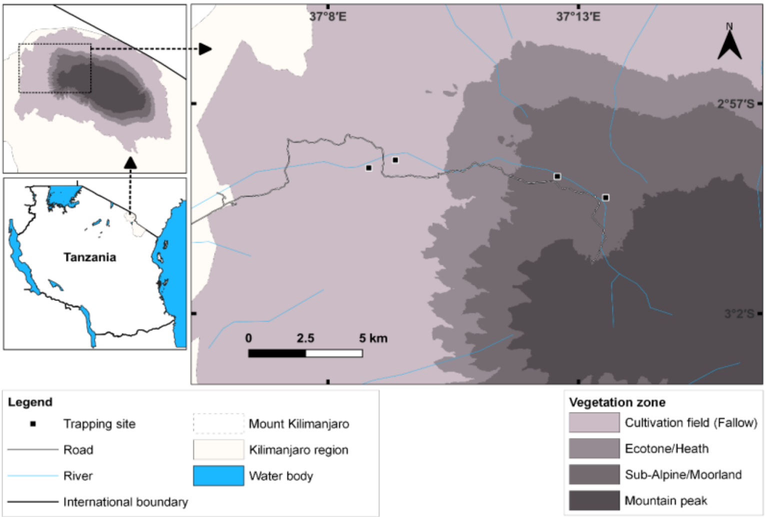


**Figure 4.1: Map of Mount Kilimanjaro, showing four grids in selected habitats (moorland and fallow).**

### 4.2.2 Rodent trapping and handling

Capture-Mark-Recapture (CMR) method was used for rodent sampling. One replicated grid 70 × 70 m was set in moorland and fallow habitat, making a total of four independent grids. In each habitat the grids were set at 500 m away to avoid mixing of the populations. Medium sized Sherman live traps (7.5 × 9 × 23 cm) were placed in 7 trapping lines each with 7 traps spaced 10 m between trapping stations resulting into a total of 49 traps per grid. Red ribbons were attached to vegetation above the traps in order to mark the trapping stations. Traps were baited with a mixture of peanut butter and maize flour and hidden under dense vegetation or covered with grasses in areas with poor vegetation. This was important for insulation and protection of trapped animals from harsh weather conditions. Trapping was conducted for 3 consecutive nights in every month (known as trapping session) from April, 2020 to March, 2022. Traps were inspected every morning from 08:00 to 10:00 a.m. Trapped animals were marked by toe-clipping which was found not to have negative impacts on the behavior and survival of rodents (Gurnell and Flowerdew, 2006; Borremans *et al*., 2015). The date, trap station number, grid number, toe clip code, species and habitat type were recorded for every individual. Animals were released at the trapping station where they were captured. Rodent species were identified in the field following Happold (2013). Moreover, species that we failed to identify in the field were collected as voucher specimens and the toe clip tissue sample preserved in 70% ethanol for molecular identification and confirmation. Weight/body size, sex and reproductive conditions of the animals were recorded following similar procedures by Makundi *et al*. (2007), Monadjem and Perrin, (2003). Assessment of age structure was conducted using body size/weight, pelage colour and texture. Animals were classified into two age classes: juveniles and adults. Juveniles were characterized by small body size, grey and soft pelage and absence of reproductive development signs (Searle, 1985; Gurnell and Flowerdew, 2006). It was difficult to distinguish between sub-adults and adults since they were both characterized by larger body size/weight and complete pelage colour and texture (varied patterns) with fully developed reproductive organs such as testis and nipples (Kingdon, 2015; Searle, 1985). Adult animals were sexed based on genitalia and presence of secondary sexual characteristics like testis and nipples. Also, by using distance between the anus and urogenital opening (shorter in females and longer in males). For sex identification of juveniles, we used descriptive characteristics by Kay and Hokestra, (2008).

Furthermore, sexual reproductive conditions were examined using testis position for males and by using vaginal condition, pregnancy, and lactation status for females. For example, scrotal or descended visible testis as a result of swollen perianal area (SV) means the animal was sexually active. Whereas abdominal and non-visible testis (AN) means the animal was not sexually active. For females, we examined the vagina (whether perforated or closed), pregnancy condition by palpation and lactation status by presence of suckling nipples. For example, if females had a closed vagina with small nipples (CSN) they were considered not sexually active. Females were considered to be sexually active if they had a perforated vagina with either small nipples (PSN) or large swollen nipples (PLN indicating lactation) and or if they were visibly pregnant with young ones (PLY). Individuals whose sex and or sexual condition could not be identified were excluded from analysis of sex ratio.

### 4.2.3 Data Analysis

#### *4.2.3.1 Sex ratio*

In this study, sex ratio was defined as the proportion of adult females to the total number of both males and females (Becker *et al*., 2016) as expressed below:
$Sr = f/m + f$

Where, Sr = sex ratio*,* *f* is number of females and *m* is number of males in a sample.

The ratio of female to male was considered because it is the females that determine potential growth of population. When sex ratio is significantly skewed towards females, there is a higher possibility of population decline and extinction (Ancona *et al.,* 2017). The data was not normally distributed (especially for *Lophuromys)*, hence non-parametric tests (MannWhitney/Wilcoxon Rank sum test and Kruskal Wallis) were used to determine the variations in sex ratio across habitats and months (Zar, 1999).

#### 4.2.3.2 Breeding activity and population fluctuations

In this study, only females were considered for breeding activity because their sexual activity depends on seasonality and availability of food resources whilst males remain sexually active throughout the year irrespective of food availability (Mulungu *et al*., 2013). Breeding activity was determined by the number of both sexually active/breeding females (PSN, PLN and PLY) and sexually inactive or non-breeding females (CSN) in all habitats and months. It was expressed as the proportion of sexually active/breeding females to the total number of females. Two way ANOVA was used to compare the number of sexually active females across habitats and months since the data were normally distributed with equal variances.

Population size was estimated in minimum number of individuals known to be alive (MNKA) (Krebs, 1966). The MNKA counts all the animals with presence. It is done by adding the animals trapped at time *t* with animals not trapped at time *t*, but were known to be alive and appeared to be trapped again in later sessions. For each grid population size was estimated per 0.5 hectare in each of the trapping session (3-days trapping) in a closed population. Population fluctuation was defined as the change in population size (MNKA) over space (habitat type) and time (month/season). Generalized linear models GLM with a negative binomial distribution were used to determine the influence of habitat type, seasons/months and the interactions between them on rodent population size. ANOVA was used to compare mean population size between habitats and seasons/months.

#### 4.2.3.3 Ethical Considerations

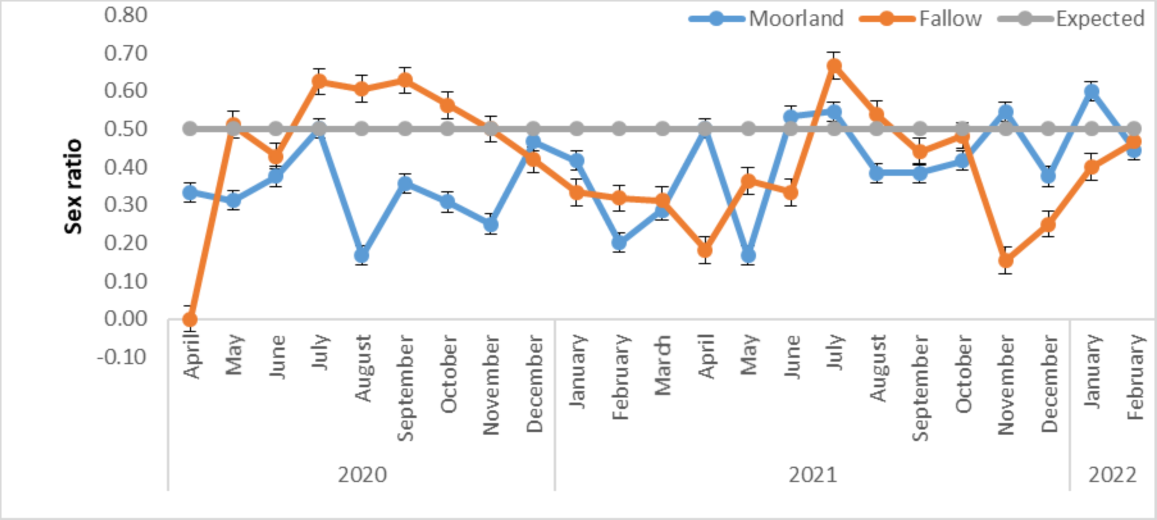
The research was approved by Sokoine University of Agriculture SUA, Tanzania (Ref no: SUA/DPRTC/PFC/D/2019/0002/1). A research permit no 2020-163-NA-2020-127 was issued by the Tanzania Commission for Science and Technology (COSTECH) in collaboration with Tanzania Wildlife Research Institute TAWIRI. A permit to conduct the research in Mt Kilimanjaro was provided by Tanzania National Parks (TANAPA).

## 4.3 RESULTS

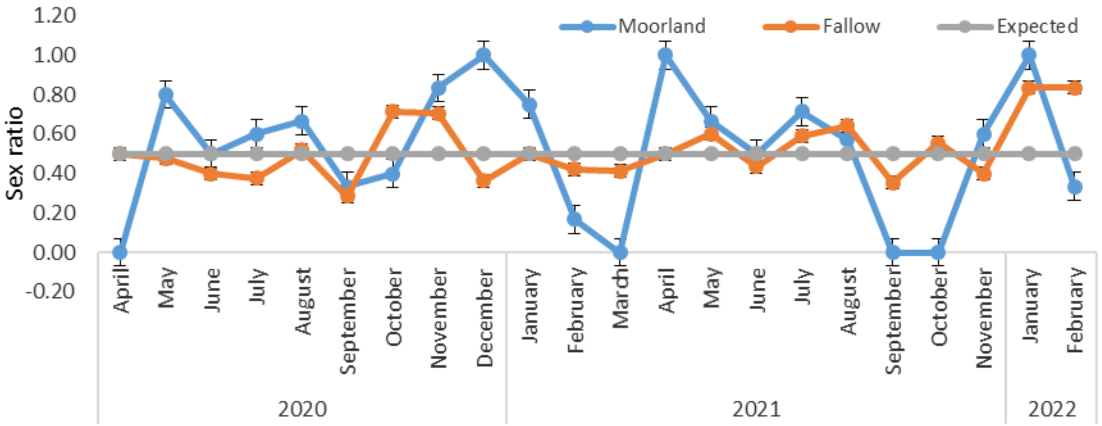
### 4.3.1 Sex ratio

Overall sex ratio of *Rhabdomys dilectus* was significantly skewed towards males in moorland (61.21% males and 38.79 % females, W= 210, $p < 0.001$) but no significant difference was observed in fallow (52.78% males and 47.22% females, W= 149.5, P = 0.237). Moreover, no significant differences in female-male sex ratio of *R. dilectus* were observed between habitats ($F_{1,22} = 0.009$, P = 0.44) and months ($F_{11,22} = 0.03$, P = 0.08). However, it was relatively higher (skewed towards females) in fallow than in moorland and was relatively higher in July which correspond to dry season. In addition, monthly sex ratio of *R. dilectus* fluctuated more from the margins in moorland and fallow (Figure 4.2a).

Overall sex ratio of *Lophuromys aquilus* was not significantly different in moorland (52.78% males and 47.22% females, W = 112, p = 0.79) and fallow (49.7% males and 50.2% females, W = 97, p = 0.936). Moreover, no significant differences in female-male sex ratio of *L. aquilus* were observed between habitats (P = 0.87) and months (P = 0.14). However, it was higher (skewed towards females) in moorland than in fallow and was relatively higher through April-May and November which corresponds to wet season. In addition, monthly sex ratio fluctuated more from the margins in moorland and was relatively stable or less fluctuating in fallow (Figure 4.2b).



(a)

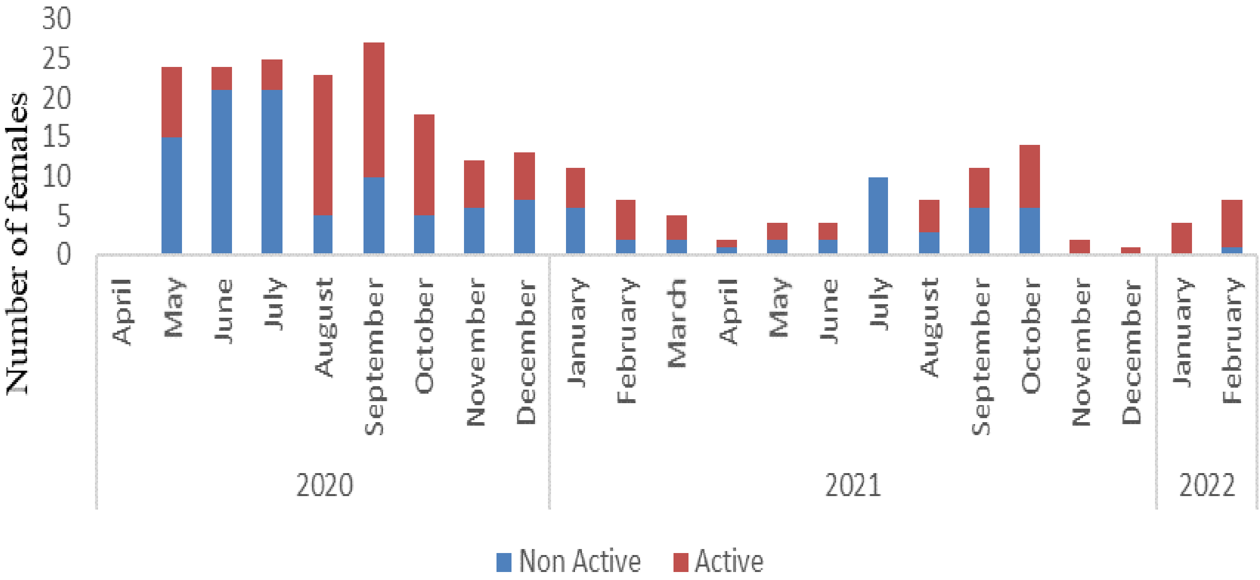


(b)

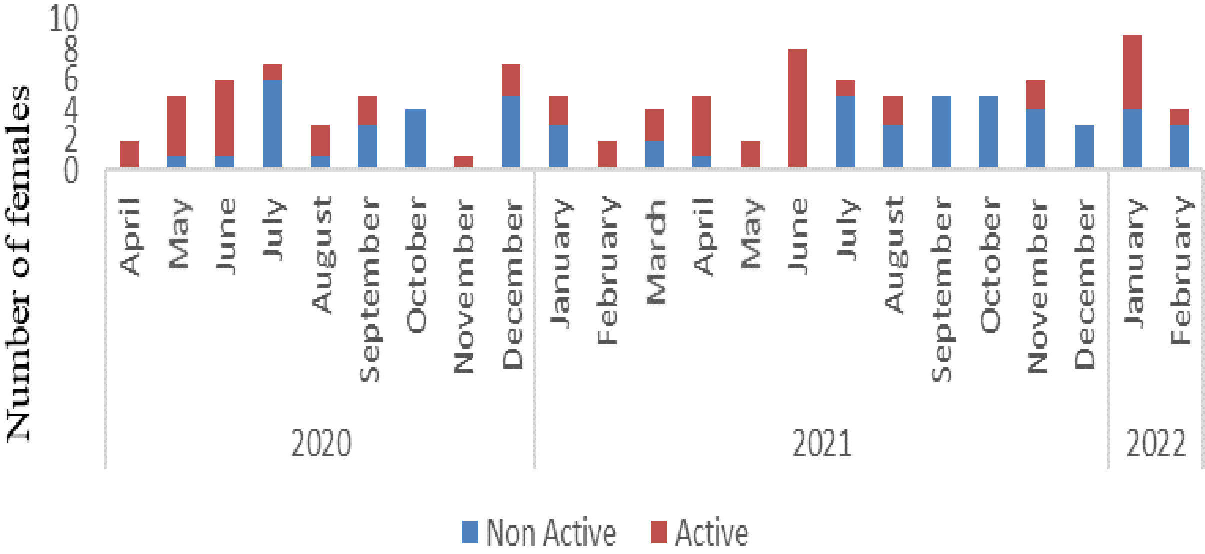
**Figure 4.2: Monthly variations in sex ratio of females to males of *Rhabdomys dilectus* (a) and *Lophuromys aquilus* (b) in both moorland and fallow habitats**

### 4.3.2 Breeding activity

There were statistically significant differences in number of sexually active females (breeding individuals) of *R. dilectus* between habitats ($P < 0.001$) but not between months ($P = 0.32$). Sexually active females were significantly higher in fallow (Estimate, SE and p-value) 1.07 ± 0.45, $P = 0.02$ than in moorland -0.87 ± 0.23, $P < 0.001$. The number of sexually active *R. dilectus* females occurred throughout the year in fallow habitat (Figure 4.3a) indicating that breeding of *R. dilectus* was year-round in fallow habitat and discrete in moorland (Figure 4.3b). There was no significant difference in number of sexually active females between months in both moorland and fallow. However, the number of sexually active females was high through April-June (which correspond to wet season).


Number of females
30
25
20
15
10
5
0
April
May
June
July
August
September
October
November
December
January
February
March
April
May
June
July
August
September
October
November
December
January
February
2020
2021
2022
Non Active
Active

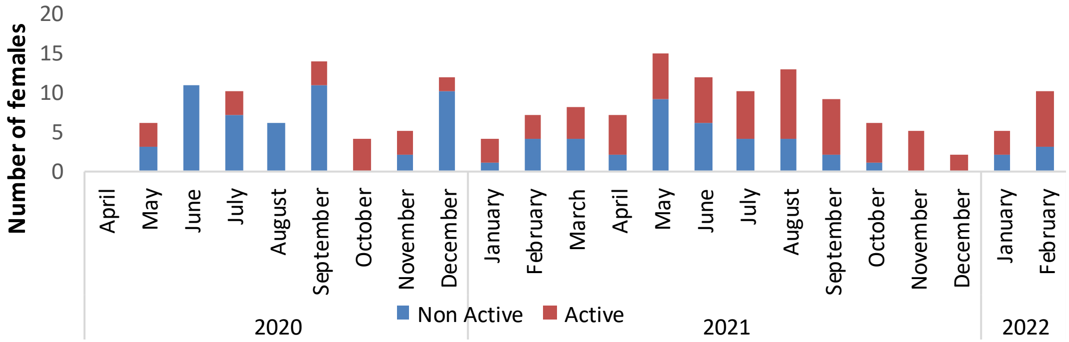
(a)



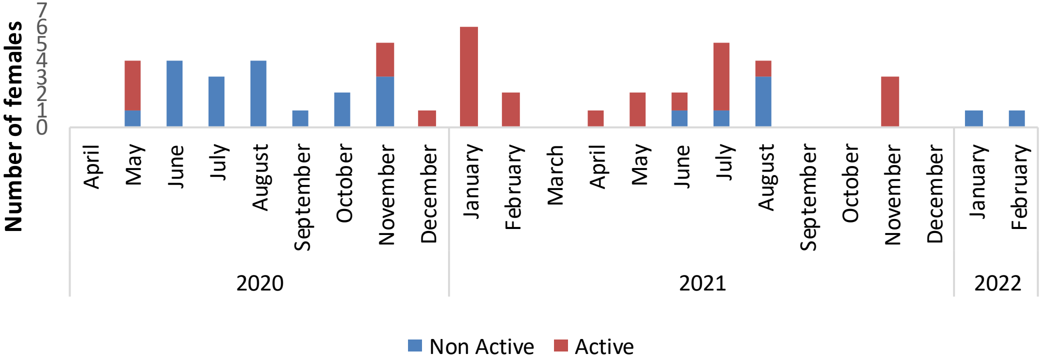
(b)

**Figure 4.3: Breeding activity of *Rhabdomys dilectus* females in fallow (a) and moorland (b) habitats on Mount Kilimanjaro**

For *Lophuromys aquilus*, the number of sexually active/breeding females was significantly different between habitats ($P$ < 0.001) but not between months ($P$ = 0.7042). Number of actively breeding females were significantly lower in moorland than in fallow habitat (-1.29 ± 0.27, $P$ < 0.001). Moreover, the breeding activity of *L. aquilus* was throughout the year in fallow (Figure 4.4a) and discrete without a clear pattern in moorland (Figure 4.4b). However, in moorland habitat the number of sexually active females peaked in January and July and no sexually active females were observed in October.



