Sokoine University of Agriculture

PhD Thesis

Ecology of Small Mammals and Their Ectoparasites in Mount Meru, Tanzania: Insights for Biodiversity Conservation

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ECOLOGY OF SMALL MAMMALS AND THEIR ECTOPARASITES IN MOUNT MERU, TANZANIA: INSIGHTS FOR BIODIVERSITY CONSERVATION

Thesis submitted to Sokoine University of Agriculture in Fulfilment of the Requirements for the Degree of Doctor of Philosophy

By

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EXTENDED ABSTRACT

This Thesis has been prepared in accordance with the Publishable Manuscripts format of the Sokoine University of Agriculture. The study on the elevational distribution of non-volant small mammals over time, their demographic characteristics, and their associations with arthropod ectoparasites was conducted between 2021 and 2022 at different elevations and habitats in Tanzania's second-highest mountain, Mount Meru. Mount Meru is one of the biodiversity hotspots in eastern Africa, hosting high level of species richness and endemism, and providing important ecosystem services. However, relatively, little is known about the ecology of small mammals and their arthropod ectoparasites. Similarly, little is known about the effects of environmental factors on the small mammal distribution, which potentially extending to the parasites they host. Tanzania is among the handful of countries in Africa where active foci of deadly zoonotic diseases that can be transmitted by small mammals and their ectoparasite vectors have been persistent. Moreover, Mount Meru is home for endemic and threatened species that are documented on the IUCN Red List. However, there is currently no available information regarding the possible role of arthropod ectoparasites of small mammals in the transmission of zoonotic disease.

The over all goal of the study was to understand the ecological dynamics and distribution patterns of small mammals and their arthropod ectoparasites across different elevations of Mount Meru in Tanzania. The study aimed at addressing three key specific objectives: i) Assesing a decade-long change in the elevational distribution of non-volant small mammals on Mount Meru; ii) determining the breeding and demographic aspects of *montemys delectorum*, an east african endemic rodent in mount Meru; iii) Examining arthropod ectoparasites of two rodent species occurring in varied elevations on Tanzania’s second highest mountain.

To address the first objective, the small mammals were surveyed from February to November 2021 at six elevations between 1500 m and 3650 m using Sherman and Havahart traps. The results show that two shrew and thirteen rodent species were recorded, including *Crocidura newmarki* and *Lophuromys verhageni*, which are endemic to the study area. Species richness was highest at mid-altitudes, in line with the general patterns globally, though less pronounced in Africa. The species *Arvicanthis niloticus, Mastomys natalensis, Lemniscomys striatus, Dasymys incomtus*, and *Cricetomys ansorgei* were not documented in 2009 but have been recorded in 2021. Upward shifts in species' ranges were observed between 2009 and 2021, suggesting the influence of climate change on the small mammal community.

It is important to note that the rodent species mentioned in Chapter 2 as *Praomys* species have been identified as *Montemys delectorum* after genetic identification and recent taxonomic revisions.

For the second objective, a Capture – mark – release studies were undertaken in dense and open patchy forests in four 70 m X 70 m grids from February 2021 to June 2022. The findings revealed that the species exhibited bimodal patterns of breeding seasonality, characterized by a low rate occurring during the short interval between December and February and a pronounced rate taking place from May to July. The population of *Montemys delectorum* was unstable in the different forest types. There was a larger population in the patchy open forest (F = 8.1; df = 1; p = 0.0001) than in dense forest, suggesting its importance as a refuge for the species.

To achieve the third objective, trapping of the two most dominant rodent species of the study area, *Montemys delectorum* and *Rhabdomys dilectus*, from five elevations (1500 to 3500 m), were examined for arthropod ectoparasite infestations. The results revealed that *Ctenophthalmus calceatus cabirus, Dinopsyllus ellobius, Varroa rindereri,* and *Xenopsylla cheopis* were recovered

from the rodents. This study demonstrates that the elevational distribution of arthropod ectoparasites is influenced by host sex, host species, and environmental temperature. With rising altitude, parasite prevalence and abundance decrease, indicating that colder environmental conditions at higher altitudes inhibit parasite reproduction and development. This indicates conservation efforts should focus on higher altitudes. Moreover, the rodents and ectoparasites reported in this study have been identified as possible vectors of medical and veterinary diseases in different parts of Africa, including Tanzania. It is crucial to take precautions in order to effectively reduce the risk of parasitic infection, which can pose an additional threat to both the endemic and threatened species listed on the IUCN Red List as well as the overall biodiversity of the study area. Furthermore, molecular results from this study reported a previously unidentified mite species within the Mesostigmata taxonomic group that had previously been recognized exclusively as a parasite of honeybees. Further research efforts may provide insights into the significance of this particular species of mite, *Varroa rindereri*. Generally, while there remains much to be learned, this particular study establishes the foundation for future initiatives in wildlife disease surveillance and biodiversity conservation management.

In abroader sense, the shift in the distribution of small mammals and their ectoparasites on Mount Meru is a microcosm of the broader challenges facing mountain ecosystems worldwide. These insights go beyond the immediate context of Mount Meru and suggest that we need to consider the long-term consequences of environmental dynamics on biodiversity conservation. As these complexities continue to shape mountain landscapes, their impact is not limited to species interactions but also touches the field of human well-being. The conservation of biodiversity is intrinsically linked to our own well-being, as biodiversity and human societies are intricately intertwined. Therefore, the findings of this research serve as an urgent reminder for effective conservation action.

IKISIRI KUU

Mkusanyiko huu wa tafiti umekamilishwa kulingana na muundo wa hati za kuchapishwa wa Chuo Kikuu cha Kilimo Sokoine. Utafiti juu ya usambazaji wa kina wa wanyama wadogo wasioruka kwa muda, tabia zao za idadi ya watu, na ushirikiano wao na vimelea vya nje vya artropodi ulifanywa kati ya 2021 na 2022 katika urefu tofauti na mazingira mbalimbali kwenye mlima wa pili kwa urefu Tanzania, Mlima Meru. Mlima Meru ni mojawapo ya maeneo yenye utajiri mkubwa wa spishi na endemiki, na hutoa huduma muhimu za mazingira. Hata hivyo, kwa ujumla, kidogo sana inajulikana kuhusu ekolojia ya wanyama wadogo na vimelea vyao vya nje vya artropodi. Vivyo hivyo, kidogo sana inajulikana kuhusu athari za sababu za mazingira kwa usambazaji wa wanyama wadogo, ambao kwa uwezekano huenda ukawa na athari kwa vimelea wanavyowahifadhi. Tanzania ni miongoni mwa nchi chache barani Afrika ambapo maeneo ya hatari ya magonjwa hatari yanayoweza kuambukizwa na wanyama wadogo na vekta zao za vimelea vya nje vimeendelea kuwepo. Zaidi ya hayo, Mlima Meru ni nyumbani kwa spishi za endemiki na zilizo hatarini ambazo zimeorodheshwa kwenye Orodha Nyekundu ya IUCN. Hata hivyo, kwa sasa hakuna habari inayopatikana kuhusu jukumu linalowezekana la vimelea vya nje vya artropodi vya wanyama wadogo katika kuambukiza magonjwa ya kuambukizwa kwa binadamu.

Lengo kuu la utafiti lilikuwa kuelewa mienendo ya ikolojia na mitindo ya usambazaji wa mamalia wadogo na wadudu wanaoishi nje mwilini (ectoparasites) kote kwenye kimo tofauti cha Mlima Meru nchini Tanzania. Utafiti ulilenga kushughulikia malengo matatu maalum muhimu: i) Kupima mabadiliko ya miongo kumi katika usambazaji wa kimo cha mamalia wadogo wasioruka katika Mlima Meru; ii) kubainisha vipengele vya uzazi na demografia ya montemys delectorum, panya wa Afrika Mashariki ambaye ni wa kipekee katika Mlima Meru; iii) Kuchunguza wadudu wanaoishi nje mwilini (ectoparasites) wa spishi mbili za panya zinazotokea katika kimo tofauti kwenye mlima wa pili kwa urefu nchini Tanzania.

Kushughulikia lengo la kwanza, mamalia wadogo walichunguzwa kuanzia Februari hadi Novemba 2021 katika kimo sita kati ya mita 1500 na 3650 kwa kutumia mitego ya Sherman na Havahart. Matokeo yanaonyesha kwamba panya wawili wa miguu na spishi kumi na tatu za panya zilirekodiwa, ikiwa ni pamoja na Crocidura newmarki na Lophuromys verhageni, ambazo ni za kipekee katika eneo la utafiti. Uwiano wa spishi ulikuwa mkubwa zaidi katika altitudes za kati, kulingana na mienendo ya kawaida duniani kote, ingawa haikuwa wazi sana barani Afrika. Spishi kama Arvicanthis niloticus, Mastomys natalensis, Lemniscomys striatus, Dasymys incomtus, na Cricetomys ansorgei hazikurekodiwa mwaka wa 2009 lakini zimeandikwa mwaka wa 2021. Mabadiliko ya juu katika maeneo ya spishi yalitambuliwa kati ya 2009 na 2021, ikionyesha ushawishi wa mabadiliko ya hali ya hewa kwenye jamii ya mamalia wadogo.

Ni muhimu kutambua kwamba spishi za panya zilizotajwa katika Sura ya 2 kama spishi za Praomys zimegunduliwa kuwa Montemys delectorum baada ya utambuzi wa jeni na marekebisho ya taksonomia ya hivi karibuni.