(a)



(b)

**Figure 4.4: Breeding activity of *Lophuromys aquilus* females in fallow (a) and moorland (b) habitats on Mount Kilimanjaro**

### 4.3.3 Population fluctuations

Mean population size of *Rhabdomys dilectus* ranged from 8 ± 0.51 during wet season to 10.75 ± 0.84 (indv/o.5 ha) during dry season in moorland. Also, it ranged from 17.10 ± 2.55 during wet season to 19.33 ± 3.05 (indv/o.5ha) during dry season in fallow. In addition, population fluctuation of *R. dilectus* was influenced by habitat types ($P < 0.001$) and season ($P = 0.034$), but no significant differences were observed between months. There was a significantly higher population size in fallow (Estimate, SE, and p-value) 2.98 ± 0.12, $P < 0.001$ than in moorland -0.63 ± 0.13, $P < 0.001$. Moreover, population size of *R. dilectus* increased during dry season (2.98 ±0.12, $P < 0.001$) and decreased during wet season (-0.27 ± 0.13, $P = 0.034$) (Figure 5a and b). Inaddition, population size of *R. dilectus* had a significant positive correlation with sex ratio ($P < 0.001$).

On the other hand, mean population of *Lophuromys aquilus* ranged from 3.5 ± 0.44 during wet season to 4 ± 0.48 (indv/o.5 ha) during dry season in moorland. Also, it ranged from 12.17 ± 2.17 during wet season to 15.25 ± 1.37 (indv/o.5 ha) during dry season in fallow. Moreover, population fluctuation of *L. aquilus* was influenced by habitat types ($P < 0.001$) and season ($P = 0.22$). However, the effect of season was not significant. Moreover, population size varied significantly between habitats but not between months. It was significantly higher in fallow (Estimate, SE, and p-value) 2.74 ± 0.11, $P < 0.001$ than in moorland -1.39 ± 0.16, $P < 0.001$ and decreased relatively during wet season -0.1808 ± 0.15, $P = 0.22$) (Figure 4.5a and 4.5.b).

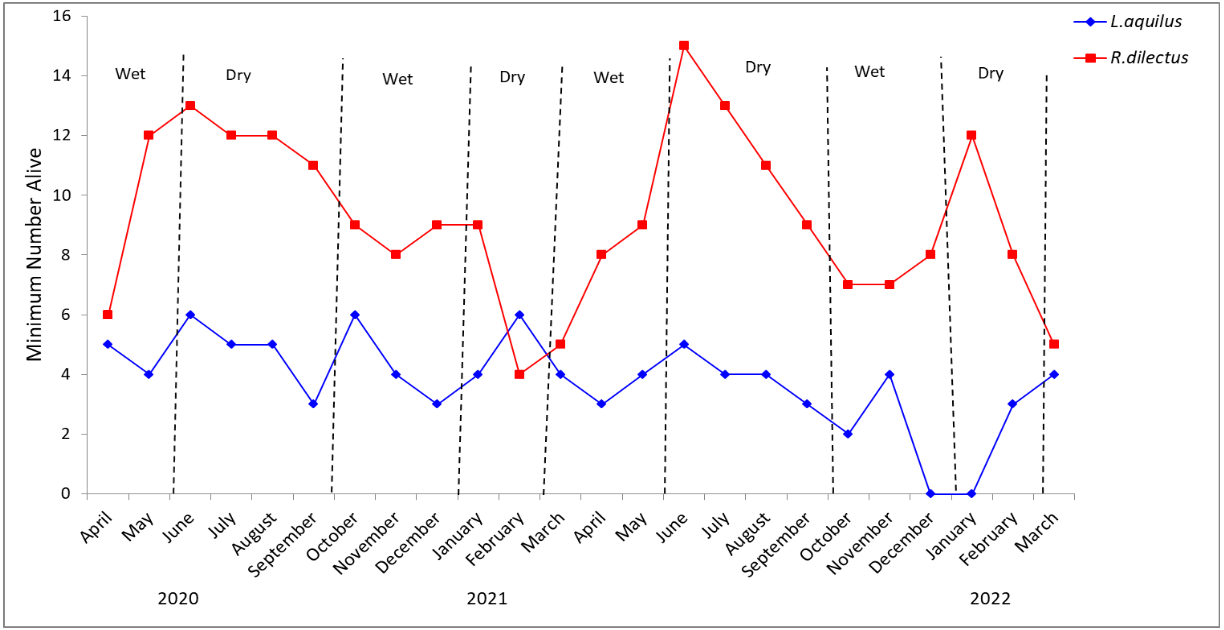


**Figure 4.5(a): Monthly and seasonal Population fluctuations of Rhabdomy *dilectus* and *Lophuromys aquilus* in moorland habitat**

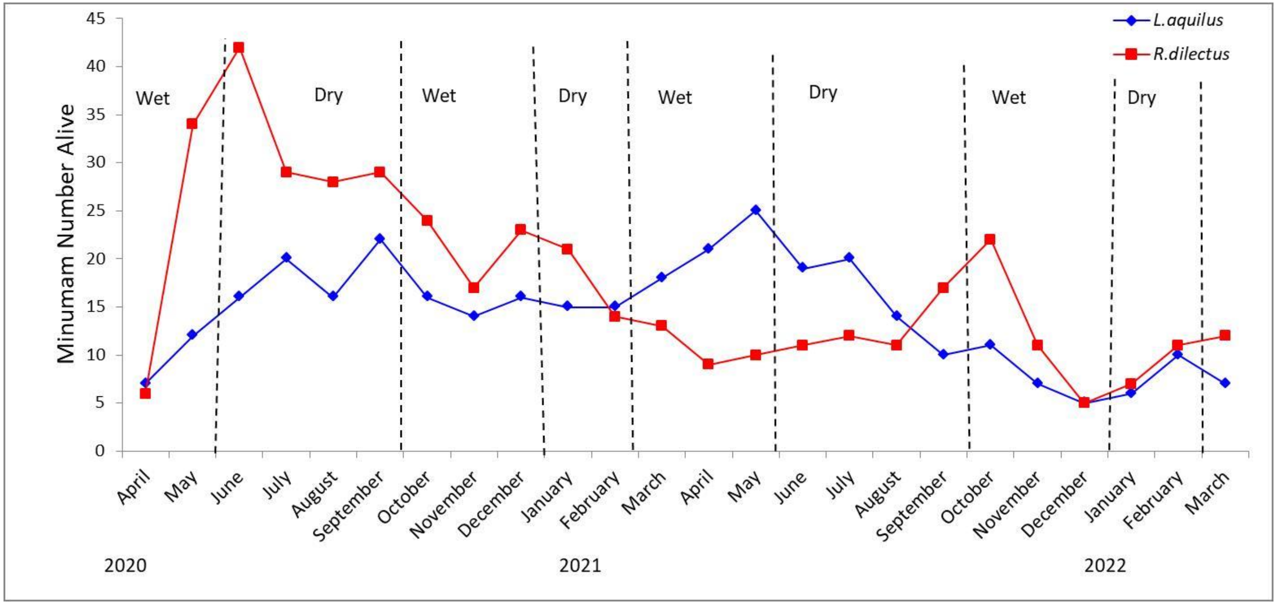


**Figure 4.5b: Monthly and seasonal Population fluctuations of Rhabdomy *dilectus* and *Lophuromys aquilus* in fallow habitat**

## 4.4 Discussion

### 4.4.1 Sex ratio

The sex ratio is an important parameter for reproductive potential of rodent populations (Shireleyo *et al*., 2020). In our study, female to male sex ratio of *R. dilectus* was unstable and highly fluctuating from the expected margin in the moorland habitat and was moderately stable (closer to the margin) in fallow. This was probably due to climate variations and food availability which limits movements and activity patterns of rodents. During dry season, moorland habitats are characterized with extremely cold and humid weather conditions which restricts the activity patterns and movements of rodents (Clausnitzer *et al.,* 2001).

In general, sex ratio of both species was skewed towards males during wet season in the moorland habitat. These observations could be due to behavioural differences and the variations in efforts and energy invested in reproduction between the two sexes. Females invest a substantial amount of time and energy during gestation, lactation and early development of juveniles (Pond, 1977). During the wet season females spend more time inside the nests during pregnancy and after giving birth, hence they are less prone to predation (Johnson *et al*., 2001; Breedveld *et al*., 2019). This improves fitness and survival of juveniles (Dickman, 1999). Therefore, reproductive success of females is constrained by resource availability and the ability to acquire them. In contrast, males devote less effort and energy to parental care.

Another possible reason for skewed sex ratio could be due to differences in movement patterns between the sexes. Males are sexually selective and have greater mobility contrary to females (Pillay, 2000). During wet season males move longer distances in search for mates hence increases the probability of being trapped (Bantihun and Bekele, 2015; D'Andrea *et al*., 1999; Phelps, 2006). In most populations, the sex ratio is balanced at birth (Rosenfeld and Roberts, 2004), however, changes in nutritional quality and stress from competition for mates might affect maternal body conditions and reduce the number of female offspring at birth (Hoffmann *et al*., 2003; Li *et al*., 2016; Hunninck *et al*., 2018).

### 4.4.2 Breeding activity

Generally, the average number of breeding females of both species was higher in fallow than in moorland habitat. Also, the breeding activity of both *Lophuromys aquilus* and *Rhabdomys dilectus* was year round in fallow and discrete in moorland. Sexually active females in fallow habitat occurred throughout the study period except in July 2021 (for *R. dilectus)* and August 2020 (for *L. aquilus)* and reached the peak in June and December, suggesting year-round breeding in fallows could be due to continuous food availability. The fallows were characterized by dense heterogenous vegetation almost throughout the year making them rich in food resources and cover (Thomas *et al*., 2022 a), hence they are presumably favourable for year-round breeding of the rodents. Similar breeding activity are observed in agro-ecosystems such as maize-fallow field mosaics, where most rodents have year round or continous breeding due to resources availability throughout the year (Mlyashimbi *et al.,* 2019; Mulungu *et al*., 2013).

Discrete or seasonal breeding of the two rodents (particularly of *R. dilectus*) in moorland could be attributed to adverse climatic conditions and poor vegetation structure which affects rodent survival and reproduction (Clausnitzer *et al.,* 2001). For example, cold temperatures and less food abundance are reported to have greater inhibitory effects on reproduction of female *Rhabdomys* (Jackson and

Bernard 2006). Hence, species of genus *Rhabdomys* are adapted to opportunistic reproduction especially in Afro-alpine environments due to spatial-temporal variations in climate (Clausnitzer *et al.*, 2001). Moreover, discrete breeding expressed by *R. dilectus* in this study concurs with studies in desert and semi-arid environments which reported that, timing of reproduction in *Rhabdomys pumilio* a species from same genus was influenced by spatial-temporal variations in climate (Jackson and Bernard, 2006; Schradin and Pillay, 2006; Krug, 2004; 2007). *Rhabdomys pumilio* has an opportunistic reproduction which occurs only when conditions are suitable (Jackson and Bernard, 2006). Consistently, it has been reported that most rodents breed only when conditions are favourable and stop when food is scarce (Leirs, 1997; Jackson and Aarde, 2004; Mohammadi, 2010).

In addition, the high number of sexually active or breeding females of both species during the study period occurred from January to June, which corresponds to rain season in the study area. The peak of rain season on Mt Kilimanjaro is between March and May and ends in early June. It is during this period when the two species *Rhabdomys dilectus* and *Lophuromys aquilus* breed. Consistently, it has been reported that breeding activity of *Lophuromys* is continous throughout the year in most places but sometimes it is seasonal (Cheeseman and Delany, 1979; Clausnitzer *et al*., 2003; Makundi *et al*., 2007). Our results coincides with previous studies in Africa and neotropical-forest which suggested that most rodents in Africa and neotropical-forest show distinct breeding seasonality **(**Field, 1975; Lacher, 1992; Lima *et al*., 2001a,b; Makundi *et al*., 2007). Moreover, adults become sexually active after the first rains in early wet season, reaching the peak during wet season when food is abundant with high quality, and reduces gradually before stopping at end of wet season (Lidicker, 1973; Mulungu *et al*., 2013). This is because, rainfall influences the abundance of insects (Linzey and Kesner, 1997) and the sprouting of fresh green vegetation which triggers the onset of reproduction in most rodents (Nicolas and Colyn, 2003; Makundi *et al*., 2007; Massawe *et al*., 2011 & 2008; Bantihun and Bekele, 2015). Also, rainfall influences reproductive success of an individual through improved ground cover for protection (Leirs, 1997; Linzey and Kesner, 1997; Ademola *et al*., 2021). Generally, the number of sexually active females of the two rodents in both moorland and fallow was high from April to early June which corresponds with wet season. Interestingly this study revealed that early rains are very important for the onset of breeding on Mt Kilimanjaro. This was evident from absence of sexually active females of both species in moorland through September-October whilst there were even more sexually active females through September-October in fallow. The observation could be attributed to delayed or little amount of rainfall in moorland compared to fallow (Thompson *et al*., 2002; Mulangu and Kraybil, 2013) which might have resulted into lower number of breeding females in November. Whereas the presence of sexually active females in fallow could be a result of high amount of rainfall, which is very important for the onset of breeding (Lidicker, 1973; Mulungu *et al*., 2013; Nicolas and Colyn, 2003; Mlyashimbi *et al*., 2018).

## 4.5 Population fluctuations

The population size of *R. dilectus* was positively correlated with female to male sex ratio, probably because sex ratio is an important parameter for reproductive potential of rodent populations. Population fluctuations are significantly impacted by unbalanced sex ratio which could be due to increased competition and mating opportunities (Marealle *et al*., 2010). Similarly, it is suggested that competition for mates occurs when the operational sex ratio (number of sexually active individuals) is skewed towards one sex

(Shilereyo *et al*., 2020). For-example, female skewed sex ratio increases the female-female competition, however, it increases the population size through increased chances of mating, because a single male can mate with several females, and increase the likelihood of successful reproduction (Shilereyo *et al*., 2020). Whilst a male-skewed sex ratio increases male-male competition for mates which reduces population growth and viability (Rankin *et al*., 2011; Grayson *et al*., 2014; López-Sepulcre *et al*., 2009).

In addition, the population size of *habdomys dilectus* was significantly higher in fallow than in moorland and significantly higher in dry season than in wet season, with highest population peaks around June and January. This observation indicates that population fluctuations of *R. dilectus* is strongly influenced by seasonality which is probably brought by rainfall distribution between the two habitats (Taylor and Green, 1976; Schradin and Pillay, 2006; Krug, 2007; Schradin, 2009). Habitats of Mt Kilimanjaro are completely distinct, for example, fallows have dense and heterogeneous vegetation with high primary productivity and food availability compared to moorland, montane forest have year-round wet conditions whilst moorland are very dry with limited rainfall (Coe, 1993; Hemp, 2006; Mulangu and Kraybill, 2013). Since rainfall has a direct impact on primary productivity and food resource quality, variations between the two habitats could affect both quantity and quality of food resources such as seeds/grains, vegetative materials, and insects, which are important for reproduction (Thomas *et al*., 2022a). Similar patterns of population fluctuations were observed on Mt Elgone by Clausnitzer *et al*. (2001) who reported that, population dynamics of rodents in the Afro-alpine environments particularly *Rhabdomys* is strongly influenced by climate, due to extremely cold and humid weather conditions which affects primary productivity.

Similarly, population size of *Lophuromys aquilus* was significantly higher in fallow than in moorland, however, no remarkable differences were observed between the seasons and months. Highest population peaks were observed in both dry and wet seasons around June-September and May respectively. Less population fluctuations of *L. aquilus* in both habitats could probably be due to habitat generalist nature of *L. aquilus* which is believed to be well adapted across a range of habitats and altitude above 500 m.a.sl. (Happold, 2013). Therefore, stable populations of *L. aquilus* in moorland and fallow could be indicative of high adaptation which results into high survival and reproduction. In addition, high population size of both species in early dry season (June-August) was probably due to newly recruited juveniles which were born on previous months, as rodents are reported to breed during wet season and the population peaks one to three months later (Mulungu *et al*., 2013).

## 4.6 Conclusion and Recommendations

The variations in breeding activity and population fluctuations of *Rhabdomys dilectus* and *Lophuromys aquilus* on Mt Kilimanjaro across the habitats might be reflective of rainfall distribution along the altitudinal gradient (between habitats). The study revealed that, seasonality and probably climate variability between moorland and fallow plays a great role in breeding activity and population fluctuations of the two species through availability and quality of food resources. This was evident from year-round breeding activity of both species in the fallow and seasonal or discrete breeding in moorland.

The present study was conducted for two years only (minimum time for studying rodent population fluctuations), it is therefore not conclusive but rather provide base line data on rodent demography. Long-term studies should be conducted for at least five years. Also, the important factors affecting rodent populations such as births and death rates, immigration and emigration, predation and intraspecific competition were not ascertained in this study. Therefore, further studies should consider the aforementioned factors for better understanding of rodent population fluctuations.

## 4.7 Acknowledgments

We would like to convene our sincere gratitude to the African Centre of Excellence for Innovative Rodent Pest Management and Biosensor Technology Development project (ACE IRPMandBTD) for funding this research work. Our special thanks, goes to the team of rodent technicians and field assistants (Ramadhan Kagunguli, Ephrahim Norbert Komba), drivers (Gervas Raphael and Sadik Kahangwa) from the Institute of Pest Management, Sokoine University of Agriculture as well as Innocent Alex and Elton Shery from Boma for their tremendous assistance in data collection. Moreover, we are more grateful to Abeid Manyonyi, Samwel Chacha and Mugabo Tuma from Mt Kilimanjaro National Park for security and protection.

## 4.8 Author’s Contribution

Suzana M. Thomas, Loth S. Mulungu, Geofrey E. Soka and Rhodes H. Makundi designed the ideas and methodology. Suzana Thomas conducted the field work (data collection), data analysis and manuscript write up. Loth S. Mulungu and Geofrey Soka supervised the work. Geofrey Soka and Rhodes H. Makundi reviewed the work and gave it final approval for submission.

## 4.9 Data Accessibility Statement

Authors agree to deposit the data associated with this study in an Institutional repository of Sokoine University of

Agriculture SUA and make it publicly available once the manuscript is accepted for publication.

## 4.10 Conflict of Interest Statement

Authors declare no conflict of interest among themselves.

## References

Ademola, O.J., B. Vanden Broecke, H. Leirs, A.W. Massawe, L.S. Mulungu and R.H. Makundi (2021) Effects of forest disturbance on the fitness of an endemic rodent in a biodiversity hotspot. *Ecology and Evolution*, 11(5): 2391-2401.

Afework B, Leirs H (1997). Population ecology of rodents of maize fields and grassland in central Ethiopia. Belg. J. Zool. 127: 39-48.

Ancona S, De´nes FV, Kru¨ger O, Sze´kely T, Beissinger SR. (2017) Estimating adult sex ratios in nature. Phil. Trans. R. Soc. B 372:

Bai Y, Xu Z, Lu B, Sun Q, Tang W, Liu X, Yang W, Xu X, Liu Q (2015). Effects of climate and rodent factors on hemorrhagic fever with renal syndrome in Chongqing, China. PLoS ONE 10(7):1997–2008.

Bantihun G, Bekele A. (2015). Diversity and habitat association of small mammals in Aridtsy forest, Awi Zone, Ethiopia. *Zoological Research 36*(2): 88-94.

Becker JB, Prendergast BJ, Liang JW (2016). Female rats are not more variable than male rats: a meta-analysis of neuroscience studies. Biology of Sex Differences 7(1):34.

Bekele, A., and Corti, M. (1994). Multivariate morphometries of the Ethiopian populations of harshfurred rat (*Lophuromys*: Mammalia, Rodentia). *Journal of Zoology*, *232*(4), 675-689.

Borremans, B., Sluydts, V., Makundi, R. H., and Leirs, H. (2015). Evaluation of short-, mid- and long-term effects of toe clipping on a wild rodent. *Wildlife Research*, 42: 143–148.

Breedveld MC, Folkertsma R, Eccard JA (2019). Rodent mothers increase vigilance behaviour when facing infanticide risk. Scientific Reports 9(1):1-10.

Cheeseman, C. L., and Delany, M. J. (1979). The population dynamics of small rodents in a tropical African grassland. *Journal of Zoology*, *188*(4), 451-475.

Clausnitzer, V., Denys, C., Granjon, L., and Poulet, A. (2001). Rodents of the afro-alpine zone of Mt. Elgon. *African small mammals*, 427-443.

Clausnitzer, V., Churchfield, S. and Hutterer, R. (2003). Habitat occurrence and feeding ecology of Crocidura montis and *Lophuromys* flavopunctatus on Mt. Elgon, Uganda. *African Journal of Ecology,* 41(1): 1-8.

Corti, M., Castiglia, R., and Verheyen, W. (2004). A note on three new cytotypes of *Lophuromys* flavopunctatus sensu lato (Rodentia, Muridae) from Tanzania.

D'Andrea PS, Gentile R, Cerqueira R, Grelle CEV, Horta C, Rey L (1999). Ecology of small mammals in a Brazilian rural area. Revista Brasileira de Zoologia 16(3): 611-620.

Dickman CR (1999). Rodent-ecosystem relationships: a review. Ecologically-based management of rodent pests. ACIAR Monograph (59):113-133.

Dufour C.M.S., Meynard C., Watson J. et al. 2015: Space use variation in co-occurring sister species:

response to environmental variation or competition? PLOS ONE 10: e0117750.

du Toit N., van Vuuren B.J., Matthee S. and Matthee C.A. 2012: Biome specificity of distinct genetic lineages within the four-striped mouse *Rhabdomys* pumilio (Rodentia: Muridae) from southern Africa with implications for taxonomy. Mol. Phylogenet. Evol. 65: 75–86.

Feldhamer GA (1979). Vegetative and edaphic factors affecting abundance and distribution of small mammals in southeast Oregon. Gre. Basi. Nat. 39: 207-218.

Field, A. C. (1975). Seasonal changes in reproduction, diet and body composition of two equatorial rodents. *African Journal of Ecology*, *13*(3-4), 221-235.

Francisco ADL, Magnusson WE, Sanaiotti TM (1995). Variation in growth and reproduction of Bolomys lasiurus (Rodentia: Muridae) in an Amazonian savanna. Journal of Tropical Ecology 11(3):419-428.

Fritzsche, K., Booksmythe, I., and Arnqvist, G. (2016). Sex ratio bias leads to the evolution of sex role reversal in honey locust beetles. *Current Biology*, *26*(18), 2522-2526.

Ganem, G., Dufour, C. M. S., Avenant, N. L., Caminade, P., Eiseb, S. J., Tougard, C., and Pillay, N. (2020). An update on the distribution and diversification of *Rhabdomys* sp.(Muridae, Rodentia). *Journal of Vertebrate Biology*, *69*(2), 20013-1.

Gebresilassie W, Bekele A, Belay G, Balakrishnan M (2006). Home range and reproduction of rodents in Maynugus irrigation field, northern Ethiopia. SINET: Ethiopian Journal of Science 29(1):57-62.

Gebrezgiher, G. B., Makundi, R. H., Meheretu, Y., Mulungu, L. S., and Katakweba, A. A. (2022). A Decade-Long

Change in the Elevational Distribution of Non-Volant Small Mammals on Mount Meru, Tanzania. *Diversity*, *14*(6), 454.

Grayson, K. L., Mitchell, N. J., Monks, J. M., Keall, S. N., Wilson, J. N., and Nelson, N. J. (2014). Sex ratio bias and extinction risk in an isolated population of tuatara (Sphenodon punctatus). *PLoS One*, *9*(4), e94214.

Gurnell J. and Flowerdew J.R. 2006: Live trapping of small mammals: a practical guide. *The Mammal Society, London, U.K.*

Happold, D. (Ed.) (2013). *Mammals of Africa.* Volume III, Rodents, Hares and Rabbits. Bloomsbury Publishing, London. 784pp.

Hemp, A. (2006). Continuum or zonation? Altitudinal gradients in the forest vegetation of Mt. Kilimanjaro. *Plant ecology, 184*(1): 27-42.

Hoffmann, I. E., Millesi, E., Huber, S., Everts, L. G., and Dittami, J. P. (2003). Population dynamics of European ground squirrels (Spermophilus citellus) in a suburban area. *Journal of Mammalogy*, *84*(2), 615-626.

Hunninck, L., Ringstad, I. H., Jackson, C. R., May, R., Fossøy, F., Uiseb, K., and Røskaft, E. (2017). Being stressed outside the Parkconservation of African elephants (Loxodonta africana) in Namibia. *Conservation Physiology*, *5*(1), cox067.

Jackson, C., and Bernard, R. T. (2006). Variation in the timing of reproduction of the four-striped field mouse, *Rhabdomys* pumilio, in the Eastern Cape Province, South Africa. *African Zoology*, *41*(2), 301-304.

Johnson M, Thomson S, Speakman JR (2001). Limits to sustained energy intake: II. Inter-relationships between resting metabolic rate, life-history traits and morphology in *Mus musculus*. Journal of Experimental Biology 204(11):1937-1946.

Kay, E. H. and Hoekstra, H. E. (2008). Rodents. *Current Biology* 18(10): R406–R410.

Kingdon J (2015). The Kingdon field guide to African mammals: Bloomsbury Publishing. p. 640.

Krebs, C. J. (1966). Demographic changes in fluctuating populations of Microtus californicus. *Ecological monographs*, *36*(3), 239-273.

Krug, Cornelia B. (2007). "Reproduction of *Rhabdomys* pumilio in the Namib desert: pattern and possible control." *Basic and Applied Dryland Research* (2007): 67-85.

Lacher, T. E. (1992). Ecological aspects of reproductive patterns in South American small rodents. In *Reproductive Biology of South American Vertebrates* (pp. 283-294). Springer, New York, NY.

Leirs, H., Verhagen, R. and Verheyen, W. (1994). The basis of reproductive seasonally in Mastomys rats (Rodentia: Muridae) in Tanzania. *Journal of Tropical Ecology*, *10*(1), 55-66.

Leirs, H., N. Stenseth, J.D. Nichols, J.E. Hines, R. Verhagen and W. verheyen (1997). Stochastic seasonality and non-linear dependent factors regulate population size in an African rodent. *Nature*, 389: 176-180.

Leirs H, Sluydts V, Makundi R (2010). Rodent outbreaks in sub-Saharan Africa. Rodent Outbreaks: Ecology and Impacts pp. 290.

Li, G., Hou, X., Wan, X., and Zhang, Z. (2016). Sheep grazing causes shift in sex ratio and cohort structure of Brandt's vole: Implication of their adaptation to food shortage. *Integrative Zoology*, *11*(1), 76-84.

Lidicker Jr, W. Z. (1973). Regulation of numbers in an island population of the California vole, a problem in community dynamics. *Ecological Monographs*, *43*(3), 271-302.

Lima M, Stenseth NC, Leirs H, Jaksic FM (2003). Population dynamics of small mammals in semi-arid regions: a comparative study of demographic variability in two rodent species. Proceedings of the Royal Society of London B: Biological Sciences 270(1528):1997-2007. https://doi.org/10.1098/rspb.2003.2448.

Lima, M., Julliard, R., Stenseth, N. C. and Jaksic, F. M. (2001a). Demographic dynamics of a neotropical small rodent (Phyllotis darwini): feedback structure , predation and climatic factors. *Journal of Animal Ecology*, 70: 761–775.

Lima, M., Stenseth, N. C., Yoccoz, N. G., and Jaksic, F. M. (2001b). Demography and population dynamics of the mouse opossum (Thylamys elegans) in semi-arid Chile: seasonality, feedback structure and climate. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1480), 2053-2064.

Linzey, A. V., and Kesner, M. H. (1997). Small mammals of a woodland-savannah ecosystem in Zimbabwe. I. Density and habitat occupancy patterns. *Journal of Zoology*, *243*(1), 137-152.

López-Sepulcre, A., Norris, K., and Kokko, H. (2009). Reproductive conflict delays the recovery of an endangered social species. *Journal of Animal Ecology*, 219-225.

Madsen, T., and Shine, R. (1999). Rainfall and rats: Climatically driven dynamics of a tropical rodent population. *Australian Journal of Ecology*, *24*(1), 80-89.

Makundi, R., Massawe, A. and Mulungu, L. (2005). Rodent population fluctuations in three ecologically heterogeneous locations in northeast, central and southwest Tanzania. *Belgium Journal of Zoology* 135: 159-165.

Makundi, R. H., Massawe, A. W., Mulungu, L. S., and Katakweba, A. (2010). Species diversity and population dynamics of rodents in a farm-fallow field mosaic system in Central Tanzania. *African Journal of Ecology* 48:13–320.

Marealle WN, Fossøy F, Holmern T, Stokke BG, Røskaft E (2010). Does illegal hunting skew Serengeti wildlife sex ratio? Wildlife Biology 16(4):419-430.

Mayamba A., R. M. Byamungu, H. Leirs, I. Moses, R. H. Makundi, D.N. Kimaro. A.W. Massawe, D. Kifumba, A. Nakiyemba, M. E. Mdangi, B. E Isabirye and L.S. Mulungu (2021) Population and breeding patterns of the rodent pest *Mastomys natalensis* in maize dominated agroecosystem in Lake Victoria crescent zone, Eastern Uganda. *African Zoology*, 56(1): 76 – 84.

Massawe AW, Mrosso FP, Makundi RH, Mulungu LS. (2008) Breeding Patterns of *Arvicanthis neumanni* in Central Tanzania. *African Journal of Ecology*, **46**(3): 320-324.

Massawe, A. W., Mulungu, L. S., Makundi, R. H., Dlamini, N., Eiseb, S. J., Kirsten, F., ... and Belmain, S. R. (2011). Spatial and temporal population dynamics of rodents in three geographically different regions in Africa: implication for ecologically-based rodent management. *African Zoology*, *46*(2), 393-405.

Meynard, C. N., Pillay, N., Perrigault, M., Caminade, P., and Ganem, G. (2012). Evidence of environmental niche differentiation in the striped mouse (*Rhabdomys* sp.): inference from its current distribution in southern Africa. *Ecology and Evolution*, *2*(5), 1008-1023.

Migula, P. 1969. Bioenergetics of pregnancy and lactation in the European common vole. - Acta Theriol. 14: 167-179.

Mulangu, F., and Kraybill, D. (2013). Climate change and the future of mountain farming on Mt. Kilimanjaro. In *The future of mountain agriculture* (pp. 73-88). Springer, Berlin, Heidelberg.

Mulungu, L. S., Makundi, R. H., Massawe, A. W., Machang'u, R. S. and Mbije, N. E. (2008). Diversity and distribution of rodent and shrew species associated with variations in altitude on Mount Kilimanjaro, Tanzania. *Journal of Mammalia* 72(3): 178-185.

Mulungu, L. S., Themb'alilahlwa, A. M., Massawe, A. W., Kennis, J., Crauwels, D., Eiseb, S., and 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, V. Ngowo, M. Mdangi, A.S. Katakweba, P. Tesha, F.P. Mrosso, M. Mchomvu, P.M. Sheyo, B.S. Kilonzo (2013) Population dynamics and breeding patterns of Multi-mammate mouse, *Mastomys natalensis* (Smith 1834) in irrigated rice field in Eastern Tanzania. *Pest Management Science*, **69**(3):371-377.

Mohammadi, S. (2010). Microhabitat Selection by Small Mammals. *Advances in Biological Research* 4 (5): 283-287.

Nicolas, V., and Colyn, M. (2003). Seasonal variations in population and community structure of small rodents in a tropical forest of Gabon. *Canadian Journal of Zoology*, *81*(6), 1034-1046.

Odhiambo RO, Makundi RH, Leirs H, Verhagen R. (2008a). Dietary selection in Mastomys natalensis (Rodentia: Muridae) in the maize agro-ecosystems of Central and South-western Tanzania. Mammalia, 72, 169–177.

Odhiambo, R. O., Makundi, R. H., Leirs, H., and Verhagen, R. (2008b). Demography, reproductive biology and diet of the bushveld gerbil Tatera leucogaster (Rodentia: Gerbillinae) in the Lake Rukwa valley, southwestern Tanzania. *Integrative Zoology*, *3*(1), 31-37. https://doi.org/10.1111/j.1749-4877.2008.00073.x

Olenev G, Grigorkina E (2011). Dynamics of sex ratio in populations of cyclomorphic mammals (rodentia, cricetidae, muridae). Biology Bulletin 38(8):797-808.

Oli MK, Dobson FS (1999). Population cycles in small mammals: the role of age at sexual maturity. Oikos 557-565.

Phelps KL (2006). *E*cological characteristics of small mammal communities inhabiting Tar Creek Superfund Site, Oklahoma. Oklahoma State University.

Pillay, N. (2000). Female mate preference and reproductive isolation in populations of the striped mouse *Rhabdomys* pumilio. *Behaviour*, *137*(11), 1431-1441.

Pond, C.M. (1977). The significance of lactation in the evolution of mammals. - Evolution 31: 177-199.

Rankin, D. J., Dieckmann, U., and Kokko, H. (2011). Sexual conflict and the tragedy of the commons. *The American Naturalist*, *177*(6), 780-791.

Rambau, R. V., Robinson, T. J., and Stanyon, R. (2003). Molecular genetics of *Rhabdomys* pumilio subspecies boundaries: mtDNA phylogeography and karyotypic analysis by fluorescence in situ hybridization. *Molecular Phylogenetics and Evolution*, *28*(3), 564-575.

Rosenfeld CS, Roberts RM (2004). Maternal diet and other factors affecting offspring sex ratio: a review. Biology of Reproduction 71(4):1063-1070.

Schärer, L., Rowe, L., and Arnqvist, G. (2012). Anisogamy, chance and the evolution of sex roles. *Trends in Ecology and Evolution*, *27*(5), 260-264.

Schradin, C., and Pillay, N. (2006). Demography of the striped mouse (*Rhabdomys* pumilio) in the succulent karoo. *Mammalian Biology*, *70*(2), 84-92.

Searle J (1985). Methods for determining the sex of common shrews (Sorex araneus). Journal of Zoology 206(2):279-282.

Shilereyo, M., Magige, F. J., Ogutu, J. O., and Røskaft, E. (2020). Small mammal community demography and reproductive seasonality under protection, pastoralism and agriculture in the Serengeti Ecosystem, Tanzania. *International Journal of Biodiversity and Conservation*, *12*(4), 253-269.

Smith, C., and Warren, M. (2019). GLMs in R for ecology.

Stanley, W. T., Rogers, M. A., Kihaule, P. M. and Munissi, M. J. (2014). Elevational distribution and ecology of small mammals on Africa's highest mountain. *PloS one, 9*(11): 1-13.

Taylor, K. D., and Green, M. G. (1976). The influence of rainfall on diet and reproduction in four African rodent species. *Journal of Zoology*, *180*(3), 367-389.

Thomas, S. M., Soka, G. E., Mulungu, L. S., and Makonda, F. (2022a). Spatial-Temporal Variations in Dietary Consumption of Two Dominant Rodent Species

(*Rhabdomys dilectus* and *Lophuromys aquilus*) on Mount Kilimanjaro, Tanzania. *Diversity*, *14*(8), 659.

Thomas, S. M., Soka, G. E., and Mulungu, L. S. (2022b). Influence of vegetation structure, seasonality, and soil properties on rodent diversity and community assemblages in west Mount Kilimanjaro, Tanzania. *Ecology and Evolution*, *12*(9), e9211

Verheyen, W., Hulselmans, J. L., Dierckx, T., and Verheyen, E. (2002). The *Lophuromys* flavopunctatus Thomas1888 sl species complex: a craniometric study, with the description and genetic characterization of two new species (Rodentia-Muridae-Africa). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique Biologie*, *72*, 141-182.

Wolff JO, Sherman PW (2007). Rodent Societies: An Ecological and Evolutionary Perspective. The University of Chicago Press, Chicago, pp. 605. http://dx.doi.org/10.7208/chicago/9780226905389.001.0001.

Wube T (2005). Reproductive rhythm of the grass rat *Arvicanthis abyssinicus*, at the Entoto Mountain, Ethiopia. Belgian Journal of Zoology 135:53-56.

Zar J.H. 1999: Biostatistical analysis, 4th ed. *Prentice Hall, New Jersey, U.S.A.*

# 5.0 CHAPTER FIVE

## Home range size and Survival probability of two major rodents (*Rhabdomys dilectus* and *Lophuromys aquilus*) on Mount Kilimanjaro.

Suzana M. Thomas[1, 2, 3,*], Geofrey E. Soka[2],
Loth S. Mulungu[4, †]

[1]The African Centre of Excellence for Innovative Rodent Pest Management and Biosensor Technology Development, Sokoine University of Agriculture, Morogoro, Tanzania.

[2]Department of Wildlife Management, Sokoine University of Agriculture,
Morogoro, Tanzania.
[3]Department of Biology, University of Dodoma, Dodoma, Tanzania.
[4]Institute of Pest Management, Sokoine University of Agriculture, Morogoro, Tanzania.