Kwa lengo la pili, utafiti wa Kukamata – Kuweka alama – Kuachilia ulifanywa katika misitu ya kanda kubwa na wazi yenye vipande katika mihimili minne ya 70 m X 70 m kuanzia Februari 2021 hadi Juni 2022. Matokeo yalionyesha kwamba spishi ilionyesha mienendo ya msimu wa kuzaa wa bimodal, ikielezewa na kiwango cha chini kinachotokea wakati wa kipindi kifupi kati ya Desemba na Februari na kiwango kikubwa kinachotokea kuanzia Mei hadi Julai. Idadi ya Montemys delectorum ilikuwa isiyo imara katika aina tofauti za misitu. Kulikuwa na idadi kubwa ya watu katika msitu wazi wenye vipande ($F = 8.1$; $df = 1$; $p = 0.0001$) kuliko katika msitu wa kuficha, ikionyesha umuhimu wake kama kimbilio kwa spishi.

Kuweza kufikia lengo la tatu, kupigwa mitego kwa spishi mbili za panya zinazodomiinant katika eneo la utafiti, Montemys delectorum na Rhabdomys dilectus, kutoka kwenye kimo cha mita 1500 hadi 3500, zilichunguzwa kwa maambukizi ya wadudu wanaoishi nje mwilini (ectoparasites). Matokeo yalionyesha kuwa Ctenophthalmus calceatus cabirus, Dinopsyllus ellobius, Varroa rindereri, na Xenopsylla cheopis walipatikana kwenye panya. Utafiti huu unaonyesha kwamba usambazaji wa kimo cha wadudu wanaoishi nje mwilini unachangiwa na jinsia ya mwenyeji, spishi ya mwenyeji, na joto la mazingira. Pamoja na kuongezeka kwa kimo, idadi na wingi wa wadudu hupungua, ikionyesha kuwa hali baridi ya mazingira katika altitudes kubwa inazuia uzazi na maendeleo ya wadudu. Hii inaonyesha juhudi za uhifadhi zinapaswa kuzingatia altitudes kubwa. Zaidi ya hayo, panya na wadudu wanaoishi nje mwilini waliotajwa katika utafiti huu wamegunduliwa kama wataoaji wa magonjwa ya matibabu na mifugo katika sehemu tofauti za Afrika, ikiwa ni pamoja na Tanzania. Ni muhimu kuchukua tahadhari ili kupunguza hatari ya maambukizi ya vimelea, ambavyo vinaweza kuwa tishio la ziada kwa spishi za kipekee na zilizotishiwa zilizoorodheshwa kwenye Orodha Nyekundu ya IUCN pamoja na bioanuwai kwa jumla ya eneo la utafiti. Zaidi ya hayo, matokeo ya molekuli kutoka kwenye utafiti huu yaliripoti spishi ya mnyoo iliyoidhinishwa hapo awali ndani ya kikundi cha kisasa cha Mesostigmata ambayo hapo awali ilitambuliwa kikamilifu kama kimelea cha nyuki. Jujuhudi za utafiti zaidi zinaweza kutoa ufahamu juu ya umuhimu wa spishi maalum ya mnyoo, Varroa rindereri. Kwa ujumla, ingawa bado kuna mengi ya kujifunza, utafiti huu maalum unaweka msingi kwa jitihada za baadaye katika ufuatiliaji wa magonjwa ya wanyama pori na usimamizi wa uhifadhi wa bioanuai.

Kwa mtazamo mpana zaidi, mabadiliko katika usambazaji wa mamalia wadogo na wadudu wanaoishi nje mwilini kwenye Mlima Meru ni mfano wa changamoto kubwa zaidi zinazokabili mfumo wa mazingira ya milima ulimwenguni kote. Maarifa haya yanavuka muktadha wa moja kwa moja wa Mlima Meru na kuashiria kwamba tunahitaji kuzingatia matokeo ya muda mrefu ya mienendo ya mazingira kwa uhifadhi wa bioanuwai. Kwa kuwa utata huu unaendelea kuunda mandhari ya milima, athari zake hazipunguzwi kwa mahusiano ya spishi bali pia huzigusa sekta ya ustawi wa kibinadamu. Uhifadhi wa bioanuwai unaunganishwa kimsingi na ustawi wetu wenyewe, kwani bioanuwai na jamii za kibinadamu zimefungamana kwa karibu. Kwa hiyo, matokeo ya utafiti huu yanatutaka kuchukua hatua za uhifadhi kwa haraka na kwa ufanisi.

DECLARATION

I, Genet Berhe Gebrezgiher, do hereby declare to the Senate of Sokoine University of Agriculture that this thesis is my own original work done within the period of registration and that it has neither been submitted nor is concurrently being submitted in any other institution.

Genet Berhe Gebrezgiher Date
(PhD Candidate)

The declaration above is confirmed by;

Prof. Rhodes Makundi Date
(Main Supervisor)

Prof. Yonas Meheretu Date
(Co-supervisor)

Prof. Abdul A. S. Katakweba Date
(Co-supervisor)

LIST OF PUBLISHED PAPERS

PAPER I: A Decade-Long Change in the Elevational Distribution of Non-Volant Small Mammals on Mount Meru, Tanzania. *Diversity 2022,* 14(6); 454. https://doi.org/10.3390/d14060454

PAPER II: Breeding and demographic aspects of Montemys delectorum, an East African endemic rodent. *African Journal of Ecology, 2023*, 00;1–9. 10.1111/aje.13172

PAPER II: Arthropod Ectoparasites of Two Rodent Species Occurring in Varied Elevations on Tanzania’s Second Highest Mountain. *Biology 2023,* 12; 394. https://doi.org/10.3390/biology12030394

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DEDICATION

Forever in my heart, forever in my art—a dedication to my lovely husband and father (late).

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LIST OF ABBREVIATIONS AND SYMBOLS

%	percent
◦C	degree Celsius
µL	micro litter
AA	afro alpine
ACE	abundance Coverage Estimator
ACE-II	African Center of Excellence
AICc	corrected Akaike’s Information Criterion
ANAPA	Arusha National Park
ANOVA	analysis of variance
CMR	capture-cark-recapture
cox1	cytochrome oxidase subunit I
cox2	cytochrome oxidase subunit II
D	ecological index of dominance
Df	degrees of freedom
DNA	deoxyribo nucleic Acid
DPX	dibutyl phthalatepolystyrene-xylene
E	evenness index
EH	ericaceous heath
g	gram
GLM	generalized linear model
GLM	generalized linear model
H’	shanno Weiner diversity index
IRPM-BTD	Innovative Rodent Pest Management and Biosensor Technology Development
IUCN	International Union for Conservation of Nature
LCL	lower confidence limit
LMF	lower montane forest
M	meter
MA	mean abundance of the ectoparasites
min	minutes
mL	milliliter
MNA	minimum number of animals live
Mt	mount

No.	number
P	probability
PAST	paleontological statistics software package
PCoA	principal Coordinate Analysis
PCR	polymerase chain reaction
QGIS	quantum Geological Information System software
R^2	coefficient of determination in regression model
RA	relative abundance
Re	number of individual rodent species infested with one or more ectoparasite species
SA	savanna
SD	standard deviation
SE	standard error
Sec	second
Sest	estimated number of species
Sobs	observed number of species
SUA	Sokoine University of Agriculture
TANAPA	Tanzania National Parks
TAWIRI	Tanzania Wildlife research Institute
TS	trap success
UCL	upper confidence limit
UMF	upper montane forest
ZINB	zero-inflated negative binomial regression models
ΔAICc	difference in AICc
χ2	Chi-square

CHAPTER ONE

1.0 GENERAL INTRODUCTION

1.1 Background Information

Steep mountain are a natural experiment to study how species respond to changing conditions because climatic conditions and habitat characteristics change rapidly as a function of elevation on a relatively small geographic scale (Vetaas, 2021). Altitudinal gradients are characterized by significant variations in temperature, rainfall, and soil, with environmental conditions at the extremes that mutually influence survival of any organism living on a gradient. (Heaney, 2001). Different mountan species are currently facing challenges maintaining their existence due to shrinking habitats attributed to climate change, ecological disturbances, and other impacts caused by human activity. Gaining insight into the distribution patterns of montane species across elevational gradients holds significant value for biodiversity conservation efforts as well as for predicting species' responses to forthcoming environmental changes and facilitating effective conservation strategies to maintain the species. Altitudinal gradients influence small mammal distribution, potentially extending to the parasites they host. Understanding parasite-host dynamics spatially is, therefore, essential for biodiversity conservation and disease management. Parasites diminish host fitness by reducing resources and immunity, which affects the host's overall well-being. Parasites can lower host density, impacting prey populations and ecosystem function. Moreover, parasites and their hosts can serve as reservoirs for medically important pathogens, posing health threats to humans. With climate change altering wildlife distribution and interactions, the spread of parasites between populations becomes a concern. Overall, understanding the ecological dynamics and distribution patterns of small mammals and their arthropod ectoparasites across different elevations of Mount Meru in Tanzania is vital for public health management and biodiversity conservation plans.

1.2 Literature Review

1.2.1 Mount Meru landscapes and its biodiversity

The Tanzanian Mountain massifs have been a subject of fascination for scientists and outdoor lovers for more than a century, offering an adventure for climbers, a breathtaking crater rim for tourists to admire, and an important location for biota research (Lovett and Wasser, 2008). The mountains can be classified into four primary groups based on their specific geologic origins (Lovett and Wasser, 2008). These groups include the Eastern Arc Mountains, which span from the Taita Hills in southern Kenya to the Udzungwa Mountains in southern Tanzania and are characterized as ancient fault block mountains. The Southern Highlands, comprising Mt. Rungwe, the Livingstone, and the Poroto Mountains, were formed as a result of both uplift and volcanism. The Mahale Mountain is part of the Albertine Rift valley. Lastly, the Northern Highlands, which encompass Kilimanjaro, Ngorongoro, and Mount Meru, are the outcome of recent volcanic activity (Lovett and Wasser, 2008).