Corresponding Author: meydancan@gmail.com

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## Abstract

Home range and survival are important parameters influencing the size and distribution of rodents. Therefore, understanding the factors that affect them is crucial for conservation and management of rodent populations. In this study, home range and survival probability of two rodent species were studied in moorland and fallow habitats of Mount Kilimanjaro, in Kilimanjrao region of northern Tanzania. Trapping was done across both dry and wet seasons using Sherman live traps in CMR grids. Home range size of *Rhabdomys dilectus* was influenced by habitat type. It was significantly higher in moorland than in fallow. *Lophuromys aquilu's* home range was influenced by the variations in habitat, season and sex. Whereby, its home range was significantly higher in moorland than in fallow. Also, male *L. aquilus* had larger home range than females but the difference was not significant. There were significant differences in survival of the two species. Whereby, survival of *L. aquilus* was higher than that of *R. dilectus*. Moreover, there were no significant differences in survival between sexes of the two species. However, for both species female's survival was higher than that of males. This was probably due to that during breeding season, females spend most of their time in the nests hence reduce the chances of encountering predators. Despite of higher survival, capture probability of *L.aquilus* was lower than that of *R.dilectus* indicating that, the former could be a trap shy whereas the latter a trap lover. This study concludes that, habitat quality and sex influences home range size and survival probabilities of rodents due to variations in food resources availability, mating behavior and reproduction fitness.

**Key words**: Home range, survival, sex, capture, reproductive fitness, vegetation structure.

## 5.1 Introduction

A home range is a specific area traversed by an animal for day-to-day activities such as foraging, nesting, resting and mating (Burt, 1943; Powell, 2000; Powell and Mitchell, 2012; Cooney *et al*., 2015; Aiken, 2019). A home range provides resources and conditions necessary for animal's survival such as food, water, shelter/cover, mates and nesting grounds. It is always difficult for the animal to protect its home range (a territory) from other cospecifics, however, if the benefits of protecting it outweighs the costs, an individual will incur the costs to protect it (Burt, 1943). Home range of small mammals are dynamics, changing in size and position over time and space due to changes in resource distribution and availability at spatial-temporal scales (Powell and Mitchell, 2012; Aiken, 2019). Moreover, home ranges may vary between individuals, species, sex, age class, season and breeding activity (Burt, 1943; Powell, 2000; Schmidt, 2002; Powell and Mitchell, 2012; Cooney *et al*., 2015; Lee and Rhim, 2016; Aiken, 2019). For example, home range differences and may be overlap between individuals of same species or sympatric species might occur as a result of competition or coexistence through resource partitioning at spatial-temporal scales (Fieberg and Kochanny, 2005; Chuyong *et al*., 2011; Morris *et al*., 2011; Thomas *et al*., 2022b).

Variations in habitat type and seasonality results into seasonal food availability and cover which in turn affects habitat selection and home range size of small mammals. For example, wood mice (*Apodemus sylvaticus*) shows seasonal differences in home range size and habitat selection (by extending the size in cultivated areas) due to change in food and cover (Flavicollis, 2006). Also, home range size of female striped mice (*Rhabdomys pumilio*) is reported to change due to seasonal variations in food resources (Schradin and Pillay, 2006). In addition, reproducing individuals have large home range size due to required food and extra energy for reproduction and caring of juveniles (Mlyashimbi *et al*., 2019). On the other hand, survival of small mammals is influenced by variations in seasonality and vegetation structure (Ademola *et al*., 2021) which affects abundance of food resources such as grains, vegetative materials, insects/termites (Ademola *et al*., 2022; Kennis *et al*., 2012). Likewise, survival of small mammals including rodents have been found to vary with sex and age class (Eccard *et al*., 2002; Previtali *et al*., 2010).

In addition, both home range size and survival are important parameters influencing behavioral and ecological characteristics of small mammals. Home range measures the space an animal uses in a habitat that reflects the energy spent to acquire food or mates and the likelihood to encounter predation (Koshev *et al*., 2005; Flavicollis, 2006). In rodent community ecology, home ranges are important factors for species breeding activity, foraging, distribution and habitat selection (Aiken, 2019). Survival on the other hand, is related with reproductive fitness of an individual. The higher the survival rate the higher the chances of reproductive fitness and higher population size (Ademola *et al*., 2021). However, human activities like agricultural land preparation practices and deforestation affect rodent species home range, survival and distribution through habitat destruction and fragmentation, which reduces habitat area and resource availability (Gehring and Swihart, 2004; Lambert *et al*., 2006; Heinze *et al*., 2010; Greenberg *et al*., 2011). Fragmentation can result into extinction of species especially for those with restricted distribution range through inbreeding depression (Gehring and Swihart, 2004). For that case, understanding home range size and survival probability of rodents is crucial for conservation of endangered/vulnerable species which has restricted home range size and distribution in a particular habitat or ecosystem (Sabuni *et al*., 2015).

Generally, home range size (Monadjem and Perrin, 1998; Gebresilassie *et al*., 2006) and survival probabilities (Julliard, *et al*., 1999; Sluydts *et al*., 2007; Mulungu *et al*., 2016; Mlyashimbi *et al*., 2019; Mayamba *et al*., 2019; Ademola *et al*., 2021) of rodents have been well studied in east Africa. However, there is scanty information on home range size and survival of rodents from the genus *Lophuromys* and *Rhabdomys* (Schradin, 2009). As reported earlier two species *Lophuromys aquilus* and *Rhabdomys dilectus* are sympatric species predominating habitats of Mt Kilimanjaro (Thomas *et al*., 2022 a,b). Their home range size and survival probabilities and the factors affecting them have not been well documented. Also, the increasing rate of human activities in unprotected areas of Mount Kilimanjaro might be of great threat to their home range and survival. Therefore, this study was aimed to determine home range size of the two species, survival and capture probability and the influencing factors. We hypothesized that, home range and survival probability of the two species would vary across habitats and seasons, and with sex (Schradin and Pillay, 2006). It was expected that, home range and survival of species would markedly differ between males and females due to different requirements for reproduction and response to changes in resource availability like food, cover and mates (Schradin and Pillay, 2006).

## 5.2 Materials and methods

### 5.2.1 Trapping

Trapping was done using Capture-Mark-Recapture (CMR) technique following similar procedures described in Thomas *et al*. (2022b). Four live trapping grids; two in each of the moorland and fallow habitat were established at approximately 500 m apart. Each grid consisted of 49 traps placed in 7 lines each with 7 traps placed at 10 m trapping station. Traps were baited with peanut butter and inspected in next morning before 10:00 a.m. Trapping was done for three nights consecutively in each trapping session (month). The continuous monthly live trapping was commenced in April 2020 and terminated in March 2022 covering both dry and wet seasons. Trapped animals were marked by toe clipping which has been scientifically tested and found not to affect animal's behaviour (Borremans *et al*., 2015). Data on the date, trap station number, grid number, habitat type, toe clip code, weight, species, sex and sex condition of each trapped animal were recorded before it was released at the point of capture. Rodent species were identified in the field following Happold (2013) and confirmed with molecular technique. Traps were washed and packed for the next trapping session.

### 5.2.2 Data analysis

Sex was determined using distance between the anus and urogenital opening (shorter in females and longer in males) and presence of secondary sexual characteristics such as testis and nipples for males and females respectively (Searle, 1985; Kay and Hokestra, 2008). Rodents were grouped into two age classes: adults and juveniles. Age of an individual was determined based on body weight and maturation status (Kay and Hokestra, 2008; Kingdon, 2015). Maturation in adults was assessed through growth of secondary sexual characteristics in both males and females, which was evident during reproductive activity (Searle, 1985; Monadjem and Perrin, 2002).

### 5.2.3 Homer range size

Home range was estimated as the total area travelled in Minimum Convex Polygon (MCP) by individuals within five different relocations. AdehabitatHR package in R program (R Core Team, 2020) was used to estimate individual's home range as MCP at 95% of relocation points. Home ranges of only two species, *Lophuromys* and *Rhabdomys* were estimated because there were few relocations from CMR capture history of other species. Non-parametric Wilcoxon/Mann-Whitney test was used to determine differences in home range between species. Moreover, home range data of individual species were log transformed and simple linear models fitted to determine the relationship between home range the with respect to season, habitat, sex, and sex conditions, and the interactions between them. Two-way Anova was used to determine the differences in home range of individual species across habitats, seasons and sex.

### 5.2.4 Survival and capture probability

Survival was defined as the probability of individual rodents to survive/persist from one month to the next. It refers to mean length of time an individual persists in the grid/study site within a trapping session, usually assigned to 1 (Mayamba *et al*., 2019; Ademola *et al*., 2021). Survival expresses the occurrence of animals that are captured in one trap session and a subsequent one. Whereas the recapture probability is fully time and trap dependent as a result of trap awareness and unawareness behavior of individual rodents. Both survival and recapture probabilities were estimated for each trapping session according to Pollock’s closed robust design, in which the population is assumed to be closed within each trapping session and open between the trap sessions. Also, it is assumed that there is no immigration or emigration of individuals from the population.

Prior to analysis, goodness-of-fit (GOF) test was carried out with the U-CARE software (Pradel *et al*., 2003; Choquet *et al*., 2009a) to assess trap dependence and transience individuals (the ones trapped only once during the entire study period). GOF test followed the assumption on transience. It did not indicate any effect of trap dependence, meaning that recapture probability of individuals was independent of their previous capture (Pradel and Sanz-Aguilar, 2012).

### 5.2.5 Survival and capture probability modelling

Survival of the two species were modelled and estimated using the multi-event capture-recapture models in E-SURGE (Pradel, 2005; Choquet *et al*., 2009a,b; Lebreton and Pradel, 2002) in which the number of states might be greater than the number of events. The multi-event capture-recapture models incorporated detection heterogeneity into our models (Pradel and Sanz-Aguilar, 2012). For capture probability, modified methods of analysis by Sluydts *et al*. (2007), and Mayamba *et al*. (2019) were used. To minimize trap dependence, capture probability of the two species was varied between trap aware individuals (captured during the previous trap session), trap unaware individuals (not captured during the previous trap session) and dead/not captured individuals. Initially, over 20 different models were constructed to test whether survival and capture probabilities of the two species is different and if whether sex has a significant impact on the differences as conducted by Mlyashimbi *et al*. (2019), hence all the models that were run included species and sex (Table 5.1). In further analysis, survival and capture probabilities of individual species were allowed to vary between sex (male and female), season (dry and wet) and between habitats (moorland and fallow). Corrected Akaike information criterion (AICc) for smaller sample size was used for ranking the models and selection. Model with lowest AICc was considered as best fit (better describes distribution of data). Also, all models with a difference of delta AICc < 2.0 were considered equally good.

### 5.3 Ethical Considerations

A proposal to conduct this research was approved by postgraduate committee of Sokoine University of Agriculture SUA, Tanzania (Ref no: SUA/DPRTC/PFC/D/2019/0002/13). Registered and provided a permit (No: 2020-163-NA-2020-127) by the Tanzania Commission for Science and Technology (COSTECH) and by Tanzania Wildlife Research Institute (TAWIRI) to research on rodents. A permit to enter into Mount Kilimanjaro National Park was provided by Tanzania National Parks (TANAPA).

## 5.4 RESULTS

### 5.4.1 Home range size

In general, mean home range size was not significantly different between the species (Mann-Whitney U = 2292.5, p = 0.217) however, *Lophuromys aquilus* had a relatively larger mean home range size (842.06 $m^2$) than *Rhabdomys dilectus* (729.05 $m^2$).

For individual species analysis; home range size of *Rhabdomys dilectus* was influenced by the variations in habitat ($F_{1,\ 115}$ = 4.61, $p$ = 0.034, $R^2$ = 0.03). Mean home range significantly differed between habitats, as it was significantly larger in moorland than in fallow habitat (Estimate, SE, P-value) (0.30 ± 0.14, $p$ = 0.034). Moreover, home range was significantly influenced by the interaction between habitats and seasons ($F_{3,\ 113}$ = 2.95, $p$ = 0.04, $R^2$ = 0.05). Whereby, mean home range significantly decreased (-0.66 ± 0.27, $p$ = 0.01) during wet season in moorland habitat.

Linear regression modeling indicated that, home range size of *Lophuromys aquilus* was influenced by habitats ($p$ = 0.001), season ($p$ = 0.062) and sex ($p$ = 0.16) ($F_{3,\ 65}$ = 6.22, $p$ = 0.0, $R^2$ = 0.19). Moreover, mean home range significantly differed between habitats, whereby, it was significantly larger in moorland than in fallow habitat (0.73 ± 0.2, *p* < 0.001). Mean home range did not differ significantly between season and sex; however, male's home range size was relatively larger than that of females (0.28 ± 0.16, *p* = 0.09). Also, mean home range was relatively larger during wet season (0.25 ± 0.16, *p* = 0.12) (Figure 5.1)

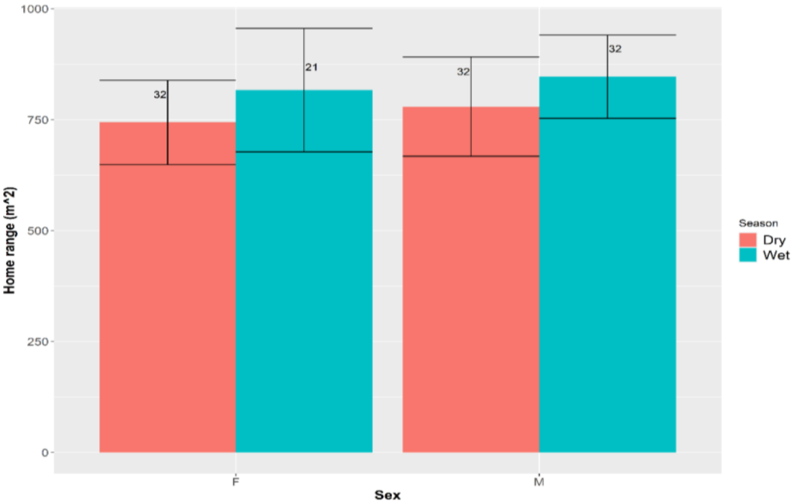

**Figure 5.1: Variations in mean home range size of *Lophuromys aquilus* between males (M) and females (F) across seasons**

### 5.4.2 Survival Probability

Comparatively, the best model indicated that survival probability was influenced by species and sex, whereas capture probability was influenced by species (Table 5.1). Also, the next best models which were well supported with (Delta AICc less than 2) indicated that survival probability was influenced by species and sex (Table 5.1).

There were significant differences in survival probability between the species. Survival probability of *Lophuromys aquilus* was significantly higher than that of *Rhabdomys dilectus* (Figure 5.2). However, there were no significant differences between sex, the survival of females of both species was relatively higher than that of males, (Mean, SE) 0.486 ± 0.031 for female *Rhabdomys dilectus* and 0.713 ± 0.235 for female *Lophuromys aquilus* (Figure 5.2). In addition, survival probability of both species (*L. aquilus* and *R. dilectus*) was significantly influenced by the variation in season when their capture probability was varied with time (Tables 5.2a and 5.2b).

**Table 5.1:** The candidate models used to estimate survival of the two species. Survival estimates (Phi) and recapture probabilities (p) of the two species were modelled with respect to time and sex (male or female). Table columns includes number of parameters (df), AICc Corrected Akaike Information Criterion due to small sample size and Delta Δ AICc, model weight and Deviance.

**Table 5.1: The candidate models used to estimate survival of the two species**

| SN | Model | df | AICc | ΔAICc | Weight | Deviance |
|---|---|---|---|---|---|---|
| 16 | Phi(~spec + sex)p(~spec) | 5 | 1947.472 | **0** | 3.27E-01 | 1937.472 |
| 12 | Phi(~spec)p(~spec) | 4 | 1948.204 | **0.732** | 2.27E-01 | 1940.204 |
| 10 | Phi(~spec)p(~spec + sex) | 5 | 1949.15 | **1.676** | 1.41E-01 | 1939.148 |
| 14 | Phi(~spec + sex)p(~spec + sex) | 6 | 1949.306 | **1.833** | 1.31E-01 | 1937.306 |
| 20 | Phi(~spec * sex)p(~spec) | 6 | 1949.434 | **1.962** | 1.23E-01 | 1937.256 |
| 18 | Phi(~spec*sex)p(~spec + sex) | 7 | 1951.256 | 3.783 | 4.93E-02 | 1937.256 |
| 28 | Phi(~time+spec)p(~spec) | 22 | 1958.554 | 11.081 | 1.28E-03 | 1914.55 |
| 26 | Phi(~time+spec)p(~spec + sex) | 23 | 1959.8 | 12.327 | 6.88E-04 | 1913.8 |
| 13 | Phi(~spec + sex)p(~1) | 4 | 1962.458 | 14.985 | 1.82E-04 | 1954.458 |
| 9 | Phi(~spec)p(~1) | 3 | 1963.145 | 15.673 | 1.29E-04 | 1957.145 |
| 17 | Phi(~spec*sex)p(~1) | 5 | 1964.427 | 16.954 | 6.80E-05 | 1954.427 |
| 15 | Phi(~spec +sex)p(~sex) | 5 | 1964.437 | 16.965 | 6.77E-05 | 1954.437 |
| 11 | Phi(~spec)p(~sex) | 4 | 1964.488 | 17.015 | 6.60E-05 | 1956.488 |
| 19 | Phi(~spec*sex)p(~sex) | 6 | 1966.408 | 18.936 | 2.53E-05 | 1954.408 |
| 32 | Phi(~time *spec)p(~spec) | 40 | 1972.824 | 25.352 | 1.02E-06 | 1892.824 |
| 25 | Phi(~time + spec)p(~1) | 21 | 1973.38 | 25.907 | 7.74E-07 | 1931.38 |

| SN | Model | df | AICc | ΔAICc | Weight | Deviance |
|---|---|---|---|---|---|---|
| 30 | Phi(~time *spec)p(~spec+ sex) | 41 | 1974.036 | 26.563 | 5.60E-07 | 1892.036 |
| 27 | Phi(~time + spec)p(~sex) | 22 | 1974.981 | 27.508 | 3.50E-07 | 1930.981 |
| 29 | Phi(~time*spec)p(~1) | 39 | 1987.722 | 40.25 | 5.95E-10 | 1909.722 |
| 31 | Phi(~time*spec)p(~sex) | 40 | 1989.226 | 41.753 | 2.80E-10 | 1909.226 |
| 5 | Phi(~sex)p(~1) | 3 | 1992.151 | 44.679 | 6.50E-11 | 1989.151 |
| 8 | Phi(~sex)p(~spec) | 4 | 1993.111 | 45.638 | 4.02E-11 | 1985.111 |
| 7 | Phi(~sex)p(~sex) | 4 | 1994.116 | 46.644 | 2.43E-11 | 1986.116 |
| 1 | Phi(~1)p(~1) | 2 | 1994.979 | 47.507 | 1.58E-11 | 1990.979 |
| 6 | Phi(~sex)p(~spec + sex) | 5 | 1995.054 | 47.582 | 1.52E-11 | 1985.054 |
| 3 | Phi(~1)p(~sex) | 3 | 1995.742 | 48.269 | 1.07E-11 | 1989.742 |
| 4 | Phi(~1)p(~spec) | 3 | 1996.168 | 48.695 | 8.72E-12 | 1990.168 |
| 2 | Phi(~1)p(~spec + sex) | 4 | 1996.815 | 49.342 | 6.31E-12 | 1988.815 |
| 21 | Phi(~time)p(~1) | 20 | 2005.238 | 57.766 | 9.35E-14 | 1965.238 |
| 24 | Phi(~time)p(~spec) | 21 | 2006.287 | 58.815 | 5.54E-14 | 1964.287 |
| 23 | Phi(~time)p(~sex) | 21 | 2006.291 | 58.818 | 5.52E-14 | 1964.291 |
| 22 | Phi(~time)p(~spec +sex) | 22 | 2007.215 | 59.742 | 3.48E-14 | 1963.215 |

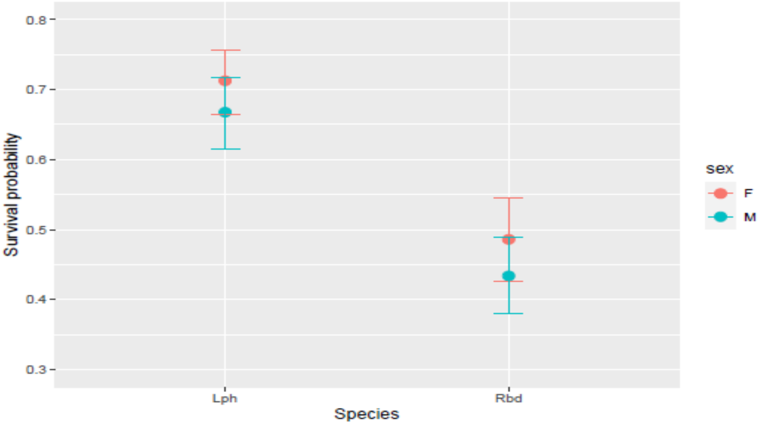

**Figure 5.2: Survival probability between the species (Lph = *Lophuromys aquilus* and Rbd = *Rhabdomys dilectus*) and sex (F = female, M = male)**

### 5.4.3 Capture probability

Capture probability differed between the two species when it was varied by time (Table 5.2a, 5.2b). Whereby, capture probability of *Rhabdomys* was significantly higher than that of (Figure 5.3). It was (Mean, SE) 429 + 0.03 for *Lophuromys aquilus* and 0.655 + 0.045 for *Rhabdomys dilectus* (Figure 5.3).

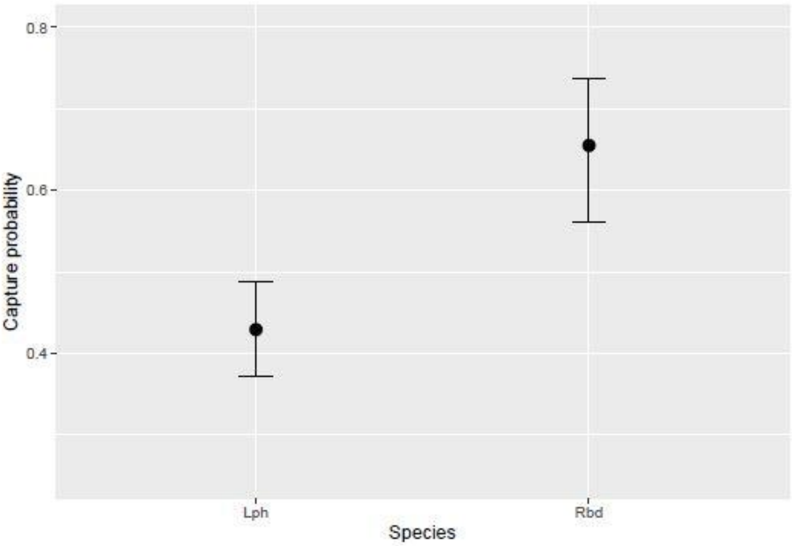

**Figure 5.3: Capture probability between species (Lph = *Lophuromys aquilus*, Rbd = *Rhabdomys dilectus*).**

**Tables (5.2a and 5.2b):** The candidate models used to estimate survival (Phi) and recapture (P) probabilities of *Rhabdomys dilectus* (5.2a) and *Lophuromys aquilus* (5.2b) were modelled with respect to time, sex (male or female), habitat type (moorland and fallow) and season (dry and wet). Table columns includes number of parameters (df), AICc Corrected Akaike Information Criterion, Delta Δ AICc, model weight and Deviance.

**Table 5.2a and 5.2b: The candidate models used to estimate survival (Phi) and recapture (P) probabilities of *Rhabdomys dilectus* (5.2a) and *Lophuromys aquilus* (5.2b) with respect to time, sex (male or female), habitat type (moorland and fallow) and season (dry and wet).**

**5.2a**

| SN | Model | df | AICc | Δ AICc | Weight | Deviance |
|---|---|---|---|---|---|---|
| 5 | Phi(~season)p(~1) | 3 | 1896.999 | 0 | 0.276 | 1890.98 |
| 7 | Phi(~sex)p(~1) | 3 | 1896.999 | 0 | 0.276 | 1890.96 |
| 6 | Phi(~season)p(~time) | 4 | 1898.282 | 1.283 | 0.145 | 1890.216 |
| 8 | Phi(~sex)p(~time) | 4 | 1898.282 | 1.283 | 0.145 | 1890.216 |
| 1 | Phi(~1)p(~1) | 2 | 1900.789 | 3.789 | 0.042 | 1896.769 |
| 3 | Phi(~habitat)p(~1) | 6 | 1901.155 | 4.156 | 0.035 | 1889.016 |
| 9 | Phi(~sex*season)p(~1) | 6 | 1901.509 | 4.509 | 0.029 | 1889.37 |
| 2 | Phi(~1)p(~time) | 3 | 1902.002 | 5.003 | 0.023 | 1895.962 |
| 4 | Phi(~habitat)p(~time) | 7 | 1902.729 | 5.729 | 0.016 | 1888.544 |
| 10 | Phi(~sex*season)p(~time) | 7 | 1903.094 | 6.095 | 0.013 | 1888.909 |

**5.2b**

| SN | Model | df | AICc | Δ AICc | Weight | Deviance |
|---|---|---|---|---|---|---|
| 1 | Phi(~1)p(~1) | 2 | 1499.966 | 0 | 0.311 | 1495.935 |
| 2 | Phi(~1)p(~time) | 3 | 1501.007 | 1.041 | 0.185 | 1494.946 |
| 5 | Phi(season)p(~1) | 3 | 1501.544 | 1.578 | 0.141 | 1495.483 |
| 7 | Phi(~sex)p(~1) | 3 | 1501.544 | 1.578 | 0.141 | 1495.483 |
| 6 | Phi(~season)p(~time) | 4 | 1502.604 | 2.638 | 0.083 | 1494.501 |
| 8 | Phi(sex)p(~time) | 4 | 1502.604 | 2.638 | 0.0831 | 1494.501 |
| 3 | Phi(habitat)p(~1) | 6 | 1505.179 | 5.213 | 0.023 | 1492.963 |
| 9 | Phi(sex*season)p(~1) | 6 | 1506.299 | 6.334 | 0.013 | 1494.083 |
| 4 | Phi(~habitat)p(~time) | 7 | 1506.4 | 6.434 | 0.012 | 1492.111 |
| 10 | Phi(~sex*season)p(~time) | 7 | 1507.501 | 7.535 | 0.007 | 1493.212 |

## 5.5 DISCUSSION

### 5.5.1 Home range size

A non-significant difference in home range size of *Lophuromys aquilus* and *Rhabdomys dilectus* indicate that the two species have overlapping home ranges and sharing of resources. Larger home range of *L. aquilus* than *R.dilectus* suggest higher accessibility to food resources and varieties, which support its generalists/opportunistic behavior. Our results support findings by Thomas *et al*. (2022a) which reported an overlap in niche breadth among the two species due to sharing of food resources. Moreover, home range size of *Lophuromys aquilus* differed between sex and season. Males had relatively larger home range size compared to females (however not significant), probably because males move longer distances especially during wet season to search for mates (Mulungu *et al*., 2013; Cooney *et al*., 2015). Unlike females who spend most of their time in the nests to nurture for the juveniles. Our findings coincide with other studies which reported significant differences in home range sizes between males and females, whereby, males moved longer distances to maximize chances of meeting sexually active females (Kennis *et al*., 2012; Borremans *et al*., 2014; Leirs *et al*., 1997). However, the results contradict those of Mlyashimbi *et al*. (2019), which reported large home range size in female *Mastomys* during breeding season due to high food requirements for reproduction.

Home range size of both species significantly differed across habitats probably due to vegetation structure and climate variability in the two habitats. Larger home range sizes of both species in moorland could be attributed to poor vegetation (ground cover) which affects food availability. Similarly, Gebresilassie *et al*. (2006) suggested that rodents have larger home ranges in habitats with limited food resources to maximize search for food to meet body requirements. Whereas small home ranges in fallow was probably due to dense vegetation and ground cover which provide food and protection from predators. Also, it could be due to crop remains from surrounding agricultural fields. Fallows are said to serve as refuge to rodents inhabiting farm-fallow mosaics, providing them with supplementary food and breeding sites (Mulungu *et al*., 2013; 2016).

In addition, seasonality has been reported as the major factor influencing home ranges of small mammals including rodents as it affects vegetation structure and food availability (Powell and Mitchell, 2012; Cooney *et al*., 2015). In most cases rodents tend to have smaller home ranges during wet season when food is abundant than in dry season when food is limited (Schradin and Pillay, 2006). Interestingly, in this study home range size of *Rhabdomys* significantly decreased during wet season (especially in the moorland) whilst that of *L. aquilus* relatively increased during wet season. An interaction between seasonality and habitat explains the variation and inconsistence in home range size between the two species in both dry and wet season. Extremely cold temperatures in moorland and behavioral adaptation of the species could be the possible explanation for a significant decrease in home range of *R. dilectus* and an increase in home range of *L. aquilus*. Cold temperatures during wet season affects movements and activity patterns of *R. dilectus* (Clausnitzer, *et al*., 2003) unlike for *L. aquilus* which prefers wet conditions and is actively moving during wet season (Happold, 2013; Kingdon, 2015).

### 5.5.2 Survival and capture probabilities

In the current study, best models for comparative and individual species analysis included species, sex, and season, indicating that survival and capture probabilities varies between species, sex and season. *Lophuromys aquilus* had higher survival probability but lower capture probability. Whilst *Rhabdomys dilectus* had lower survival probability but higher capture probability. Higher survival of the latter indicates that *L. aquilus* is a habitat generalist that is more adapted across a range of habitats and altitudinal gradients which is evident from its distribution on Mt Kilimanjaro and elsewhere (Clausnitzer *et al*., 2003; Banthiun and Bekele 2015; Thomas *et al*., 2022b). *Lophuromys* species are reported to colonize disturbed and less suitable habitats and are opportunistically able to utilize resources in vicinity because of human disturbance (Happold, 2013; Gitonga *et al*., 2015; Monadjem *et al*., 2015). Similarly, Ademola *et al*. (2021) reported high survival rate of *praomys delectorum* in disturbed forest due to high food resources because of anthropogenic disturbance. High survival probability improves individual's fitness through successful reproduction which results into stable populations (Ademola *et al*., 2021; Mulungu *et al*., 2016 & 2013;). Hence, survival is a vital component and an important factor that influences rodent population size (Mulungu *et al*., 2016; Mlyashimbi *et al*., 2019). Moreover, it is reported that, rodent population size is directly dependent on rain fall patterns (Leirs *et al*., 1994), also, rodent breeding occurs during rainy season when conditions are suitable (Mulungu *et al*. 2013). For that case, rodents' survival is higher in high quality habitats which has stable conditions and high food resources than in poor quality habitats (Kennis *et al*., 2012). Moreover, low survival probability of *Rhabdomys dilectus* especially during wet season was probably due to variations in breeding and population size which are highly influenced by seasonality. Moreover, the lower survival probability could be due to high predation risk since the species is moderately associated with ground cover and preferably inhabits patchy grasses which exposes it to predation (Schradin and Pillay, 2006; Clausnitzer *et al*., 2003). Despite that information, low capture probability of *L. aquilus* and high capture probability of *R. dilectus* suggests that the former could be a trap shy species whilst the latter is a trap loving species.

In addition, the higher survival rate of the females of both species was probably due to the differences in time and energy invested in reproduction between the two sexes. Females spend most of their time inside the nests nurturing for their newborn juveniles, hence encounter less chances of predation (Norrdahl and Korpimäki, 1998) and mortality from extreme harsh weather conditions (Clausnitzer *et al*., 2003). However, our findings are contrary to Oli and Dobson, (1999) which found lower survival of females compared to males due to post-natal stress, as it is suggested that, female's reproduction success depends on spatial-temporal availability and distribution of food resources (Ostfeld, 1985).

## 5.6 Conclusion and Recommendations

Home range size and survival are important demographic parameters that influences rodent population fluctuations and viability. Our study indicated that, home range and survival varied between the species whereby *Lophuromys aquilus* had larger home range and higher survival probability than *Rhabdomys dilectus*. Moreover, home range size and survival probabilities of the two species were influenced by habitat type, season, and sex. Male *Lophuromys aquilus* had larger home range size and lower survival rates than females. The study results suggest that distinct vegetation structure and climate variability between the habitats could have played a great role on influencing home range size and survival probability of the two species through food availability and protection from predators which in turn influence rodent movements, reproduction and population size.

From the current study, larger home range size and higher survival probability of *L. aquilus* than that of *R. dilectus*, may indicate the former is well adapted on Mt Kilimanjaro. However, the current study could not provide clear proof of other reasons behind its high survival. Despite of the large home range size and high survival probability of *L. aquilus*, its conservation status still remains uncertain. The species could be threatened from anthropogenic activities which result into habitat destruction and fragmentation. Therefore, further studies on behavioral adaptations of the species are highly recommended.

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### 5.8 Author’s contribution

Suzana Thomas, Loth S Mulungu and Geofrey Soka designed the ideas and the methodology. Suzana Thomas collected the data. Thomas and Vincent Slyudts analysed the data. Geofrey Soka supervised and reviewed the work.

### 5.9 Conflict of Interest Statement

Authors declare no conflicting interests among themselves.

## 5.10 Data accessibility statement

Authors agree to provide the data associated with this study upon request once the manuscript is accepted for publication.

## References

Ademola, O. J., Vanden Broecke, B., Leirs, H., Massawe, A. W., Mulungu, L. S., and Makundi, R. H. (2021). Effects of forest disturbance on the fitness of an endemic rodent in a biodiversity hotspot. *Ecology and Evolution*, *11*(5), 2391–2401.

Aiken, K. (2019). Personality in Small Mammals: From Home Range to Microhabitat Selection. https://digitalcommons.library.umaine.edu/honors/494

Borremans, B., Hughes, N.K., Reijniers, J., Sluydts, V., Katakweba, A.A.S., Mulungu, L.S., Sabuni, C.A., Makundi, R.H. and Leirs, H. (2014) Happily together forever: temporal variation in spatial patterns and complete lack of territoriality in a promiscuous rodent. Popul. Ecol. 56, 109–118.

Borremans, B., Sluydts, V., Makundi, R. H., and Leirs, H. (2015). Evaluation of short-, mid- and long-term effects of toe clipping on a wild rodent. *Wildlife Research*, 42: 143–148.

Burt, W. H. (1943) Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*. 24:346–352.

Cooney, S. A., Schauber, E. M. and Hellgren, E. (2015). Ranging Behavior of Marsh Rice Rats in a Southern Illinois Wetland Complex. *Journal of*

*Mammalogy* 96, No. 4: 732-741. doi:10.1093/jmammal/gyv069.

Choquet, R., Lebreton, J.-D., Gimenez, O., Reboulet, A.-M., and Pradel, R. (2009a). U-CARE: Utilities for performing goodness of fit tests and manipulating CApture REcapture data. *Ecography*, 32(6): 1071–1074. https://doi.org/10.1111/j.1600-0587.2009.05968.

Choquet, R., Rouan, L., and Pradel, R. (2009b). Program E-Surge: A Software Application for Fitting Multievent Models. In D. L. Thomson, E. G. Cooch, and M. J. Conroy (Eds.): *Modeling Demographic Processes In Marked Populations* (pp. 845–865). https://doi.org/10.1007/978-0-387-78151-8_39

Chuyong, G. B., Kenfack, D., Kyle E. Harms, K. E., Thomas, D. W., Condit, R., Comita, L. S. (2011). Habitat specificity and diversity of tree species in an African wet tropical forest. Journal of Plant Ecology: 212:1363–1374.

Eccard, J. A., Klemme, I., Horne, T. J., and Hannu, Y. (2002). Effects of competition and season on survival and maturation of young bank vole females. *Evolutionary Ecology*, 16: 85–99. https://doi.org/10.1023/A

Fieberg, J. and Kochanny, C.O. (2005) Quantifying home-range overlap: the importance of the utilization distribution. *Journal of Wildlife Management*, 69, 1346–1359.

Flavicollis, O. A. (2006). Spatial organization and home range of Apodemus flavicollis and A. agrarius on Mt. Avala, Serbia. *Acta Zoologica Academiae Scientiarum Hungaricae*, *52*(1), 81-96.

Gebresilassie, W., Bekele, A., Belay, G. and Balakrishnan, M. (2006). Home Range and Reproduction of Rodents in Maynugus Irrigation Field, Northern Ethiopia. Ethiopian Journal of Science. 29(1):57–62.

Gehring, T. M., and Swihart R. K. (2004). Home Range and Movements of Long-Tailed Weasels in a Landscape Fragmented by Agriculture. *Journal of Mammalogy*, 85(1):79–86, 2004.

Gitonga, J., Simbauni, J., and Oguge, N. (2015). Effect of habitat fragmentation on food habits and gastrointestinal tract of Praomys delectorum sub-populations in the Taita and Kyulu hills , Kenya. *International Journal of Current Research*, 4(1): 63–72.

Greenberg, C. H., Perry, R. W., Harper, C. A., Levey, D. J., and Mccord, J. M. (2011). The role of young, recently disturbed upland hardwood forest as high quality food patches. In C. H. Greenberg, B. Collins, and F. Thompson III (Eds.): *Sustaining young forest communities*: *ecology and management of early successional habitats in the Central Hardwood Region, USA.* pp. 121–141. https://doi.org/10.1007/978-94-007-1620-9

Happold, D. C. D. (Ed.). (2013). *Mammals of Africa. Volume III: Rodents, Hares and Rabbits.* London, United Kingdom: Bloomsbury Publishing, London. 784pp.

Heinze, E., Boch, S., Fischer, M. Müller, J., Prati, D., Socher, S., Kalko, E. K. V. and Halle, S.Halle, S. (2010). Large Scale Monitoring of Small Mammals in Relation to Different Land Use Types and Habitat Structure. In: Distribution and Habitat Use of Selected Small and Large

Mammal Species in Relation to Different Land Use. Dissertation for Award of PhD Degree at Institute of Ecology, Friedrich Schiller University, Jena, Germany. 100pp.

Julliard, R., Leirs, H., Chr, N., Yoccoz, N. G., Caroline, A., Vot, P. R. E., Julliard, R., Leirs, H., Chr, N., Yoccoz, N.G., Caroline, A., Vot, P.R.E., Verhagen, R.O.N. and Verheyen, W. (1999). Survival-variation within and between functional categories of the African multimammate rat. *Journal of Animal Ecology*, 68: 550–561.