Mount Meru, which stands as the second-highest peak in Tanzania after Mount Kilimanjaro, is a notable geographical landmark among the East African massifs (Stanley and Kihaule, 2016). This region is known for its diverse flora and fauna, with sizeable endemics. The topography of the area exhibits a predominantly rugged terrain, which can be attributed to past volcanic events. The elevation gradually increases from the Momela Lakes in the northeast and the Ngurdoto crater in the southeast, situated at an approximate altitude of 1 400 meters, to the Meru crater and summit located at the western end, reaching an elevation of 4 566 meters (Stanley and Kihaule, 2016). The value of the Mount Meru ecosystem is derived from the diverse array of landscapes and habitats it encompasses. It is characterized by distinct vegetation zones, encompassing grasslands and deciduous open woodlands at lower altitudes, followed by montane forests spanning from 1 700 to 3 000 m. Higher up, there is a presence of evergreen ericaceous scrub that serves as a transitional zone to afro-alpine vegetation (Bussmann, 2006). As the centerpiece of the Arusha National Park (which covers an area of 552 km^2), Mount Meru is a popular ecotourism destination in the nation. It's a pretty popular spot for tourists and researchers because of its biodiversity and numerous trails, which cater to the interests of nature enthusiasts (Stanley and Kihaule, 2016). It receives an average of 53 433 visitors per year, according to the last six years of data. The rapid expansion of the human population surrounding the mountains has resulted in greater pressures on the natural forests and their vertebrate fauna due to human activities such as grazing, agricultural encroachment, and firewood collection (Maleko *et al*., 2012). The mountain range harbors a wide array of flora and fauna, including endemic species and those listed in the IUCN red lists (Stanley and Kihaule, 2016). The lower and central slopes of the mountain exhibit significant breadth and support a diverse range of mammalian fauna, such as vulnerable African elephants (*Loxodonta africana*), Giraffe (*Giraffa camelopardalis*), African buffalo (*Syncerus caffer*), Leopard (*Panthera pardus*), Warthog (*Phacochoerus africanus*), Baboon (*Papio anubis*), and Monkey (Cercopithecidae) (Maleko *et al*., 2012; Kahana *et al*., 2013). Additionally, this region is home to over 400 species of birds, 10 species of amphibians, and approximately 24 reptiles (Scoon, 2018). Small mammals are also integral components of the biodiversity within the Mount Meru ecosystem (Demeter and Hutterer, 1989; Stanley and Kihaule, 2016).

1.2.2 Non-volant small mammals

Non-volant small mammals refer to mammals weighing less than 500 g that encompass non-flying species such as rodents and shrews, excluding bats (Hoffmann *et al*., 2010). Because of their extensive range of morphological, physiological, feeding, and life-history strategies, these organisms have demonstrated remarkable adaptability to various environmental conditions (Hope and Parmenter, 2007; Alemayehu and Bekele, 2013). They exhibit a higher degree of elusiveness, often occupying isolated areas within rainforests, mountains, and deserts, and play a crucial role in ecosystems all over the world (Gazzard *et al*., 2023). In Africa, about 17% of the rodent species are pests (Monadjem *et al*., 2015; Mulungu, 2017; Swanepoel *et al*., 2017), which have a detrimental impact on agriculture and stored products while also serving as reservoirs and hosts for zoonotic diseases (Meerburg *et al*., 2009; Mulungu, 2017). On the other hand, small mammals in general, including rodents and other small mammals, are an invaluable link in the food chain; they serve as food for vertebrates as prey, and they regulate the population dynamics of insects and other invertebrates by acting as predators (Ojeda and Chazarreta, 2018; Gazzard *et al*., 2023). Furthermore, small mammals contribute to various ecological functions such as vegetation pruning, soil aeration, and the dispersal of pollen, fungal spores, and seeds (Wang and Ives, 2016; Geng *et al*., 2018). Certain species of burrowing rodents play a crucial role in the creation of subterranean habitats, which can be utilized by various other animals. Additionally, certain species serve as ecosystem engineers by constructing dams that contribute to the purification of water systems and the regulation of floods and droughts (Gazzard *et al.,* 2023). In addition, rodents are susceptible to environmental changes at a smaller scale because of their limited dispersal capacity and high affinity for particular types of habitats (Stirnemann *et al*., 2015; Cuypers *et al.,* 2022). Hence, they serve as excellent indicators of environmental change for landscape ecologists. Overall, regardless of how we look at them, they are more than mere vermin and are very important creatures in the natural world, and they deserve to be recognized for their positive contribution to the environment. Therefore, assessing them is a crucial part of studying terrestrial ecosystems.

1.2.3 Altitudinal distribution of small mammals

Mountain ranges provide an exceptional opportunity to investigate how species respond to changing conditions due to the rapid variation in climatic conditions and related productivity measures over short distances (Vetaas, 2021). Altitudinal gradients are characterized by significant variations in temperature, rainfall, and soil, with environmental conditions at the extremes that pose considerable challenges to species' ability to adapt and tolerate in terms of evolutionary and physiological contexts (Heaney, 2001). Different montane species, including rodents and shrews, are currently facing challenges maintaining their existence due to shrinking habitats (Gazzard *et al*., 2023) attributed to climate change, ecological disturbances, and other impacts caused by human activity (Willig and Presley, 2015; Neate–Clegg *et al.,* 2018; Rogora *et al*., 2018; Gazzard *et al*., 2023). Gaining insight into the distribution patterns of montane species across elevational gradients holds significant value for biodiversity conservation efforts as well as for predicting species' responses to forthcoming environmental changes and facilitating effective conservation strategies to maintain the species (Rogora *et al*., 2018). To this end, ecologists have become increasingly interested in learning about the elevational distribution of small mammals in different mountain ranges across the globe (Moritz *et al*., 2008; Benedek and Sirbu, 2019; Chen *et al*., 2020; Craig *et al*., 2020; Mena and Pacheco, 2020). These studies are notable for the comprehensive insight they provide into the specific and general patterns of mammalian elevational distribution. Undoubtedly, a reassessment of species distribution serves as a vital benchmark for assessing the impact of climate and other environmental changes over a period of time.

Temporal variations in the elevational distributions of natural communities provide valuable insights into the rate of change that takes place (Rogora *et al*., 2018). In order to make precise predictions regarding the ecological impacts of habitat changes, it is essential to possess a comprehensive understanding of the interplay between biotic and abiotic factors as well as the occurrence patterns of different species. Recent evidence suggests that there is a tendency for greater species richness to occur at mid-elevations in mountain landscapes (Brown, 2001; Heaney, 2001; McCain, 2004), which challenges the previously established notion that species richness increases with elevation and that richness and elevation are inversely related (MacArthur, 1972). The mid-elevational peak pattern, initially identified by Rahbek (1995), was further verified in 2005 through the analysis of 56 published montane diversity surveys. Out of these surveys, only four did not report the highest species richness at mid-elevations (McCain, 2005). However, despite the increasing amount of global evidence supporting this general pattern, the documentation of mid-elevation distributions of small mammals in Africa has been relatively rare (Taylor *et al*., 2015). Considering the influences of climate change and the human pressure from the lower altitudes surrounding the African mountains, assessment of species distribution along elevational gradients is most important.

1.2.4 Demographic characteristics of small mammals

The populations of small mammals frequently display significant fluctuations in both abundance and composition over space and time (Leirs *et al*., 1997; Makundi *et al*., 2005). These variations are influenced by a multitude of factors, such as the quality of their habitat in terms of available cover and food resources, the level of predation they experience, as well as environmental factors like temperature, humidity, and rainfall (Lin and Batzli, 2001; Getz *et al*., 2006). In the region of sub-Saharan Africa, however, the regulation of demographic processes and population dynamics is predominantly influenced by rainfall, as it directly affects primary productivity and food availability (Lima *et al*., 2001b; Makundi *et al*., 2006; Massawe *et al.,* 2007). Rainfall seems to be the most influential factor in the breeding patterns and population size of rodents due to its effect on the onset of reproduction, the duration of the breeding season, and the survival of offspring (Leirs *et al*., 1997; Makundi *et al*., 2007, 2010; Meheretu *et al*., 2015; Lock and Wilson, 2017). The main argument centers on the notion that the presence of fresh vegetation immediately following seasonal rainfall stimulates the seasonal breeding of rodents and that the quality and quantity of plant biomass affect the rodent's reproductive success. By understanding how these factors influence breeding patterns, population dynamics, and reproductive success, we gain valuable insights into the complex mechanisms that drive species survival and abundance. Such knowledge not only enhances our understanding of fundamental ecological processes but also has practical implications for biodiversity conservation and ecosystem health.