Kay, E.H. and Hoekstra, H.E., 2008. Rodents. *Current Biology*, *18*(10), pp.R406-R410.

Kennis, J., Laurent, C., Amundala, N. D., Migimiru, A., and Leirs, H. (2012). Survival and movement of the Congo forest mouse (Deomys ferrugineus): a comparison of primary rainforest and fallow in Kisangani, Democratic Republic of Congo. *African Zoology*, 47(1): 147–159. https://doi.org/10.1080/15627020.2012.11407533.

Kingdom, J. (2015). *The Kingdon Field Guide to African Mammals*. Second Edition. Bloomsbury Publishing Plc, 50 Bedford Square London WC1B 3DP. 640pp.

Koshev, Y., Atanassov, N. and Kocheva, M. (2005). Relation between Body Mass and Home Range Size of Small Mammals. Proceedings of the Balkan Scientific Conference of Biology in Plovdiv (Bulgaria) from 19 – 21 May, 2005 (Eds B. Gruev, M. Nikolova And A. Donev), 2005 (P. 437–444).

Lambert, T. D., Malcom, J. R., and Zimmerman, B. L. (2006). Amazonian small mammal abundances in relation to habitat structure and resource abundance. *Journal of Mammalogy*, 87(4): 766–776.

Lee, E. and Rhim, S. (2016). Seasonal home ranges and activity of three rodent species in a post-fire planted stand. *Journal of Folia Zooligica*. 65(2): 101- 106.

Leirs, H., Stenseth, N. C., Nichols, J. D., Hines, J. E., Verhagen, R., and Verheyen, W. (1997). Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent. *Nature*, 389(September): 176–180.

Leirs, Herwig, Verhagen, R., and Verheyen, W. (1994). The basis of reproductive seasonality in Mastomys rats (Rodentia: Muridae) in Tanzania. *Journal of Tropical Ecology*, 10: 55–66.

Massawe, A. W., Rwamugira, W., Leirs, H., Makundi, R., and Mulungu, L.S., (2005). Influence of land preparation methods and vegetation cover on population abundance of *Mastomys natalensis* in Morogoro, Tanzania. *Journal of Belgium Zoology*: 135: 187-190.

Mayamba, A., Broecke, B. Vanden, Leirs, H., Isabirye, B. E., Byamungu, R. M., Nakiyemba, A., … Crescent, L. V. (2019). Fitness of the pestiferous small rodent Mastomys natalensis in an agroecosystem in Mayuge district, Lake Victoria Crescent, Uganda. *Mammalia*, 1–10.

Mlyashimbi E.C.M., B. Vanden Broecke, J. Mariën[3], D.N. Kimaro, A.J.P. Tarimo, R.S. Machang'u, M. Isabirye, R.H. Makundi A.W. Massawe, P. Hieronimo, D. Kifumba, H. Leirs, M.E. Mdangi, S.R. Belmain, L.S. Mulungu (2019) Influences of soil types on the population dynamics and survival of Multimammate rat (*Mastomys natalensis*, Smith 1832) in semi-arid areas in Tanzania. *Crop Protection*, 124:104829. https://doi.org/10.1016/j.cropro.2019.05.023.

Monadjem A. and Perrin, M. (2002). Population fluctuations and community structure of small mammals in a Swaziland grassland over a three-year period. *African Zoology* 38(1): 127–137.

Monadjem, A. and Perrin, M. (1998). The effect of supplementary food on the home range of the multi-mammate mouse Mastomys natalensis. S. Afr. J. Wildl. Res. 28, 1–3.

Monadjem, A., Taylor, P. J., Denys, C., and Cotterill, F. P. D. (2015). *Rodents of Sub-Saharan Africa. A biogeographic and taxonomic synthesis*. Berlin/Munich/Boston: Walter de Gruyter.

Morris, G., Hostetler, J. A., Conner, L. M., and Oli, L. K. (2011). Effects of prescribed fire, supplemental feeding and mammalian predator exclusion on hispid cotton rat populations. *Oecologia* 167:1005-1016. DOI 10.1007/s00442-011-2053-6.

Mulungu, L. S., Mahlaba, T., Massawe, A. W., Kennis, J., Crauwels, D., Eiseb, S., Monadjem, A., Makundi, R. H., Katakweba, A.S., Leirs, H., and Belmain, S. (2011). Dietary differences of the multimammate mouse, *Mastomys natalensis* (Smith, 1834), across different habitats and seasons in Tanzania and Swaziland. *Journal of Wildlife Research*. 38: 640–646.

Mulungu, L.S., Ngowo, V., Mdangi, M., Katakweba, A. S., Tesha, P., Mrosso, P., Mchomvu, M., Sheyo, P., and Kilonzo, B. S., (2013). Population dynamics and breeding patterns of multimammate mouse, *Mastomys natalensis* (Smith 1834), in irrigated rice fields in Eastern Tanzania. *Pest Management Science* 69, 371–377.

Mulungu, L. S., Ngowo, V., Mdangi, M. E., Katakweba, A. S., Tesha, P., Mrosso, F. P. and Belmain, S. R. (2016). Survival and recruitment of the multimammate mouse, Mastomys natalensis (Smith 1834), in a rice agro ecosystem. *Mammalia*, *80*(2), 205-210. doi:10.1515/mammalia-2014-0150.

Norrdahl, K., and Korpimaki, E. (1998). Does mobility or sex of voles affect risk of predation by mammalian predators? *Ecology*, 79(1): 226–232.

Ogada, D., Kerbis. J., and Agwanda, B. (2009). Preliminary report of shrews and rodents

in and around Lake Bogoria National Reserve, Kenya. *Journal of East African Natural History* 98(1): 129–139.

Oli, M. K., and Dobson, F. S. (1999). Population cycles in small mammals: the role of age at sexual maturity. *OIKOS*, (86): 557–565.

Ostfeld, R. S. (1985). Limiting resources and territoriality in microtine rodents. *The American Naturalist*, 126(1): 1–15.

Lebreton, J.D., Pradel, R., 2002. Multistate recapture models: modelling incomplete individual histories. J. Appl. Stat. 29 (1–4), 353–369.

Powell, R. (2000). Animal home range and territories and home range estimators. Research Techniques in Animal Ecology. Controversies and Consequences. Columbia University Press.

Powell, R. A. and Mitchell, S. M. (2012). What is home range? *Journal of Mammalogy*, 93(4):948–958, 2012. DOI: 10.1644/11-MAMM-S-177.

Pradel, R., Wintrebert, C. M. A., and Gimenez, O. (2003). A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture-recapture model. *Biometrics*, 59(1): 43–53.

Pradel, R. (2005). Multievent: An Extension of Multistate Capture-Recapture Models to Uncertain States. *Biometrics*, 61(2): 442–447. https://doi.org/10.1111/j.1541-0420.2005.00318.x.

Pradel, R., and Sanz-Aguilar, A. (2012). Modeling Trap-Awareness and Related Phenomena in Capture-Recapture Studies. *PLoS ONE*, 7(3): 1–4. https://doi.org/10.1371/journal.pone.0032666.

Previtali, M. A., Lehmer, E. M., Pearce-Duvet, J. M. C., Jones, J. D., Clay, C. A., Wood, B. A., Ely, P.W., Laverty, S.M. and Dearing, D. M. (2010). Roles of human disturbance, precipitation, and a pathogen on the survival and reproductive probabilities of deer mice. *Ecology*, 91(2): 582–592.

Sabuni, C. A., Sluydts, V., Mulungu, L. S., Maganga, S. L., Makundi, R. H., and Leirs, H. (2015). Distribution and ecology of lesser pouched rat, Beamys hindei, in Tanzanian coastal forests. *Integrative Zoology*, *10*(6), 531-542.

Schmidt, N. M., Berg, T. B., Jensen, T. S. (2002). The Influence of Body Mass on Daily Movement nd Home Range of the Collared Lemming (*Dicrostonyx Groenlandicus*). *Canadian Journal of Zoology*. 80: 64-69.

Schradin, C. and Pillay, N. (2006) Female striped mice (*Rhabdomys* pumilio) change their home ranges in response to seasonal variation in food availability. *Behav. Ecol.*, *17*, 452–458. https://doi.org/10.1093/beheco/arj047.

Schradin, C., Schneider, C., and Yuen, C. H. (2009). Age at puberty in male African striped mice: the impact of food, population density and the presence of the father. *Functional Ecology*, *23*(5), 1004-1013.

Searle, J.B., 1985. Methods for determining the sex of common shrews (Sorex araneus). *Journal of Zoology*, *206*(2), pp.279-282.

Shilereyo, M., Magige, F. J., Ogutu, J. O., and Røskaft, E. (2020). Small mammal community demography and reproductive seasonality under protection, pastoralism and agriculture in the Serengeti Ecosystem, Tanzania. *International Journal of Biodiversity and Conservation*, *12*(4), 253-269.

Sluydts, V., Crespin, L., Davis, S. and Lima, M. (2007). Survival and maturation rates of the African rodent, Mastomys natalensis: density-dependence and rainfall. *Integrative Zoology*, 2: 220–232. https://doi.org/10.1111/j.1749-4877.2007.00065.x.

Thomas, S.M., Soka, G.E., Mulungu, L.S. and Makonda, F.B. (2022a). Spatial-Temporal Variations in Dietary Consumption of Two Dominant Rodent Species (*Rhabdomys dilectus* and *Lophuromys aquilus*) on Mount Kilimanjaro, Tanzania. *Diversity*, *14*(8), p.659.

Thomas, S.M., Soka, G.E. and Mulungu, L.S. (2022b). Influence of vegetation structure, seasonality, and soil properties on rodent diversity and community assemblages in west Mount Kilimanjaro, Tanzania. *Ecology and Evolution*, *12*(9), p.e9211. 10.22541/au.163842979.99861775/v1.

Torre Corominas, I. (2004). Distribution, population dynamics and habitat selection of small mammals in Mediterranean environments: the role of climate, vegetation structure, and predation risk. A PhD thesis submitted at the Department of Animal Biology, Universitat de Barcelona, Spain. 178pp.

Verheyen, W. N., Hulselmans Jan, L. J., Dierckx, T., Mulungu, L., Leirs, H., Corti, M., and Verheyen, E. (2007). The characterization of the Kilimanjaro *Lophuromys aquilus* true 1892 population and description of five new *Lophuromys* species (Rodentia, Muridae). *Bulletin L'Insitut Royal des Sciences Naturalles de Belgique, Biologie*, *77*, 23–75.

# 6.0 CHAPTER SIX

# GENERAL DISCUSSION

## General Discussion

First and foremost, large number of rodent species (more than fourteen) and *Crocidura* spp were recorded in high abundance. *Rhabdomys dilectus, Praomys delectorum* and *Lophuromys aquilus* were the most abundant species comprising 69.35% of the total rodents, however percentage composition of other species did not differ across habitats and seasons. *Pelomys fallax* (not previously reported) had least composition hence termed as a rare species (Mlyashimbi *et al*., 2019). In addition, *Lophuromys aquilus* was the only endemic rodent reported in this study (Verheyen *et al.,* 2007). It occurred across all habitats suggesting that it is a habitat generalist (Mulungu *et al*., 2008; Happold, 2013; Bantihun and Bekele, 2015). On the other hand, *Praomys delectorum* predominated montane forests indicating that it is a forest specialist. *Rhabdomys dilectus* predominated agricultural fields and moorland but its occurrence was restricted from montane forest. This observation could be due to its preference on sparse grasses with drier conditions (Clausnitzer *et al*., 2001), whilst montane forests have dense canopy and are mostly wet. *Mastomys natalensis* predominated agricultural fields because it is the most common crop pest and an opportunistic species mostly associated with human disturbances (Mulungu *et al*., 2013).

Nonetheless, rodent species richness and abundance were influenced differently by the variations in vegetation structure, seasonality, and soil properties such as texture and bulk density. Rodent abundance and richness were highest in fallow and montane forest and lowest in agricultural fields and plantation forests. High richness, abundance and diversity in fallows was attributed to high vegetation density and ground cover which provides food and shelter (Mulungu *et al*., 2011b). Fallows (interspersed between agricultural fields and plantation forest) were more heterogeneous with dense vegetation and canopy cover providing niches to many species (Cramer and Willig, 2002; Makundi *et al*., 2003). Also, montane forests were characterized by dense vegetation, high canopy cover with high diversity of plant species, hence, ensures high richness of food resources and maintains microclimate suitable for forest specialists (Kisingo *et al*., 2005). Also, species richness was influenced by seasonality and soil bulk density as well as soil type. Clay and loamy soils had higher abundance than sandy and volcanic ash soils of Mt Kilimanjaro, probably due to good structure of clay soils which does not collapse easily (Nanzyo *et al*., 1993; Massawe *et al*., 2008). Also, it showed that over all distributuion abundance of rodents on Mt. Kilimanjaro is Hump shaped, increasing towards the middle, where it peaks and dcreasing afterwards (Mulungu *et al*., 2008).

Moreover, this study has identified two distinct rodent communities on Mt. Kilimanjaro. The first one is the habitat generalist community predominated by *Rhabdomys dilectus*, *Lophuromys aquilus* and *Mastomys natalensis* mainly occurring in fallows, agricultural fields and plantation forest. Whereas the second one was habitat specialist community predominated by *Praomys delectorum*, *Graphiurus murinus* and *Grammomys dolichurus* occurring in montane forest. Occurrence of the two communities indicate that community assemblage reflects species response to variations in habitat type and vegetation structure (rodent-habitat association) (Cramer and Willig, 2002; Bantihun and Bekele, 2015).

Being the first study on Mt Kilimanjaro, to investigate and shed light on dietary variations and resource partitioning of *Lophuromys aquilus* and *Rhabdomys dilectus*, the study has demonstrated that the two species coexist through differential use of food resources across habitats and seasons. Both species were superficially similar in consumption of plant materials but varied markedly in proportions of invertebrates and seeds/starch, an indication that they are omnivores which could be a reason for their successful distribution. The species also differed in niche breadth and diet diversity. *Lophuromys aquilus* had a significantly higher diet diversity and niche breadth than *Rhabdomys dilectus*. Large niche breadth of *L. aquilus* was due to consumption of food varieties in higher proportions, although it specialized on invertebrates during wet season (Clausnitzer *et al*., 2003). Whilst small niche breadth of *R. dilectus* was due to preference on seeds as primary source of food (Curtis and Perrin, 1979). Also, the species differed in body weight and activity patterns which enabled differential utilization of food resources (Perrin and Kotler, 2005). *Rhabdomys dilectus* is smaller in body size and strictly diurnal (Christian, 1977; Krug, 2004), whilst *Lophuromys aquilus* is larger and nocturnal but sometimes it forages during the day (Bekele and Corti, 1994; Claustnizer *et al*., 2003), hence serving as another mechanism of coexistence. In addition, there was niche overlap between the species across habitats and seasons, however, it didi not indicate competition, this could be due to differential utilization of food resources and foraging behavior which could have served as a mechanism of coexistence.

Furthermore, this is the first study in Mount Kilimanjaro and Tanzania at large to document on the breeding activity and population fluctuations of *Lophuromys aquilus* and *Rhabdomys dilectus*. It shows that monthly sex ratio of the two species did not differ between habitats and seasons. However, sex ratio of both *R. dilectus* nd *L. aquuilus* was skewed towards males during wet season and highly fluctuating in moorland. This was probably due to different sex roles. Females reproduces and nurture the juveniles (Pond, 1977), hence spends more time in the nests. Higher fluctuations in moorland were attributed to cold weather which limits movement and activity pattern of rodents (Clausnitzer *et al.,* 2001). Moreover, results of this study indicate that, the number of sexually active females of *Rhabdomys dilectus* significantly differed between habitats and seasons. However, for *Lophuromys aquilus* the difference was not significant between seasons. For both species there was high number of breeding females around June which correspond to wet season, indicating that breeding of rodents in Mt Kilimanjaro starts in early wet season and peaks at end of wet season. Rainfall influences food resources and ground cover which provides protection to newly recruited juveniles from predators and harsh weather (Leirs, 1997). Apart from that, the number of sexually active females of both species was significantly higher in fallow habitat than in moorland and their breeding activity was throughout the year, and mainly discrete or seasonal in moorland. This was probably due to poor vegetation structure and less food availability in the moorland (Jackson and Bernard, 2006). Similarly, other studies have reported that species of genus *Rhabdomys* have opportunistic reproduction. For example, breeding activity of *Rhabdomys pumilio* is highly influenced by spatial-temporal availability of food resources, hence it breeds only when conditions are favourable (Krug, 2007; Jackson and Bernard, 2006). Population size of *Rhabdomys dilectus* also differed between habitats and seasons. It was significantly higher in fallow than in moorland, it was also higher in dry season than wet season. In contrast, population size of *L. aquilus* differed between habitats but no differences were observed between season indicating that *R. dilectus* has seasonal population fluctuations whilst *L. aquilus* have stable populations (Taylor and Green, 197; Schradin and Pillay, 2006).

In objective number four, this study revealed that, home range, survival and capture probability probability differed significantly between species. Whereby, *Lophuromys aquilus* had larger home range and higher survival probability than *Rhabdomys dilectus*. Large home range and high survival probability of *L. aquilus* indicate that the species has high accessibility to food resources which could have resulted into higher population size and an adaptation to live in many habitats (Happold, 2013). The study also, demonstrates that, *L. aquilus* had a significantly lower capture probability over time which suggest it could be a trap shy species. Being a trap shy could serve as a mechanism to avoid predation. Because the species spend longer time to acclimatize to the traps and normally prefer areas with moist and dense cover. Whilst high capture probability of *R. dilectus* could suggest it is a trap loving species, which put the species at high risk of predation, as it quickly get familiar with the traps and prefers open grasslands with sparse vegetation (Claustnizer *et al*., 2001).

Survival probability also, differed between sexes although it was not significant, it was relatively higher for females of both species than males and was relatively higher during wet season than dry season. Results indicate that survival probability between the sexes was attributed to movement patterns because females spend more time inside the nest than males which move longer distance to search for mates, hence males have a higher risk of predation compared to females (Norrdahl and Korpimäki, 1998). Also, high availability of food resources during wet season could have resulted into improved growth and survival of the rodents during wet season.

# 7.0 CHAPTER SEVEN

## GENERAL CONCLUSION AND RECOMMENDATIONS

### 7.1 Conclusions

i. Large number of rodent species recorded in high abundance and the presence of an endemic (*Lophuromys aquilus*) and a rare species *Pelomys fallax* (not previously reported), suggest that habitats of Mt Kilimanjaro support high diversity of rodents. Also, the high abundance recorded in this study could be due to extensive and intensive sampling methods.

ii. The study also concluded that, rodent species richness and abundance were influenced by the variations in vegetation structure, seasonality, and soil properties such as texture and bulk density.

iii. Concurring with previous studies, this study concludes that, habitat heterogeneity was the most important factor for rodent diversity and community assemblages on Mt Kilimanjaro. However, increasing agricultural intensification and expansion of forest plantations in west Kilimanjaro could favour habitat generalists at the expense of forest natives like *Praomys delectorum* due to habitat fragmentation.

iv. The study has shed light on dietary variations and resource partitioning of the two sympatric species. It indicates that despite of the niche overlap, differential use of food resources and foraging behavior of the species serve as the mechanisms of coexistence in a community. Both species consumed more of vegetative materials, seeds and invertebrates. However, invertebrates were more important to the diet of *L. acquilus* than *R. dilectus*. Preference of *Rhabdomys dilectus* on seeds might play a great role in seed dispersal and development of savanna grasslands and might be indicative of potential pest status in agricultural fields. Generally, the study concludes that dietary consumption of *L. acquilus* and *R. dilectus* on Mount Kilimanjaro is reflective of the spatial-temporal variations in food availability.

v. Furthermore, the results confirm that breeding activity and population fluctuations of rodents in tropical mountains including Mt Kilimanjaro is highly influenced by seasonality. Species breed either seasonally or throughout the year and stop when conditions are unfavourable. Furthermore, the study confirms *Rhabdomys dilectus* has opportunistic breeding (specially in the Afro-alpine environments i.e. moorland) which is highly influenced by spatial-temporal variation in food resources. Moreover, the study proposes that, distinct climate between habitats of Mt Kilimanjaro along the altitudinal gradient could have major influence on breeding activity and population fluctuations of both species especially in the moorland which is characterized by extremely cold temperatures and less primary productivity.

vi. This study revealed that, *Lophuromys aquilus* had larger home range and higher survival probability than *Rhabdomys dilectus*. Large home range and high survival probability of *L. aquilus* indicate that the species has high accessibility to food resources which could have resulted into higher population size and its adaptation to live across habitats. It concludes that habitat type and seasonality are major factors affecting home range and survival of rodents through provision of food and cover.

## 7.2 General Recommendations

For effective conservation and management of rodent communities on Mt Kilimanjaro. This study recommends the following.

i. Continuous monitoring of rodent community to determine the long-term effects of habitat heterogeneity on rodent diversity and community.

ii. For management implications, it is recommended that buffer zones with natural vegetation should be established in agricultural fields and tree plantations. This is very important for maintaining rodent communities because uncultivated land serve as refuge to habitat generalists inhabiting agroforestry and farm-fallow mosaics providing them with nesting grounds and alternative foods.

iii. Non-invasive and advanced methods of diet analysis like DNA meta-barcoding is recommended for further identification of rodent niche (i.e identification of plant and animal species that are mostly consumed by rodents) using scat samples.

iv. Further experimental studies on rodent behaviour are recommended to ascertain the effects of behavioural adaptations of the species on home range size and survival which were not covered in this study.

v. Further studies are recommended to determine the possible effects of climate change and habitat alterations on rodent populations. Because, increasing climate change, habitat destruction and fragmentation could result into elevational range shift of rodents towards higher altitudes, hence it is importatnt to ascertain this in future studies.

vi. Moreover, the least concern conservation status of rodents needs to be reassigned by the IUCN RedList because *Lophuromys aquilus* is reported to be endemic to Mt Kilimanjaro, however, its conservation status is unknown due to data deficiency.

vii. The duration of rodent trapping should be prolonged for at least five years. This will provide robust data with enough recaptures for better understanding of population ecology of other species. For example, estimation of home range using MCP was not applicable to other rodents because it required more than five trap relocations per individual.

viii. For management and conservation of the two populations, it is recommended that population genetics should be studied to provide insightful information on the effects of habitat fragmentation to rodent populations. Preliminary findings of this study suggest that *Rhabdomys dilectus* have a disjoint distribution on Mt. Kilimanjaro unlike *Lophuromys aquilus* with continuous distribution in all habitats. Therefore, it would be interesting to study genetic diversity within and between these populations especially in fallow and moorland that are spatially isolated by montane forest.

# REFERENCES

Alibhai, S. K. (1986). Reproductive response of *Gerbillus harwoodii* to 6-MBOA in the Kora National Reserve, Kenya. *Journal of Tropical Ecology*, 2: 377–379.

Admas, A. and Yihune, M. (2016). Species composition, relative abundance and habitat association of rodents in Yekoche Forest, East Gojjam, Ethiopia. *International Journal of Biodiversity and Conservation 8*(9): 216-223.

Ademola, O.J., B. Vanden Broecke, H. Leirs, A.W. Massawe, L.S. Mulungu and R.H. Makundi (2021) Effects of forest disturbance on the fitness of an endemic rodent in a biodiversity hotspot. *Ecology and Evolution*, 11(5): 2391-2401.

Ademola, O. J., Massawe, A. W., Mulungu, L. S., and Makundi, R. H. (2022). Dietary composition of rodents across different habitats in the Ukaguru Mountains, Tanzania. *African Journal of Ecology*, *60*(4), 958-968.s.

Andrews, P. and Brien, E. M. O. (2000). Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. *Journal of Zoology London*, 251: 205–231.

Aplin, K. P., Brown, P. R., Jacob, J., Krebs, C. J. and Singleton, G. R. (2003). *Field methods for rodent studies in Asia and the Indo-Pacific*. Canberra, Australia: Australian Centre for International Agricultural Research.

August, P. V. (1983). The role of habitat complexity and heterogeneity in structuring tropical mammal communities. *Ecology*, 64(6): 1495-1507.

Avenant, N.L. (2003). The use of small mammal community characteristics as an indicator of ecological disturbance in the Korannaberg Conservancy. Pp 95-98. In: Singleton, G.R.; Hinds, L.A., Krebs, C.J.; and Spratt, D.M. (Eds.) Rats, Mice and People: Rodent Biology and Management. ACIAR Monograph No. 96, 564 Pp.

Avenant, N. L. and Cavallini, P. (2007). Correlating rodent community structure with ecological integrity, Tussen-die-Riviere Nature Reserve, Free State province, South Africa. *Integrative Zoology*, 2: 212–219. https://doi.org/10.1111/j.1749-4877.2007.00064.x.

Avenant, N. L., Watson, J. P. and Schulze, E. (2008). Correlating small mammal community characteristics and habitat integrity in the Caledon Nature Reserve, South Africa. *Mammalia*, 72: 186–191. https://doi.org/10.1515/MAMM.2008.023.

Avenant, N. (2011). The potential utility of rodents and other small mammals as indicators of ecosystem ‘integrity’of South African grasslands. *Wildlife Research*, *38*(7), 626-639.

Bantihun G, Bekele A. (2015). Diversity and habitat association of small mammals in Aridtsy forest, Awi Zone, Ethiopia. *Zoological Research 36*(2): 88-94.

Benthem, K. J. Van, Froy, H., Coulson, T., Getz, L. L., Oli, M. K. and Ozgul, A. (2017). Trait – demography relationships underlying small mammal population fluctuations. Journal of Ecology, 86: 348–358. https://doi.org/10.1111/1365-2656.12627

Bekele, A., and Corti, M. (1994). Multivariate morphometries of the Ethiopian populations of harsh-furred rat (Lophuromys: Mammalia, Rodentia). *Journal of Zoology*, *232*(4), 675-689.

Brewer, S. W. and Rejmánek, M. (1999). Small rodents as significant dispersers of tree seeds in a Neotropical forest. *Journal of Vegetation Science*, 10: 165–174

Burgess, N. D., Fjeldså, J. and Botterweg, R. (1998). Faunal Importance of the Eastern Arc Mountains of Kenya and Tanzania. *Journal of East African Natural History*, 87(1): 37–58.

Burgess, N. D., Butynski, T. M., Cordeiro, N. J., Doggart, N. H., Fjeldsa, J., Howell, K. M., Kilahama, F.B., Loader, S.P., Lovett, J.C., Mbilinyi, B., Menegon, M., Moyer, D. C., Nashanda, E., Perkin, A., Rovero, F., Stanley, W. T. and Stuart, S. N. (2007). The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biological Conservation*, 134(2): 209–231. https://doi.org/10.1016/j.biocon.2006.08.015.

Bryja, J., Mikula, O., Patzenhauerová, H., Oguge, N. O., Šumbera, R. and Verheyen, E. (2014). The role of dispersal and vicariance in the Pleistocene history of an East African mountain rodent, Praomys delectorum. *Journal of Biogeography*, 41(1): 196–208. https://doi.org/10.1111/jbi.12195.

Byrom, A. E., Nkwabi, A. J., Metzger, K., Mduma, S. A., Forrester, G. J., Ruscoe, W. A. And Sinclair, A. R. E. (2015). Anthropogenic stressors influence small mammal communities in tropical East African savanna at multiple spatial scales. Wildlife Research, 42(2), 119-131.

Carleton, M. D. and Stanley, W. T. (2012). Species limits within the *Praomys delectorum* group (Rodentia: Muridae: Murinae) of East Africa: a morphometric reassessment and biogeographical implications. *Zoological Journal of the Linnean Society*, 165: 420–469. https://doi.org/10.1111/j.1096-3642.2012.00817.x

Caro, T. M. (2001). Species richness and abundance of small mammals inside and outside an African national Park. *Biological Conservation*, 98: 251–257

Cassola, F. (2016). *Praomys delectorum. The IUCN Red List of Threatened Species 2016: e.T18114A22418403*.https://doi.org/10.2305/IUCN.UK.20162.RLTS.T18114A22418403.en.

Chazal C, Patton JL, Conroy CJ, Parra JL, White GC, et al. (2008) Impact of a Century of Climate Change on Small-Mammal Communities in Yosemite National Park, USA. Science 322: 261–264.

Chidodo, S, Kilawe, C.J., Mnyone, L.L., Vanden Broecke, B. and Mulungu, L. S. (2020) Factors affecting the composition of rodent assemblages in North Uluguru Mountains, Tanzania. *Journal of Vertebrate Biology*, 69(2), 20047.1-10, https://doi.org/10.25225/jvb.20047

Clausnitzer, V., Denys, C., Granjon, L., and Poulet, A. (2001). Rodents of the afro-alpine zone of Mt. Elgon. *African small mammals*, 427-443.

Clausnitzer, V., Churchfield, S. and Hutterer, R. (2003). Habitat occurrence and feeding ecology of Crocidura montis and *Lophuromys* flavopunctatus on Mt. Elgon, Uganda. *African Journal of Ecology,* 41(1): 1-8.

Coe, M. (1993). The conservation of Mount Kilimanjaro: In: Edited by William D. Newmark. IUCN, The World Conservation Union, Gland, Switzerland and Cambridge, UK. 1991. 136 pp. ISBN 2-8317-0070-1 (Pbk).

Corlett, R. T. and Hughes, A. C. (2015). Mammals in forest ecosystems. In K. S.-H. Peh, R. T. Corlett and Y. Bergeron (Eds.): *The Routledge Handbook of Forest Ecology* (pp. 264–278). Oxford, UK: Routledge

Cramer, M.J. and Willig, M.R. (2002). Habitat heterogeneity, habitat associations and rodent species diversity in a Sand-Shinnery-Oak Landscape. *Journal of Mammalia* 83: 743-753.

Christian, D. P. (1977). Diurnal activity of the four-striped mouse, Rhabdomys pumilio. *African Zoology*, *12*(1), 238-239.

Currie, D. J. (2010). Energy and large-scale patterns of animal- and plant-species richness. The American Naturalist, 137(1): 27–49.

Curtis, B. A., and Perrin, M. R. (1979). Food preferences of the vlei rat (Otomys irroratus) and the four-striped mouse (Rhabdomys pumilio). *African Zoology*, *14*(4), 224-229.

Degen, A. A., Khokhlova, I. S., Kam, M. and Snider, I. (2004). Water budget during reproduction in female common spiny mice (Acomys cahirinus). *Journal of Mammalogy*, 85(6): 1106–1110.

Delany, M. J. (1972). The ecology of small rodents in tropical Africa. *Mammal Review*, 2(1): 1–42.

Ecke, F., Lofgren, O., Hornfeldt, B., Eklund, U., Ericsson, P. and Sorlin, D. (2001). Abundance and diversity of small mammals in relation to structural habitat factors. *Ecological Bulletins*, 49: 165–171.

Elsen, P. R., Monahan, W. B., and Merenlender, A. M. (2020). Topography and human pressure in mountain ranges alter expected species responses to climate change. *Nature Communications*, *11*(1), 1974.

Field, A. C. (1975). Seasonal changes in reproduction , diet and body composition of two equatorial rodents. *East African Wildlife Journal*, 13: 221–235.

Forestry and Beekeeping Division. (2005). Forest condition assessment of the Eastern Arc Mountains forests of Tanzania. In S. S. Madoffe and P. K. T. Munishi (Eds.): *Conservation and Management of the Eastern Arc Mountain Forests* (p. 127). Dar es Salaam.

Gebrezgiher, G. B., Makundi, R. H., Meheretu, Y., Mulungu, L. S., and Katakweba, A. A. (2022). A Decade-Long Change in the Elevational Distribution of Non-Volant Small Mammals on Mount Meru, Tanzania. *Diversity*, *14*(6), 454.

Getz, L. L., Hofmann, J. E., McGuire, B. and Oli, M. K. (2004). Vole population dynamics: factors affecting amplitudes of fluctuation. *Oikos*, 1–45.

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C.J. A., Laurance, W.F., Lovejoy, T. E. and Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 478(7369): 378–381. https://doi.org/10.1038/nature10425

Gitonga, J., Simbauni, J. and Oguge, N. (2016). Effect of habitat fragmentation on some aspects of reproduction among Praomys delectorum sub-populations in the Taita and Kyulu hills, Kenya. *International Journal of Advanced Research in Biological Sciences*, 3(4): 143–151.

Gratz, N. G. (1997). The burden of rodent-borne diseases in Africa South of the Sahara. *Belgian Journal of Zoology*, 127(supplement 1): 71–84.

Grelle, C. E. V. (2003). Forest structure and vertical stratification of small mammals in a secondary Atlantic forest, southeastern Brazil. *Studies on Neotropical Fauna and Environment*, 38(2): 81-85.

Grimshaw, IM. And Foley, C.A.H. 1991. *Kilimanjaro Elephant Project 1990 - Final Report.* Friends of Conservation, London.

Grimshaw, J. M., Cordeiro, N. J., and Foley, C. A. H. (1995). The mammals of Kilimanjaro. *Journal of East African Natural History*, *84*(2), 105-139

Happold, D. C. D. (Ed.). (2013). *Mammals of Africa. Volume III: Rodents, Hares and Rabbits.* London, United Kingdom: Bloomsbury Publishing, London. 784pp.

Hemp, A. (2006). Continuum or zonation? Altitudinal gradients in the forest vegetation of Mt. Kilimanjaro. *Plant ecology, 184*(1): 27-42

Jackson, C., and Bernard, R. T. (2006). Variation in the timing of reproduction of the four-striped field mouse, *Rhabdomys* pumilio, in the Eastern Cape Province, South Africa. *African Zoology*, *41*(2), 301-304.

Jackson, T. P. and Aarde, R. J. V. A. N. (2004). Diet quality differentially affects breeding effort of Mastomys coucha and M. natalensis: Implications for rodent pests. *Journal of Experimental Zoology*, 301*A*, 97–108. https://doi.org/10.1002/jez.a.

Kasangaki, A., Kityo, R. and Kerbis, J. (2003). Diversity of rodents and shrews along an elevational gradient in Bwindi Impenetrable National Park, south-western Uganda. *African Journal of Ecology*, 41: 115–123.

Kisingo, A. W., Sabuni, C. A., Coiffait, L., Hayhow, B. and

Larsen, B. (2005). Effects of habitat fragmentation on diversity of small mammals in Lulanda Forest in Mufindi, Tanzania. *Belgian Journal of Zoology*, 135: 109–112

Krug, C. B. (2004). Survival in the Namib: Adaptations of the striped mouse to an arid environment. *Transactions of the Royal Society of South Africa*, *59*(2), 93-98.

Krug, Cornelia B. "Reproduction of *Rhabdomys* pumilio in the Namib desert: pattern and possible control." *Basic and Applied Dryland Research* (2007): 67-85.

Joel L. Meliyo, Boniface H.J. Massawe, Balthazar M. Msanya, Didas N. Kimaro, Proches Hieronimo, Loth S. Mulungu, Nganga I. Kihupi, Jozef A. Deckers, Hubert Gulinck and Herwig Leirs (2014) Landform and surface attributes for prediction of rodent burrows in the West Usambara Mountains, Tanzania. *Tanzania Journal of Health Research,* 16(3). Doi: http://dx.doi.org/10.4314/thrb.v16i3.5.

Johnson, S. D., Burgoyne, P. M., Harder, L. D., and Dötterl, S. (2011). Mammal pollinators lured by the scent of a parasitic plant. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1716), 2303-2310.

Kay, E. H. and Hoekstra, H. E. (2008). Rodents. *Current Biology* 18(10): R406–R410.

Kideghesho, J. R. (2015). Realities on Deforestation in Tanzania — Trends, Drivers, Implications and the Way Forward. [http://dx.doi.org/10.5772/61002 ]. Site visited on 28/11/2017.

Leirs, H., N. Stenseth, J.D. Nichols, J.E. Hines, R. Verhagen and W. verheyen (1997). Stochastic seasonality and non-linear dependent factors regulate population size in an African rodent. *Nature*, 389: 176-180.

Lema, R.and Magige, F. J. (2018). The influence of agricultural activities on the diversity of rodents in Kindoroko forest reserve and surrounding areas, North Pare Mountains, Tanzania. *Tanzania Journal of Science, 44*(1); 97-106.

Lima, M., Julliard, R., Stenseth, N. C. and Jaksic, F. M. (2001a). Demographic dynamics of a neotropical small rodent (Phyllotis darwini): feedback structure , predation and climatic factors. *Journal of Animal Ecology*, 70: 761–775.

Lima, M., Stenseth, N. C., Yoccoz, N. G. and Jaksic, F. M. (2001b). Demography and population dynamics of the mouse opossum (Thylamys elegans) in semi-arid Chile: seasonality, feedback structure and climate. *Proceedings of the Royal Society of London Series B*: *Biological Sciences*, 268: 2053–2064. https://doi.org/10.1098/rspb.2001.1735.

Lima, M., Stenseth, N. C., Leirs, H. and Jaksic, F. M. (2003). Population dynamics of small mammals in semi-arid regions: a comparative study of demographic variability in two rodent species. *Proceedings of the Royal Society of London Series B*: *Biological Sciences.*, 270: 1997–2007. https://doi.org/10.1098/rspb.2003.2448.

Linn, I. J. (1991). Influence of 6-methoxybenzoxazolinone and green vegetation on reproduction of the multimammate rat Mastomys coucha. *South African Journal of Wildlife Research*, 21(2): 33–37.

Linzey, A. V. and Kesner, M. H. (1997). Small mammals of a woodland-savannah ecosystem in Zimbabwe .I. Density and habitat occupancy patterns. *Journal of*

*Zoology, London*, 243: 137–152.

Luo, J. I. A., and FOX, B. J. (1996). Seasonal and successional dietary shifts of two sympatric rodents in coastal heathland: a possible mechanism for coexistence. *Australian Journal of Ecology*, *21*(2), 121-132.

Maeda, E. E., and Hurskainen, P. (2014). Spatiotemporal characterization of land surface temperature in Mount Kilimanjaro using satellite data. *Theoretical and Applied Climatology*, *118*, 497-509.

Makundi, R. H., Kilonzo, B. S. and Massawe, A. W. (2003). Interaction between rodent species in agro-forestry habitats in the western Usambara Mountains, north-eastern Tanzania, and its potential for plague transmission to humans. *Rats, Mice and People*: *Rodent Biology and Management*, 20–24.