1.2.5 Arthropod ectoparasites of small mammals

The ecological interactions of small mammals are not only limited to humans and other wildlife but also involve organisms that inhibit their bodies, commonly referred to as parasites (Krasnov *et al*., 2007). This suggests that the host functions as a suitable environment for the parasite, offering it sustenance, living space, and opportunities for reproduction, irrespective of whether the parasite resides internally or externally within the host (Wall and Shearer, 2001; Krasnov *et al*., 2007). Ectoparasites are a diverse and well-adapted group of invertebrates. These organisms exhibit a spectrum of characteristics, including obligate or facultative parasitism, permanent or intermittent attachment, and infestation of both surface and subcutaneous parts of the host’s body. Their primary hosts are predominantly vertebrates, including small mammals. However, some arthropod ectoparasites, such as the *Varroa* spp. (Mesostigmata mite), have been observed to parasitize invertebrates, such as honey bees (Anderson and Trueman, 2000; Reyes-Quintana *et al*., 2019).

Ectoparasites have gained considerable attention in ecological research due to their significant impact on the regulation of host populations, the structuring of host communities, and their role as vectors of diseases. According to Schmid-Hempel (2021), parasites reduce the overall fitness of their hosts by depleting the resources available to them. The act of consuming energy by certain entities frequently results in a decrease in the energy reserves of the host, leading to detrimental effects on the host's physical well-being (Hakkarainen *et al*., 2007; Mougeot *et al*., 2009). This phenomenon is associated with a reduction in immunity and an elevation in mortality rates (Comas, 2020). Parasites possess the capacity to diminish host density (Ebert *et al*., 2000), thereby resulting in the decline of prey populations and subsequent repercussions on ecosystem function. Moreover, the diminished immune response of the host, heightened contact with potential sources of infection, and heightened burden of additional infestations and infections collectively augment the likelihood of transmitting the pathogens to other individuals within the community (Solak *et al*., 2020). This is attributed to the fact that rodents and their associated ectoparasites are recognized as medically and veterinary important due to their role as reservoirs for pathogens that pose a threat to human health (Makundi *et al*., 2015; Haikukutu *et al*., 2022). In addition, climate change forecasting models indicate that alterations in wildlife population distribution, such as migration to elevated mountainous regions, may lead to unprecedented interactions with other populations. Consequently, the transmission of parasites between these populations could potentially impose detrimental consequences on susceptible and unexposed hosts (Lvarez-Ruiz *et al*., 2018). Over all, it is of utmost importance to understand the spatial variation in parasite-host dynamics in order to gain insights into the ecological and evolutionary processes that affect host populations as well as for the effective management of species conservation and zoonotic disease (Poisot *et al*., 2017).

Approximately 10.7% of rodent species are implicated in the transmission of zoonotic diseases (Kimbrough, 2021). In Africa, many rodent species, including but not limited to *Montemys, Cricetomys, Arvicanthis, Mastomys, Rattus, Lemniscomys, Rhabdomys, Mus,* and *Lophuromys,* are known hosts of medically important pathogens and vectors (Makundi *et al*., 2015; Haikukutu *et al*., 2022). The risk of transmission varies significantly across different habitats and is influenced by human behavior and the degree of contact rates (Meerburg *et al.,* 2009). However, small mammals possess the capability to transmit infectious agents through multiple pathways: horizontally to other rodents living close to anthropized environments; from anthropized areas to wild animals; and as reservoirs on which intermediate arthropod vectors such as flea, mite, louse, bug, tick, mosquito, Tsatsefly, and sandfly and other vectors feed and get infected before transmitting the infectious agent to humans, livestock, and wildlife (Makundi *et al*., 2015; Eisen *et al*., 2020). Overall transmission of the pathogens from rodent to human is adapted and modified from Meerburg *et al.* (2009) in Figure 1.1.

Compared to other wildlife, the relationship between parasites and their environment is much more complex (Wilson *et al.*, 2002). Parasites do not spread evenly across their range but rather congregate on hosts. They exhibit a non-uniform distribution within their habitat, tending to aggregate on specific hosts rather than being evenly dispersed (Wilson *et al.*, 2002). Such an uneven distribution is attributed to the influence of host and parasite characteristics on the host's exposure to and susceptibility to parasites (Wilson *et al*., 2002). Host-related factors are partly intrinsic and include sex, age, body size, breeding status, and fur type and color (Viljoen *et al*., 2011; Postawa and Nagy, 2016). Furthermore, parasite distribution affected by climatic conditions and landscape of the environment. Altitudinal gradients influence small mammal distribution (Rahbek, 1995; Brown, 2001; Heaney, 2001; Thomas *et al*., 2022), potentially extending to their arthropod ectoparasites. Understanding these patterns is crucial for understanding community dynamics.

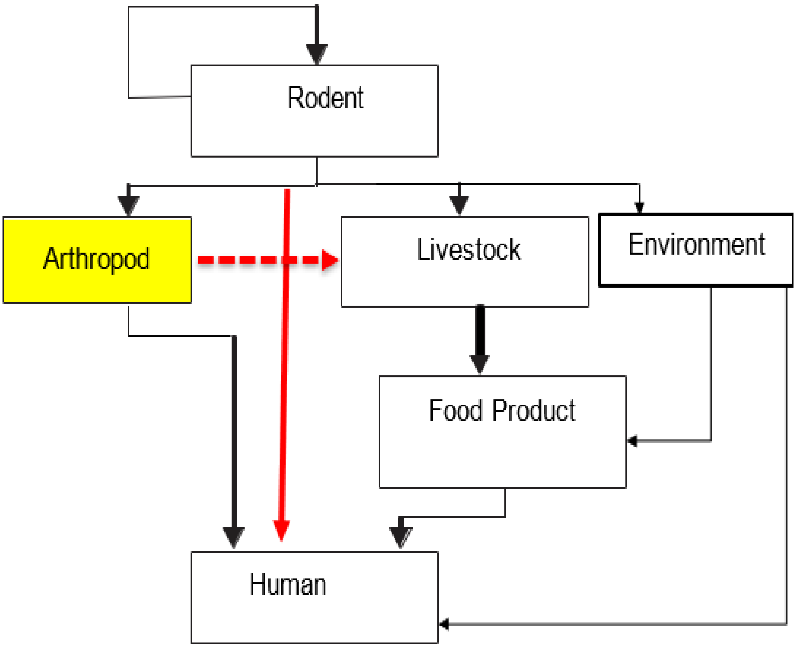

Figure 1.1: Pathogen transmission routs from rodents to humans. Adapted and modified from Meerburg *et al.* (2009)

1.3 Statement of the Problem and Justification of the Study

Mount Meru is one of the eastern Africa hotspots for biodiversity, a refugia for numerous taxa and providing important ecosystem services (Demeter and Hutterer, 1986). There is very little published on small mammals from this mountain, while other mountains in Tanzania, such as Kilimanjaro (Mulungu *et al*., 2008; Stanley *et al*., 2014; Thomas *et al*., 2022), Udzungwa (Stanley and Hutterer, 2007), and Usambara (Stanley and Goodman, 2011), appear to have diverted the attention of most ecologists, thereby overshadowing the lesser-known mountain in its neighborhood. One of the first reports concerning Mount Meru is that of Demeter and Hutterer (1986), in which the authors provided scattered records of species occurrence, mainly from the lower vicinity of the mountain. Only Stanley and Kihaule (2016) employed a systematic survey to document the species distribution data of small mammals in the study area, but they did not include the habitat at the lower altitudes and did not apply Havahart traps to consider large-bodied species. Updated and more detailed information from all habitat types is crucial to having a full data set on the small mammal diversity of this ecosystem. A survey of small mammals has consistently shown changes in the elevational distribution of species as a response to climate change and other impacts caused by human-related activity (Moritz *et al*., 2008; Rowe *et al*., 2010), but limited reports in case of Africa. The lower altitude of Mount Meru has been experiencing human pressures such as grazing and deforestation (Maleko *et al*., 2012). Therefore, the survey of species distribution results of this study might also help to predict species responses to future environmental changes and establish conservation strategies for small mammal biodiversity and ecosystem functionality in the future.

Despite the ecological importance of small mammals, research conducted in Tanzania has shown a tendency to focus primarily on pest species (Mulungu *et al*., 2013; Monadjem *et al*., 2015; Mulungu, 2017), leading to a scarcity of available data regarding other non-pest forest species. In order to ensure effective pest control or conservation management for forest species, studying their demographic characteristics is crucial. Understanding these demographic factors, such as population dynamics and breeding patterns, is important not only for the conservation and management of the species but also for gaining insights into the dynamics of wildlife-borne diseases due to the fact that small mammals are known hosts of parasites that cause disease in humans and livestock (Makundi *et al*., 2015).

Tanzania is among the handful of countries in Africa where active foci of deadly zoonotic diseases that can be transmitted by small mammals and their ectoparasite vectors have been persistent (Makundi *et al*., 2015). Mount Meru is a refuge for a number of endemic and threatened species that are documented on the International Union for Conservation of Nature's (IUCN) Red List

(Demeter and Hutterer, 1989; Stanley and Kihaule, 2016). Parasitic infection poses an additional threat to a critical species and overall biodiversity (Pedersen *et al*., 2007); however, there is currently no available information regarding the possible role of arthropod ectoparasites in the transmission of zoonotic infectious agents in the Mount Meru ecosystem.

Mount Meru is a popular ecotourism destination that attracts a huge number of Tourists and Researchers (Stanley and Kihaule, 2016). The wildlife present in the park could interact with these parties, which subsequently increases the likelihood of their engagement with the surrounding community. Furthermore, different wildlife, including rodents and shrews, cross the boundaries of the park and enter human habitations, thereby establishing direct or indirect interactions with humans and livestock residing in close proximity to the park's periphery (Mawanda *et al.,* 2020). All these interactions contribute to an increased probability of transmission of pathogens between humans and animals, thereby modifying the risk of zoonotic infections in the biodiversity of the ecosystem. Furthermore, according to the United Nations (UN Health Agency, 2022), there has been a 65% increase in zoonotic disease outbreaks in Africa over the past ten years. In light of the overall increase in human-wildlife-interaction, it is important to put the assessment of small mammals for arthropod ectoparasites at the top of the list; a key foundation for future wildlife disease surveillance efforts and the development of effective biodiversity conservation management plans. In addition, molecular-based ectoparasite species identification is of very importance in the management of wildlife-borne diseases. However, there is currently a lack of molecular data for ectoparasite species from Tanzanian rodents. Thus, the use of molecular approaches to identify ectoparasite species will be vital in addressing the scarcity of sequencing data for African rodent ectoparasites in GenBank. In essence, this study addresses gaps in knowledge, aids conservation planning, and informs disease management efforts in the face of changing ecological dynamics and increasing zoonotic risks.

1.4 Objectives

1.4.1 Overall objective

The study aimed to understand the ecological dynamics and distribution patterns of small mammals and their arthropod ectoparasites across different elevations of Mount Meru in Tanzania.

1.4.2 Specific objectives

The specific objectives of this study were:

i. To assess changes in the elevational distribution of small mammals over temporal spans;
ii. To determine the breeding patterns and demographic aspects of the dominant small mammal species inhabiting the Mount Meru ecosystem;
iii. To examine the elevational distribution of arthropod ectoparasites infesting the two dominant small mammal species.

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CHAPTER TWO

A DECADE-LONG CHANGE IN THE ELEVATIONAL DISTRIBUTION OF NON-VOLANT SMALL MAMMALS ON MOUNT MERU, TANZANIA

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A Decade-Long Change in the Elevational Distribution of Non-Volant Small Mammals on Mount Meru, Tanzania

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Abstract: Understanding species distribution across elevational gradients is crucial for developing conservation strategies for montane biotic systems. A survey of small mammals was conducted on Mount Meru at six elevations, ranging between 1500 m and 3650 m. A total of 803 small mammal individuals, including 2 shrew species and 13 rodent species, were documented. Of these, *Crocidura newmarki* and *Lophuromys verhageni* were endemic on Mount Meru. Species richness was highest at mid–elevations, which is in line with the global pattern for small mammals. Prior to our study, the most complete data on small mammals on Mount Meru was collected in 2009. Our study provides an opportunity to show how small mammal elevational distribution has changed, over the last decade. We found six species (*Arvicanthis niloticus*, *Mastomys natalensis*, *Lemniscomys striatus*, *Dasymys incomtus*, *Cricetomys ansorgei*, and *Montemys delectorum*), which were not documented in 2009, but did not find *Otomys tropicalis*. Interestingly, the community composition at higher elevations in 2021 resembles that at lower elevations in 2009, suggesting that small mammal species have moved their range upward over time. Climate change could be a factor associated with the distributional shift found.

Keywords: elevational distribution; rodents; shrews; species composition; climate changes

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1. Introduction

Tropical mountains are key habitats for biodiversity; they harbour a high level of species richness and endemism [1,2]. However, due to climate change, ecological disturbances, and other human–induced changes, montane species are, increasingly, under threat [3–5]. Understanding the distribution of montane species along an elevational gradient enables the development of conservation strategies and foresees species's responses to future environmental changes [6–8]. Over the last decades, there has been an increase in studies that document the elevational distribution of small mammals worldwide (China [6], Ethiopia [9], Peru [10], Philippines [11,12], Slovakia [13], Romania [14], the USA [15], and Tanzania [16,17]). The understanding of specific and general patterns of mammalian elevational distribution provided by these studies is noteworthy, and it serves as a vital benchmark for assessing the effect of environmental change over time. For instance, Craig et al. [9] recently revealed that changes in climate have resulted in in upward elevational changes in the ranges of rodent and shrew species in Simien Mountains National Park, Ethiopia, after 88 years.

Many East African mountain ranges have been the focus of research on the elevational distribution of small animals, including Mount Elgon in Uganda [18,19], Simien Mountain

National Parks in Ethiopia [9], Mount Kenya in Kenya [20], and the Udzungwa [21] and Kilimanjaro mountains in Tanzania [16,17]. There are, of course, other topographically important massifs that have attracted less scientific attention.

Mount Meru (4566 m) is the second highest mountain in Tanzania, after Kilimanjaro, and the centrepiece of Arusha National Park. The high diversity of landscapes, from open grassland to montane and Afroalpine forests, are home to a highly diverse wildlife community [22]. The lower and central slopes are particularly broad and provide a potential refuge, for a great array of large mammalian fauna [23]. Small mammals, including rodents and shrews, are, also, important components of this mountain ecosystem, where they play a vital role in the distribution and abundance of other animal taxa through top–down and bottom–up control. Meanwhile, they function as soil aerators, pollinators, and seed dispersers [24]. Despite their key contribution to the ecosystem, very little is known about them on Mount Meru.

The first reports of small mammal fauna on Mount Meru are those of Demeter and Hutterer [25], who provided scattered records of species occurrence, mainly from the lower altitudes. Only Stanley and Kihaule [26], in 2009, employed a systematic survey to document small-mammal distribution along elevational gradients in the study area. Updated and more detailed information about this ecosystem is, therefore, required, since, as the climate changes over time, so does the distribution of species [27]. Resurveys of small mammals across the world have revealed elevational shifts in species ranges, in response to climate change [9,15,28]. However, we found limited references in Africa. We, therefore, sought to: (i) determine the current elevational distribution and diversity of small mammal species and (ii) compare our findings to those from the 2009 survey [26], to assess community composition changes over time along an elevational gradient.

2. Materials and Methods

2.1. Study Area

The study was conducted on Mount Meru (3°14′48″ and 36°44′54″), located in the northeastern part of Tanzania, about 35 km northeast of Arusha town (Figure 1). The topography is, generally, rugged, as a result of historical volcanic activity, and rises from the Momela Lakes (northeast) and Ngurdoto crater (southeast), lying at 1400 m, to the Meru crater and summit (west end), at 4566 m. The rainfall pattern is bimodal and varies with the altitude. The short rain period occurs between October and December, and the long rainy season is between March and May. The dry season is from June to September. In lower, drier areas, annual rainfall ranges between 600 mm and 1300 mm, and at 2590 m a.s.l. in the Meru crater, between 1400 mm and 2400 mm [23].

2.2. Sampling Sites and Vegetation Types

There is a single path, which provides access to climbers from the lowlands, and runs up the southeastern slope of the massif. Six sites were sampled for small mammals, between February and November 2021, along this route, with an elevation ranging from roughly 1500–3650 m a.s.l. Sites were selected based on altitude and the major vegetation type. Each site and elevation was centered at the corresponding campsite. Details on habitat notes related to each site, trapping altitude, coordinates, and date of sampling are given below (representative habitats photographed at each site are provided in Figure 2). Vegetation identification in each site was based on [29,30]. All sampling sites span along the Arusha National Park.

Savanna (SA): 1500 m; 3°13′20.766″ S, 36°52′30.076″ E; 11–16 February 2021. This site is located at the foot of Mount Meru. The vegetation cover of this site varies from grassland, thicket, and bushland to woodland. The conspicuous plant species include *Caesalpinia decapetala*, *Croton macrostachyus*, *Jacaranda mimosifolia*, *Senna spectabilis*, *Ocimum gratissimum*, *Orthosiphon parvifolius*, *Solanum incanum*, *Aerva lanata*, *Lantana trifolia*, and tussock grasses. Scattered patches of *Acacia xanthophloea* trees are, also, common on this site.

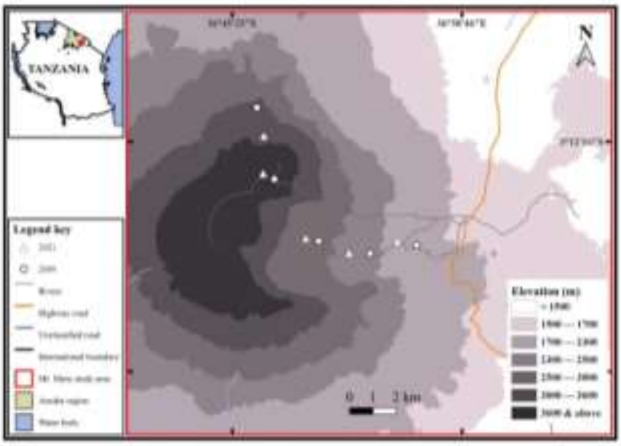

Figure 1. Map of Mount Meru, Tanzania, showing sampling points. Symbols indicate trapping elevations for 2009 (circle) and 2021 (triangle) studies. Elevation zones are represented with color in the legend.

Lower montane forest (LMF): 2000 m; 3°14′33.102″ S, 36°49′15.528″ E; 4–9 July 2021. This site is in a lower montane forest, with a closed canopy of tall and medium–height trees of various species, such as *Diospyros abyssinica*, *Olea hochstetteri*, *Rhamnus prinoides*, *Ficus thonningii*, *Nuxia*, and *Podocarpus*.

Upper montane forest (UMF): 2500 m; 3°14′32.892″ S, 36°47′25.644″ E; 4–9 July 2021. This site is positioned in the upper montane forest dominated by *Juniperus procera and Podocarpus gracilior*, which is followed by a small band of cloud forest with *Hagenia abyssinica*. In much of this type of forest, there was dense undergrowth of herbaceous plants, lianas of different species, and shrubs, and the trees were festooned with epiphytes. Mosses were common on dead wood and live trees. The site, also, included rivers and swamp areas that were rounded off by Papyrus and Miscanthusas plant species.