Massawe, A W, Mrosso, F. P., Makundi, R. H. and Mulungu, L. S. (2007). Breeding patterns of Arvicanthis neumanni in central Tanzania. *Afrrican Journal of Ecology*, 46: 320–324.

Massawe, A. W., Rwamugira, W., Leirs, H., Makundi, R. H., Mulungu, L., Ngowo, V. and Machang'u, R. (2008). Soil type limits population abundance of rodents in crop fields: case study of the multimammate rat Mastomys natalensis Smith, 1834 in Tanzania. *Integrative Zoology, 3*(1): 27-30.

Massawe, A. W, Makundi, R. H., Mulungu, L. S., Katakweba, A. and Shayo, T. N. (2012). Breeding Dynamics of Rodent Species Inhabiting Farm — Fallow Mosaic Fields in Central Tanzania. *African Zoology*, 47(1): 128–137.

Mason-Romo, E. D., Ceballos, G., Lima, M., Martínez-Yrízar, A., Jaramillo, V. J. and Maass, M. (2018). Long-term population dynamics of small mammals in tropical dry forests, effects of unusual climate events, and implications for management and conservation ☆. *Forest Ecology and Management*, 426: 123–133. https://doi.org/10.1016/j.foreco.2018.05.058.

Mbugua, S. M. (2002). Influence of land use patterns on diversity, distribution and abundance of small mammals in Gachoka dvision of Mbeere District, Kenya. *LUCID Working Paper.*

Mbonile, M. J., Misana, S., and Sokoni, C. (2003). Land use change patterns and root causes of land use change on the southern slopes of Mount Kilimanjaro, Tanzania. *LUCID Working Paper.*

Meerburg, B. G., Singleton, G. R. and Kijlstra, A. (2009). Rodent-borne diseases and their risks for public health. *Critical Reviews in Microbiology*, 35(3): 221–270. https://doi.org/10.1080/10408410902989837.

Men, X., Guo, X., Dong, W., Ding, N., and Qian, T. (2015). Influence of human disturbance to the small mammal communities in the forests. *Open Journal of Forestry*, 5: 1–9.

Mlyashimbi, E. C. M; J. Mariën; D. N. Kimaro; A. J. P. Tarimo; M. Isabirye; R. H. Makundi; A. W. Massawe; M. E. Mdangi; D. Kifumba, A. Nakiyemba; H. Leirs; S. R. Belmain and L. S. Mulungu. (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):1-13

Mlyashimbi E.C.M., B. Vanden Broecke, J. Mariën[3], D.N. Kimaro, A.J.P. Tarimo, R.S. Machang'u, M. Isabirye, R.H. Makundi A.W. Massawe, P. Hieronimo, D. Kifumba, H. Leirs, M.E. Mdangi, S.R. Belmain, L.S. Mulungu (2019) Influences of soil types on the population dynamics and survival of Multimammate rat (*Mastomys natalensis*, Smith 1832) in semi-arid areas in Tanzania. *Crop Protection*, 124:104829. https://doi.org/10.1016/j.cropro.2019.05.023

Mwanjabe, P. S., Sirima, F. B., & Lusingu, J. (2002). Crop losses due to outbreaks of Mastomys natalensis (Smith, 1834) Muridae, Rodentia, in the Lindi Region of Tanzania. International Biodeterioration & Biodegradation, 49(2-3), 133-137

Monadjem, A., Taylor, P. J., Denys, C., and Cotterill, F. P. (2015). *Rodents of sub-Saharan Africa: a biogeographic and taxonomic synthesis*. Walter de Gruyter GmbH and Co KG.

Mulangu, F., and Kraybill, D. (2013). Climate change and the future of mountain farming on Mt. Kilimanjaro. In *The future of mountain agriculture* (pp. 73-88). Springer, Berlin, Heidelberg

Mulungu, L. S., Makundi, R. H., Massawe, A. W., Machang'u, R. S. and Mbije, N. E. (2008). Diversity and distribution of rodent and shrew species associated with variations in altitude on Mount Kilimanjaro, Tanzania. *Journal of Mammalia* 72(3): 178-185.

Mulungu, L. S., Mahlaba, T., Massawe, A. W., Kennis, J., Crauwels, D., Eiseb, S., Monadjem, A., Makundi, R. H., Katakweba, A.S., Leirs, H., and Belmain, S. (2011a). Dietary differences of the multimammate mouse, *Mastomys natalensis* (Smith, 1834), across different habitats and seasons in Tanzania and Swaziland. *Journal of Wildlife Research*. 38: 640–646.

Mulungu, L. S., Massawe, A. W., Kennis, J., Crauwels, D., Eiseb, S., Mahlaba, T. A. A., and Belmain, S. R. (2011b). Differences in diet between two rodent species, Mastomys natalensis and Gerbilliscus vicinus, in fallow habitats in central Tanzania. *African Zoology*, *46*(2), 387-392.

Mulungu, L.S., Ngowo, V., Mdangi, M., Katakweba, A. S., Tesha, P., Mrosso, P., Mchomvu, M., Sheyo, P., and Kilonzo, B. S., (2013). Population dynamics and breeding patterns of multimammate mouse, *Mastomys natalensis* (Smith 1834), in irrigated rice fields in Eastern Tanzania. *Pest Management Science* 69, 371–377.

Monadjem, A., Taylor, P. J., Denys, C. and Cotterill, F. P. D. (2015). *Rodents of Sub-Saharan Africa. A biogeographic and taxonomic synthesis*. Berlin/Munich/Boston: Walter de Gruyter.

Mortelliti, A. and Boitani, L. (2006). Patterns of rodent species diversity and abundance in a Kenyan relict tropical rainforest. *Biodiversity and Conservation*, 15: 1425–1440. https://doi.org/10.1007/s10531-005-0310-x.

Moritz, C., Patton, J. L., Conroy, C. J., Parra, J. L., White, G. C., and Beissinger, S. R. (2008). Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science*, *322*(5899), 261-264.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B. and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403: 853–858.

Nanzyo, M., Shoji, S., and Dahlgren, R. (1993). Physical characteristics of volcanic ash soils. In *Developments in soil science* (Vol. 21, pp. 189-207). Elsevier.

Neal, B. R. and Alibhai, S. K. (1991). Reproductive response of Tatera leucogaster (Rodentia) to supplemental food and 6-methoxybenzoxazolinone in Zimbabwe. *Journal of Zoology London*, 223: 469–473.

Newmark, W. D. (Ed.). (1991). *The Conservation of Mount Kilimanjaro* (Vol. 16). Iucn. Oli, M. K. and Dobson, F. S. (1999). Population cycles in small mammals: the role of age at sexual maturity. *OIKOS*, (86): 557–565.

Norrdahl, K., and Korpimaki, E. (1998). Does mobility or sex of voles affect risk of predation by mammalian predators? *Ecology*, 79(1): 226–232.

Pinotti, B. T., Naxara, L. and Pardini, R. (2011). Diet and food selection by small mammals in an old- growth Atlantic forest of south-eastern Brazil. *Studies on Neotropical Fauna and Environment*, 46(1): 37–41. https://doi.org/10.1080/01650521.2010.535250.

Odhiambo RO, Makundi RH, Leirs H, Verhagen R. (2008a). Dietary selection in Mastomys natalensis (Rodentia: Muridae) in the maize agro ecosystems of Central and South-western Tanzania. Mammalia, 72, 169–177.

Odhiambo, R. O., Makundi, R. H., Leirs, H., and Verhagen, R. (2008b). Demography, reproductive biology and diet of the bushveld gerbil Tatera leucogaster (Rodentia: Gerbillinae) in the Lake Rukwa valley, southwestern Tanzania. *Integrative Zoology*, *3*(1), 31-37. https://doi.org/10.1111/j.1749-4877.2008.00073.x.

Oguge, N. O. (1995). Diet, seasonal abundance and microhabitats of Praomys (Mastomys) natalensis (Rodentia: Muridae) and other small rodents in a Kenyan sub-humid grassland community. *African Journal of Ecology*, *33*(3), 211-223.

Ostfeld, R. S. (1985). Limiting resources and territoriality in microtine rodents. *The American Naturalist*, 126(1):

1–15.

Ostfeld, R. S., Lidicker, W. Z., and Heske, E. J. (1985). The Relationship between Habitat Heterogeneity, Space Use, and Demography in a Population of California Voles. *OIKOS*, 45(3): 433–442.

Pianka, E. R. (1974). Niche Overlap and Diffuse Competition (desert lizards/resource partitioning/community structure/species diversity). *Proceedings of National Academy of Sciences*, 71(5): 2141–2145.

Perrin, M. R., and Kotler, B. P. (2005). A test of five mechanisms of species coexistence between rodents in a southern African savanna. *African Zoology*, *40*(1), 55-61.

Pond, C.M. (1977). The significance of lactation in the evolution of mammals. - Evolution 31: 177-199.

Rahbek, C., Borregaard, M. K., Colwell, R. K., Dalsgaard, B. O., Holt, B. G., Morueta-Holme, N., ... and Fjeldså, J. (2019). Humboldt's enigma: What causes global patterns of mountain biodiversity? *Science*, *365*(6458), 1108-1113.

Richard, U., Byamungu, R. M., Magige, F., and Makonda, F. B. (2022). Microhabitat, altitude and seasonal influence on the abundance of non-volant small mammals in Mount Rungwe forest nature reserve. *Global Ecology and Conservation*, *35*, e02069.

Rogora, M., Frate, L., Carranza, M. L., Freppaz, M., Stanisci, A., Bertani, I., and Matteucci, G. (2018). Assessment of climate change effects on mountain ecosystems through a cross-site analysis in the Alps and Apennines. *Science of the total environment*, *624*, 1429-1442.

Rovero, F., Menegon, M., Fjelds, J., Collett, L., Doggart, N., Leonard, C., Norton, G., Owen, N., Perkin, A., Spitale, D., Ahrends, A. and Burgess, N. D. (2014). Targeted vertebrate surveys enhance the faunal importance and improve explanatory models within the Eastern Arc Mountains of Kenya and Tanzania. *Diversity and Distributions*, 20: 1438–1449. https://doi.org/10.1111/ddi.12246

Rowe, R. J., Finarelli, J. A., and Rickart, E. A. (2010). Range dynamics of small mammals along an elevational gradient over an 80-year interval. *Global Change Biology*, *16*(11), 2930-2943

Sato, J. J., Shimada, T., Kyogoku, D., Komura, T., Uemura, S., Saitoh, T. and Isagi, Y. (2018). Dietary niche partitioning between sympatric wood mouse species ( Muridae : Apodemus ) revealed by DNA meta-barcoding analysis. *Journal of Mammalogy*, 99(4): 952–964. https://doi.org/10.1093/jmammal/gyy063

Schradin, C., and Pillay, N. (2005). Demography of the striped mouse (*Rhabdomys* pumilio) in the succulent karoo. *Mammalian Biology*, *70*(2), 84-92.

Sicard, B., Fuminier, F., Maurel, D. and Boissin, J. (1993). Temperature and water conditions mediate the effects of day length on the breeding cycle of a Sahelian rodent, Arvicanthis niloticus. *Biology of Reproduction*, 49: 716–722.

Shiels, A. B., Flores, C. A., Khamsing, A., Krushelnycky, P. D., Mosher, S. M., and Drake, D. R. (2013). Dietary niche differentiation among three species of invasive rodents (Rattus rattus, R. exulans, Mus musculus). *Biological invasions*, *15*, 1037-1048.

Shilereyo, M., Magige, F. J., Ogutu, J. O., and Røskaft, E. (2020). Small mammal community demography and reproductive seasonality under protection, pastoralism and agriculture in the Serengeti Ecosystem, Tanzania. *International Journal of Biodiversity and Conservation*, *12*(4), 253-269.

Smith, V. R. and Avenant, N. L. (2004). Seasonal changes in age class structure and reproductive status of house mice on Marion Island (sub-Antarctic). *Polar Biology*, 27: 99–111. https://doi.org/10.1007/s00300-002-0405-8.

Shore, R. F. and Garbett, S. D. (1991). Notes on the small mammals of the Shira Plateau, Mt. Kilimanjaro. *Mammalia 55*(4): 601-608.

Soininen, E. M., Ravolainen, V. T., Bråthen, K. A., Yoccoz, N. G., Gielly, L., and Ims, R. A. (2013). Arctic small rodents have diverse diets and flexible food selection. *PLoS One*, *8*(6), e68128.

Stanley, W. T., Kihaule, P. M., Howell, K. M., and Hutterer, R. (1998). Small mammals of the Eastern Arc Mountains, Tanzania. *Journal of East African Natural History*, *87*(1), 91-1001.

Stanley, W. T., Rogers, M. A., and Hutterer, R. (2005). A morphological assessment of Myosorex zinki, an endemic shrew on Mount Kilimanjaro. *Belgian Journal of Zoology*, *135*(supplement), 141-144.

Stanley, W. T. and Hutterer, R. (2007). Differences in abundance and species richness between shrews and rodents along an elevational gradient in the Udzungwa Mountains, Tanzania. *Acta Theriologica*, *52*(3), 261-275.

Stanley WT, Goodman, SM. (2011) Small mammal inventories in the East and West Usambara Mountains, Tanzania. 4. Rodentia. In: Stanley WT, editor. Studies of Montane Vertebrates of Tanzania. Fieldiana Life Earth Sci 4: 53–73.

Stanley, W. T., Rogers, M. A., Kihaule, P. M. and Munissi, M. J. (2014). Elevational distribution and ecology of small mammals on Africa’s highest mountain. *PloS one, 9*(11): 1-13.

Stanley, W. T., and Kihaule, P. M. (2016). Elevational distribution and ecology of small mammals on Tanzania's second highest mountain. *Plos one*, *11*(9), e016200.

Stein, A. and Kreft, H. (2015). Terminology and quantification of environmental heterogeneity in speciesrichness research. *Biological Reviews,* 90(3): 815-836.

Stirnemann, I., Mortelliti, A., Gibbons, P., and Lindenmayer, D. B. (2015). Fine-Scale Habitat Heterogeneity Influences Occupancy in Terrestrial Mammals in a Temperate Region of Australia. *Plos one*, *10*(10), e0140802.

Stenseth, N. C., Samia, N. I., Viljugrein, H., Kausrud, K. L., Begon, M., Davis, S., Leirs, H., Dubyanskiy, V. M., Esper, J., Ageyev, V. S., Klassovskiy, N. L., Pole, S.B., and Chan, K. S. (2006). Plague dynamics are driven by climate variation. *Proc Natl Acad Sci* U S A. 2006 Aug 29;103(35):13110-5. doi:10.1073/pnas.0602447103. Epub 2006 Aug 21. PMID: 16924109; PMCID: PMC1559761.

Stevens, R. D., and Tello, J. S. (2011). Diversity begets diversity: relative roles of structural and resource heterogeneity in determining rodent community structure. *Journal of Mammalogy*, *92*(2), 387-395.

Swanepoel, L. H., Swanepoel, C. M., Brown, P. R., Eiseb, S. J., Goodman, S. M., Keith, M., Kirsten, F., Leirs, H., Mahlaba, T.A.M., Makundi, R.H., Malebane, P., von Maltitz, E. F., Massawe, A.W., Monadjem, A., Mulungu, L. S., Singleton, G. R., Taylor, P.

J., Soarimalala, V. and Belmain, S. R. (2017). A systematic review of rodent pest research in Afro-Malagasy small-holder farming systems: Are we asking the right questions? *PLoS ONE*, 12(3): 1–20.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C. and Schwager, M. (2004). Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *Journal of Biogeography*, 31: 79–92. https://doi.org/10.1046/j.0305-0270.2003.00994.x.

Thomas, S. M., Soka, G. E., Mulungu, L. S., and Makonda, F. B. (2022). Spatial-Temporal Variations in Dietary Consumption of Two Dominant Rodent Species (Rhabdomys dilectus and Lophuromys acquilus) on Mount Kilimanjaro, Tanzania. *Diversity*, *14*(8), 659.

Thompson, L. Mikhalenko, V., Mosley-Thompson, E., Davis, M., Brecher, H., Lin, P., Hardy, D. and Zagorodnov, V. (2002). Kilimanjaro ice core records: evidence of Holocene climate change in tropical Africa. Science, 298, 589-593

Taylor, K. D., and Green, M. G. (1976). The influence of rainfall on diet and reproduction in four African rodent species. *Journal of Zoology*, *180*(3), 367-389.

Verheyen, W.N., Hulselmans Jan L.J., Dierckx, T., Mulungu, L., Leirs, H., Corti, M. and Verheyen, E. (2007). The characterization of the Kilimanjaro *Lophuromys aquilus* True 1892 population and description of five new *Lophuromys* species (Rodentia, Muridae). *Bulletin L'Insitut Royal des Sciences Naturalles de Belgique, Biologie* 77: 23-75.

Willig, M. R., and Presley, S. J. (2016). Biodiversity and metacommunity structure of animals along altitudinal gradients in tropical montane forests. *Journal of Tropical Ecology*, *32*(5), 421-436.

Wimberly, M. C. and Ohmann, J. L. (2004). A multi-scale assessment of human and environmental constraints on forest land cover change on the Oregon (USA) coast range. *Landscape Ecology*, 19: 631–646.

Wimberly, M. C. and Spies, T. A. (2001). Influences of environment and disturbance on forest patterns in coastal Oregon watersheds. *Ecology*, 82(5): 1443–1459.

Yihune, M., and Bekele, A. (2012). Diversity, distribution and abundance of rodent community in the afro-alpine habitats of the Simien Mountains National Park, Ethiopia. *International Journal of Zoological Research*, *8*(4), 137.

Zu, K., Wang, Z., Zhu, X., Lenoir, J., Shrestha, N., Lyu, T., and Zhou, J. (2021). Upward shift and elevational range contractions of subtropical mountain plants in response to climate change. *Science of the Total Environment*, *783*, 146896.

## Kuhusu Tasnifu Hii

Utafiti huu ulihusisha ikolojia ya panya magharibi mwa Mlima Kilimanjaro. Uliangalia namna tofauti za kiikolojia kama vile aina za makazi na msimu huathiri aina na jamii za panya. Pia uliangalia mgawanyo wa chakula, kuzaliana na uwezekano wa kuishi miongoni mwa panya waliopatikana kwa wingi zaidi. Njia ya kukamata na kurudisha pamoja na kuondoa zilitumika kutega panya kwenye mashamba, misitu (asili na kupanda), maeneo yasiyolimwa na uoto wa vichaka vifupi kipindi cha mvua na kiangazi. Utafiti ulibaini aina zipatazo kumi na nne za panya zilizounda jamii kubwa mbili (panya wa msituni na makazi mbalimbali). Pia, imebainika kuwa panya aina ya *Lophuromys aquilus* na *Rhabdomys dilectus* wanamuingiliano mkubwa wa kiikolojia na uwezo wa kuishi pamoja kutokana na mgawanyo wa vyakula katika viwango na nyakati tofauti. Vilevile, huzaliana kwa wingi kipindi cha mvua kutokana na upatikanaji wa chakula na usalama wa malazi. Hivyo, utafiti unapendekeza uhifadhi na usimamizi bora wa makazi ya panya.