Upper montane forest/Ericaceous heath (UMF/EH); 2950 m: 3°13′28.724″ S, 36°47′7.782″ E; 3–8 August 2021. This site is located in a transitional zone between upper montane forest and ericaceous heath habitats, conquered by *Hagenia abyssinica*, *Erica arborea*, *Stoebe kilimandscharica*, and some *Lobelia* species.

Ericaceous heath (EH); 3500 m: 3°13′6.192″ S, 36°46′24.042″ E; 3–8 August 2021. This site was situated in the ericaceous heathland, where *Erica reunionensis*, *Pennisetum setaceum, and Santolina* species dominated the habitat. The majority of the forests on this site were dried, due to the experienced firebreak.

Afroalpine (AA); 3650 m: 3°12′6.193″ S, 36°46′9.294″ E; 11–16 November 2021. This highest point is in the Afroalpine zone. Tussock grass and some scrubs were found on this site.

Figure 2. Photographs of representative habitats for each site sampled on Mount Meru, Tanzania. SA (savanna grassland), LMF (lower montane forest), UMF (upper montane forest), UMF/EH (upper montane forest/Ericaceous heathland), EH (ericaceous heathland), and AA (Afroalpine).

2.3. Trapping Techniques and Identification

The trapping of small mammals was carried out in trap lines, consisting of medium–sized Sherman, 7.5 × 9 × 23 cm (H.B. Sherman Traps Inc., Tallahassee, FL, USA), and Havahart traps. At the SA, LMF, UMF, and UMF/EH, four trap lines were established, each with 50 traps. In the EH and AA sites, a total of 38 Sherman traps only were employed in five trap lines. The trap lines in all sites were established from 30 m to 50 m apart, as described in the literature, with trap stations spaced up to 10 m apart, with one trap per station. There were six days of sampling at each site, accumulating a total of 1140–1200 trap nights (Table 1). The Sherman traps were baited, using peanut butter mixed with maize flour and avocado, whereas the Havahart traps were baited with a combination of fresh banana, green maize, and avocado. Traps were inspected every morning at 07:00–08:00 h and rebaited. Animals were euthanized with Diethyl ether, using a piece of cotton wool, in the temporary laboratory in the field, and handled following the ethical policies and guidelines approved by the committee for Animal Care and Use of Sokoine University of Agriculture. For each representative species, muscle/or kidney tissues were preserved, in 96% ethanol, for further research. For all trapped animals, standard external body measurements (body, tail, hindfoot, and left ear) and weight were recorded. This study considered only non–flying small mammals, including shrews and rodents. Animals were handled following the guidelines of the American Society of Mammalogists [31]. Each captured species was identified in the field, using distributional data from Happold [32], Stanley and Kihaule [26], and experts from Sokoine University of Agriculture's Institute of Pest Management. Representative samples for each species are kept at the Institute of Pest Management, Sokoine University of Agriculture, Tanzania.

2.4. Data Analysis

We compiled the number of individuals of each small mammal species per site and calculated the sampling effort in terms of trap nights. Unequal trapping effort among sites was accounted for, by using as a measure of species abundance a capture index, i.e., trap success. We calculated percentage of trap success, by dividing the number of individuals caught by the number of trap nights (i.e., the number of traps used, multiplying by number of trapping days) and multiplying by 100. A trap night is defined as a single trap set for 24 h. Species composition is given by the relative abundances of species, i.e., their proportions within the assemblage. A linear regression model was used to test the relationship between species relative abundance and elevation. To assess completeness of sampling, we generated species accumulation curves and calculated estimated species richness, using Estimate S version 9.1.0 [33]. We used the Chao non–parametric estimator, to estimate the number of missing species in the overall survey pool. For individual sites, species richness was estimated, using the Abundance Coverage Estimator (ACE), due to its capability to knob species abundance data with low observed richness. Diversity and evenness were, also, calculated for each site. To evaluate species diversity, we used the Shannon diversity index, H' [34], and derived evenness, E (H'/lnS), to show how the species are distributed in the community.

2.5. Analysing and Comparing the 2009 and 2021 Surveys

We compared the present elevational distribution of small mammals with prior surveys on Mount Meru, using a diversity and distribution dataset collected by William T. Stanley and Philip M. Kihaule in 2009 (hereafter, 2009 survey) and published in 2016 [26]. Between 16 July 2009 and 19 August 2009, the authors surveyed small mammals at five different elevations (1950 m, 2300 m, 2650 m, 3000 m, and 3600 m) along the southeastern aspect of Mount Meru using Sherman traps, Victor Rat traps, Museum Special traps, and pitfall buckets. Bait for each trap consisted of freshly fried coconut coated in peanut butter. We used the generated species distribution and abundance data of the 2009 survey to determine small mammal distributions, for each site over time. To account for the inconsistency in the trapping efforts between the two surveys, the species's trap success and percentage of relative abundance were used for comparison. The absolute abundances for both studies are given in Appendix A Table A1. All of the 2009 small mammal data, on which our study was based, are publicly available [26]. All the sites sampled in 2009 were included within the boundary of our survey. To make direct comparisons between the 2009 and 2021 surveys, sites from both surveys were consolidated into six elevational sampling bands. The elevational zone is established, based on the major vegetation belts of Mount Meru: (a) savanna (SA; 1500–1700 m; this site was not surveyed in the 2009 study), (b) lower montane forest (LMF; 1700–2300 m), (c) upper montane forest (UMF; 2300–2550 m), (d) upper montane forest/ericaceous heathland (UMF/EH; 2550–3000 m), (e) ericaceous heathland (EH; 3000–3600 m), and (f) Afroalpine (AA; 3600 m and above) [29]. QGIS software was used to create these digital elevation models of the study sites.

To assess changes in small mammal community composition for each site and time period, we conducted a Principal Coordinate Analysis (PCoA) using a Paleontological Statistics Software (PAST) Package. The Bray–Curtis dissimilarity matrix was used to quantify the compositional dissimilarity within each zone, between the two surveys. A paired t–test was used to compare the distribution of sites between the 2009 and 2021 surveys along the first major axis. To estimate changes in climate between the two surveys, we downloaded 43 years (1979–2021) of historical climate data from Arusha National Park, the core of Mount Meru, from the data source ERA5, the fifth–generation ECMWF atmospheric reanalysis of global climate, with a spatial resolution of 30 km [35]. We converted the yearly data to about 10–year averages (1979–1988, 1989–1998, 1999–2008, and 2009–2021), and the average mean temperature for each interval was calculated, to determine the mean increase temperature per decade. We regressed the annual mean temperature against the year for a period of 43 years, to see the trend of changing temperatures over time. Changes in climate over time were evaluated with simple linear regression, where the year was used as an explanatory variable and the yearly mean temperature variable as a response.

3. Results

3.1. Abundance and Species Richness across Elevation Gradient

We recorded 803 small mammal captures in 7080 trap nights, with a total trap success of 11.3%, ranging from 4.5% to 21.9%. Of the small mammals captured, 595 were rodents (Rodentia) and 208 were shrews (Insectivora). While rodents belonged to 13 species under 12 genera, the shrews belonged to 2 species under 1 genus (Table 1). Only two of the species (*Lophuromys verhageni* and *Crocidura newmarki*) were endemic to the study area. *Praomys taitae* was the most abundant species, with 40% ($n = 321$) contribution of the total small mammals. *Crocidura newmarki* was the second most abundant species, with a percentage of relative abundance of 15.8% ($n = 127$). *Mus triton* 0.5% ($n = 4$), *Lemniscomys striatus* 0.5 % ($n = 4$), and *Montemys delectorum* 0.4% ($n = 3$) were the three most infrequently captured species. In the SA sites, *Mastomys natalensis* was the most abundant, accounting for 51.8% of the total individual in the habitat, where as in the LMF and UMF, *Praomys taitae* were the dominant species, with 57.1% and 73.0%, respectively, for each site. As for the EH, *Crocidura* species and *Lophuromys verhageni* were frequent. A linear regression model of species richness, total percentage of trap success, and total percent contribution in relation to elevation were not significant (all $p > 0.05$). The chi–squared (X^2) analysis results in Table 2 show that the species composition of small mammals in all habitats were significantly different ($p < 0.05$), except the UMF/EH ($X^2 = 6.27$, df = 10, $p = 0.134$).

Table 1. Percentage contribution and total abundance (in parentheses) of small mammals in different sites on Mount Meru.

	Sites						
	SA	**LMF**	**UMF**	**UMF/EH**	**EH**	**AA**	**Totals**
Rodents							
Rhabdomys dilectus	3.6(2)	0.8(1)	1.1(3)	17.4(26)	12.7(20)	70.6(36)	11.0(88)
Praomys taitae	–	57.1(72)	73.0(192)	26.2(39)	11.4(18)	–	40.0(321)
Montemys delectorum *	–	–	0.8(2)	0.7(1)	–	–	0.4(3)
Mus triton	–	–	–	–	–	7.8(4)	0.5(4)
Mastomys natalensis	51.8(29)	–	–	–	–	–	3.6(29)
Lophuromys verhageni	–	–	–	8.1(12)	23.4(37)	9.8(5)	6.7(54)
Lemniscomys striatus	–	–	1.1(3)	0.7(1)	–	–	0.5(4)
Graphiurus murinus	–	–	–	14.1(21)	3.2(5)	–	3.2(26)
Grammomys dolichurus	10.7(6)	2.4(3)	1.9(5)	2.7(4)	1.9(3)	–	2.6(21)
Dendromus insignis	–	–	–	–	2.5(4)	5.9(3)	0.9(7)
Dasymys incomtus	–	2.4(3)	1.1(3)	0.7(1)	–	–	0.9(7)
Cricetomys ansorgei	–	3.2(4)	1.1(3)	1.3(2)	¥	¥	1.1(9)
Arvicanthis niloticus	30.4(17)	4(5)	–	–	–	–	2.7(22)
Shrews							
Crocidura newmarki	3.6(2)	30.2(38)	7.2(19)	15.4(23)	26.6(42)	5.9(3)	15.8(127)
Crocidura allex	–	–	12.5(33)	12.8(19)	29(18.4)	–	10.1(81)
Rodent abundance	96.4(54)	69.8(88)	80.2(211)	71.80(107)	55.1(87)	94.1(48)	74.1(595)
Shrew abundance	3.6(2)	30.2(38)	19.8(52)	28.2(42)	44.9(71)	5.9(3)	25.9(208)
Rodent species	4	6	7	9	6	4	13
Shrew species	1	1	2	2	2	1	2
Trap success (%)	4.7	10.5	21.9	12.4	13.9	4.5	11.3
Trap effort	1200	1200	1200	1200	1140	1140	7080

* As *Praomys delectorum* in previous studies (but see Nicolas et al., 2021) "–"Not recorded; ¥ Not assessed. SA (savanna); LMF (lower montane forest); UMF (upper montane forest); UMF/EH (upper montane forest/Ericaceous heathland); EH (ericaceous heathland); and AA (Afroalpine).

Table 2. Chi-squared (X^2) statistical results of species composition in each sites.

	SA	LMF	UMF	UMF/EH	EH	AA
X^2	27.00	22.87	15.00	6.27	19.20	27.00
df	5	7	9	10	8	5
p-value	**0.000**	**0.001**	**0.035**	0.134	**0.003**	**0.00**

SA (savanna); LMF (lower montane forest); UMF (upper montane forest); UMF/EH (upper montane forest/Ericaceous heathland); EH (ericaceous heathland); and AA (Afroalpine). Bold indicates statistically significant.

Our results show that the distribution of species varies between sites (Table 3). The percentage of relative abundance of *Rhabdomys dilectus* and *Mus triton* was higher in the AA, whereas *Lophuromys verhageni*, *Crocidura newmarki*, and *Dendromus insignis* showed higher percentage of relative abundance in the EH. For *Graphiurus murinus*, 80.8% of the total was found in the UMF/EH. *Praomys taitae*, *Montemys delectorum*, and *Lemniscomys striatus* were highest in the UMF habitat. *Dasymys incomtus* and *Cricetomys ansorgei* were recorded in the LMF. In addition, high abundances of *Mastomys natalensis* (100%), *Arvicanthis niloticus*, and *Grammomys dolichurus* were recorded in the SA habitats. Based on the result of a linear regression model, the distribution of *Rhabdomys dilectus* showed a strong positive relationship with elevation ($R^2 = 0.89$, $p = 0.016$). The distribution of *Dendromus insignis* was, also, strongly related with elevation ($R^2 = 0.80$, $p = 0.05$). Similarly, the association between *Arvicanthis niloticus* and elevation was strong ($R^2 = -0.78$, $p = 0.04$) but negative, indicating a decrease with elevation (Table 3)

Table 3. Percentage of relative abundance of small mammal species across sites on Mount Meru. A linear regression model (R^2) was used to check the relationship between the percentage of relative abundance of each species and elevation.

Small Mammal Species	SA	LMF	UMF	UMF/EH	EH	AA	Total (R^2)
Rhabdomys dilectus	2.3	1.1	3.4	29.5	22.7	**40.9**	11.0(88) [††]
Praomys taitae	0.0	22.4	**59.8**	12.1	5.6	0.0	40.0(321)
Montemys delectorum	0.0	0.0	**66.7**	33.3	0.0	0.0	0.4(3)
Mus triton	0.0	0.0	0.0	0.0	0.0	**100.0**	0.5(4)
Mastomys natalensis	**100.0**	0.0	0.0	0.0	0.0	0.0	3.6(29)
Lophuromys verhageni	0.0	0.0	0.0	22.2	**68.5**	9.3	6.7(54)
Lemniscomys striatus	0.0	0.0	**75.0**	25.0	0.0	0.0	0.5(4)
Graphiurus murinus	0.0	0.0	0.0	**80.8**	19.2	0.0	3.2(26)
Grammomys dolichurus	**28.6**	14.3	23.8	19.0	14.3	0.0	2.6(21)
Dendromus insignis	0.0	0.0	0.0	0.0	**57.1**	42.9	0.9(7) [††]
Dasymys incomtus	0.0	**42.9**	42.9	14.3	0.0	0.0	0.9(7)
Cricetomys ansorgei	0.0	**44.4**	33.3	22.2	[¥]	[¥]	1.1(9) [¥]
Arvicanthis niloticus	**77.3**	22.7	0.0	0.0	0.0	0.0	2.7(22) [††]
Crocidura newmarki	1.6	29.9	15.0	18.1	**33.1**	2.4	15.8(127)
Crocidura allex	0.0	0.0	**40.7**	23.5	35.8	0.0	10.1(81)

[††] $p < 0.05$; Bold indicates highest percentage of relative abundance of the species between sites. [¥] not determined. SA (savanna); LMF (lower montane forest); UMF (upper montane forest); UMF/EH (upper montane forest/Ericaceous heathland); EH (ericaceous heathland); and AA (Afroalpine).

The Shannon–Wiener index of diversity was highest in the UMF/EH (H' = 1.94), and lowest in the UMF (H' = 0.90), as shown in Figure 3A. Values for evenness, also, varied across elevations, with a relatively higher value at the EH (E = 0.75). Figure 3B depicts that there is a tendency for total small-mammals-species and rodent-species richness to be greatest at the UMF/EH and decline substantially at the highest elevations. Likewise, total percentage contribution and percentage of trap success were higher at the UMF and lower in the SA and AA sites (Figure 4). Except for the UMF/EH sites (Figure 5), where *Lemniscomys striatus* was collected on the fourth day, the total number of species reported at each elevation had achieved an asymptote by the third day of trapping. The estimated number of species (Sest) was equal to the observed number of species (Sobs) at all sites, except at the UMF/EH, where it was slightly greater (11.5 species, SE ± 1.10). The total number of species in the overall survey pool was estimated to be 16.2 (SE ± 0.18).

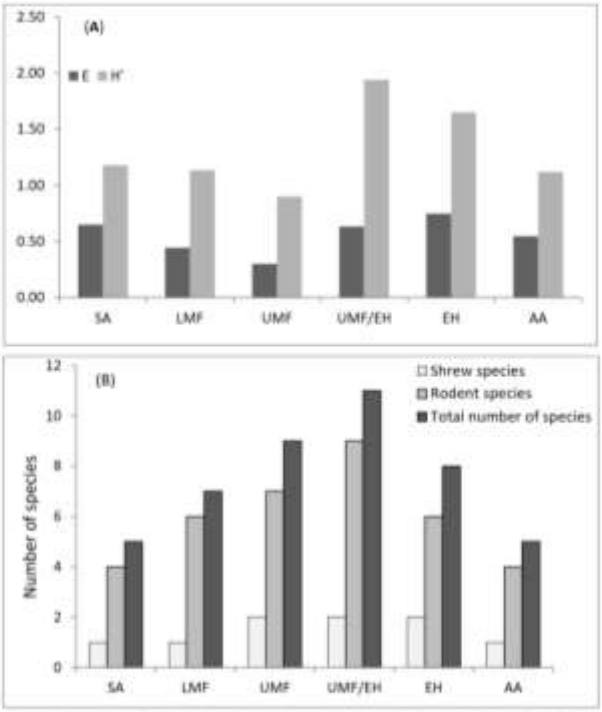

Figure 3. Diversity of small mammals across sites. (**A**) Species diversity evaluated with Shannon diversity index (H') and evenness (E), and (**B**) species richness.

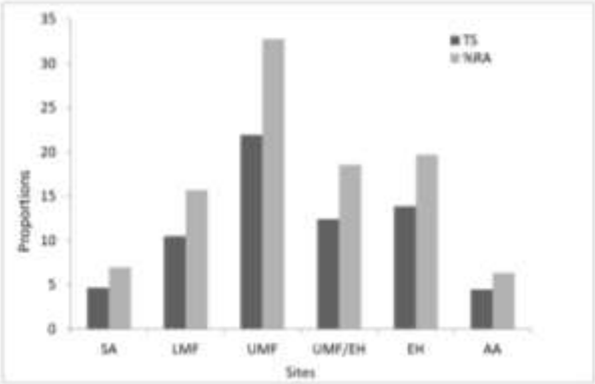

Figure 4. Small mammals's percentage of relative abundance (%RA) and percentage of trap success (TS) across sites.

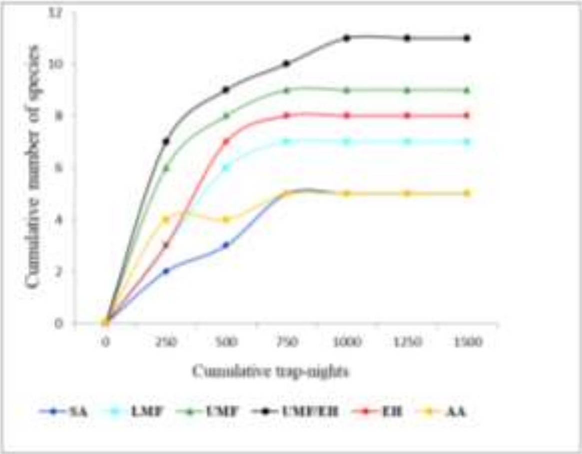

Figure 5. Species accumulation curves for elevations surveyed. The AS and AA sites had the same number of cumulative species starting from the third day of trapping. Asymptote reached on all sites. Trapping effort expressed as trap-nights. SA (savanna); LMF (lower montane forest); UMF (upper montane forest); UMF/EH (upper montane forest/Ericaceous heathland); EH (ericaceous heathland); and AA (Afroalpine).

3.2. Changes in Community Composition in the Last Decade, between 2009 and 2021

We compared small mammal species composition in 2021 against species composition recorded in 2009 (Table 4). Except for the SA, which was sampled only in 2021, both surveys sampled the LMF, UMF, UMF/EH, EH, and AA. The 2009 dataset included 751 small mammal captures (475 rodents and 276 shrews) in 7111 trap nights, with trap success ranging from 3.5% to 18.0% [26]. The rodents and shrews were represented by eight and two species, respectively. The total small mammal species richness in the study area was higher in our survey (15 species) than in 2009 (10 species). *Praomys taitae* was the most abundant species, accounting for 40.7% of total small mammal captures in 2009. The trap success of 2021 was slightly higher than 2009, in most of the sites (Figure 6). The highest percentage of trap success in the 2009 (18.0%) and 2021 (21.9%) surveys was recorded in the UMF zone.

Table 4. Occurrence data in terms of percentage of relative abundance for each species, by elevation zone, in 2009 (numerator) and 2021 (denominator) on Mount Meru.

Species	SA **	LMF	UMF	UMF/EH	EH	AA
Rhabdomys dilectus	–/3.6	–/0.8	–/1.1	19.7/17.4	4.5/12.7	48/70.6
Otomys tropicali	–/0.0	–/–	–/–	1.6/–	0.6/–	2.0/–
Praomys taitae [D]	–/0.0	47.3/57.1	72.0/73.0	31.1/26.2	2.6/11.4	–/–
Montemys delectorum	–/0.0	–/–	–/0.8	–/0.7	–/–	–/–
Mus triton	–/0.0	–/–	–/–	–/–	0.6/–	–/7.8
Mastomys natalensis [d]	–/51.8	–/–	–/–	–/–	–/–	–/–
Lophuromys verhageni	–/0.0	–/–	7.0/–	7.4/8.1	19.4/23.4	4.1/9.8
Lemniscomys striatus [D]	–/0.0	–/–	–/1.1	–/0.7	–/–	–/–
Graphiurus murinus [D]	–/0.0	3.0/–	0.4/–	4.9/14.1	9.7/3.2	–/–
Grammomys dolichurus [D]	–/10.7	1.8/2.4	1.6/1.9	1.6/ /2.7	2.6/1.9	–/–
Dendromus insignis	–/0.0	–/–	–/–	0.8/–	4.5/2.5	4/5.9
Dasymys incomtus	–/0.0	–/2.4	–/1.1	–/0.7	–/–	–/–
Cricetomys ansorgei	–/0.0	–/3.2	–/1.1	–/1.3	–/–	–/–
Arvicanthis niloticus	–/30.4	–/4.0	–/–	–/–	–/–	–/–
Crocidura newmarki	–/3.6	29.3/30.2	7.0/7.2	18.0/15.4	32.9/26.6	8.0/5.9
Crocidura allex [D]	–/0.0	18.6/–	12.1/12.5	14.8/12.8	23.2/18.4	32.0/–
Percentage of contribution per site	–/7.0	22.2/15.7	34.2/32.8	16.2/18.6	20.6/19.7	6.7/6.4
Total number of species	–/5	5/7	6/9	9/11	10/8	6/5
Total number of captures	–/56	167/126	257/263	122/149	156/158	49/51
Trap effort	–/1200	1426/1200	1426/1200	1426/1200	1426/1140	1407/1140
Trap success (%)	–/4.7	11.7/10.5	18.0/21.9	8.6/12.4	10.9/13.9	3.5/4.5

"–" Not recorded. ** Site not surveyed in 2009, results from 2021 are given for context. [D] Species recorded by Demeter and Hutterer [25] within the elevational range of our study. [d] Species recorded by Demeter and Hutterer [25] below the elevational range of our study. The faunal lists of Demeter and Hutterer [25] are detailed in Stanley and Kihaule [26]. LMF (lower montane forest); UMF (upper montane forest); UMF/EH (upper montane forest/Ericaceous heathland); EH (ericaceous heathland); and AA (Afroalpine).

Except for *Otomys tropicalis*, there were no small mammal species recorded in 2009 that were not found in our survey. On the contrary, we collected a total of six rodent species (*Arvicanthis niloticus*, *Mastomys natalensis*, *Lemniscomys striatus*, *Dasymys incomtus*, *Cricetomys ansorgei*, and *Montemys delectorum*), which were not reported in the 2009 survey. Of these, *Mastomys natalensis* was recorded exclusively in the SA, whereas *Arvicanthis niloticus* was recorded in the SA and the LMF zones. *Montemys delectorum*, *Dasymys incomtus*, *Lemniscomys striatus*, and *Cricetomys ansorgei* species were distributed between the LMF and UMF/EH zones.

In total, 9 out of the 16 small mammal species recorded (*Rhabdomys dilectus*, *Praomys taitae*, *Mus triton*, *Lophuromys verhageni*, *Graphiurus murinus*, *Grammomys dolichurus*, *Dendromus insignis*, *Crocidura newmarki and Crocidura allex*) were documented in both surveys. Of the nine species present in both studies, five species (*Graphiurus murinus*, *Lophuromys verha-*

geni, *Crocidura allex*, *Dendromus insignis*, and *Mus triton*) were recorded at higher elevation zones in 2021 than they were in 2009 (Table 4). The 2009 survey collected *Crocidura allex* across all elevational zones sampled, but they were missing in the LMF and AA zones in our survey. *Graphiurus murinus* was captured from the lowest elevational zones, the LMF (3%; $n = 5$) and UMF (4%; $n = 1$), in the 2009 survey, but we captured *Graphiurus murinus* at higher altitudes in the UMF/EH (4.9%; $n = 1$) and the EH (9.7%; $n = 5$). Similarly, in the 2009 survey, *Lophuromys verhageni* was recorded between the UMF and AA zones, along the elevational gradients, but we began collecting *Lophuromys verhageni* in the UMF/EH (8.1%; $n = 12$). *Dendromus insignis* was collected in the UMF/EH, EH, and AA, whereas our survey started recording at the EH (2.5%; $n = 4$). A single specimen of *Mus triton* was collected from the EH (2.0%; $n = 1$) in 2009, whereas all individuals (7.8%; $n = 4$) in our survey were from the AA zone.

No species recorded at higher elevation zones in 2009 than in 2021. The degree and direction of community compositional changes between the 2009 and 2021 surveys are portrayed with an arrow in Figure 8. The length of the arrows indicates the degree of observed changes in species composition over time. Closer points show a higher degree of similarity in species makeup. Thus, our results revealed that the greater observed changes in species composition occurred in the LMF and UMF. According to PCoA on the Bray–Curtis dissimilarity matrix (Figure 8), 74% of the difference in community dissimilarity is explained by the first two axes. The elevational distribution of species was largely (51%) explained by the first axis of species composition, with the species composition of sites at higher elevations having higher values along Axis 1. Based on correlation analysis, the elevation of sites was positively correlated with the values of Axis 1 (Pearson's $r = 0.93$, $p < 0.001$). Using a paired t–test of Axis 1 values, to compare the 2009 and 2021 community makeup, we found that the 2021 species composition had more negative values in all elevation sites than the 2009 community composition ($t = -3.74$, $p = 0.020$). Hence, over time, the species composition has changed in the negative direction along the first main axis. This indicates that the species composition at higher elevations in 2021 resembles the species composition at lower elevations in 2009.

Meteorological data from Mount Meru showed a trend in increasing temperatures since 1979 (Figure 7). Between 2009 and 2021, it showed a significant increase in mean temperature by 0.37 °C ($p < 0.05$, SE = 0. 20). Increases in temperature are, also, evident in the neighbouring region of Mount Kilimanjaro, with an increase of 0.27 °C per decade [36], although the extent of change varies from one area to another.

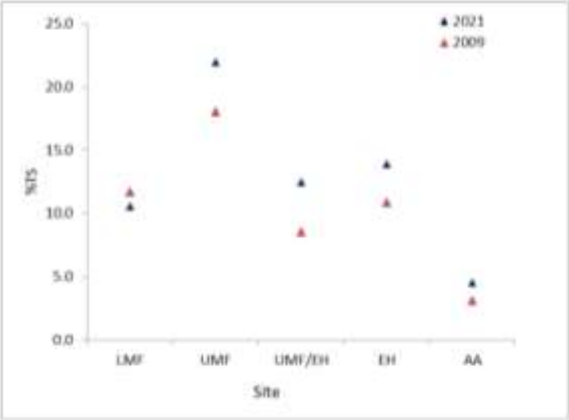

Figure 6. Percentage of trap success (%TS) between the two studies, across sites. LMF (lower montane forest); UMF (upper montane forest); UMF/EH (upper montane forest/Ericaceous heathland); EH (ericaceous heathland); and AA (Afroalpine).

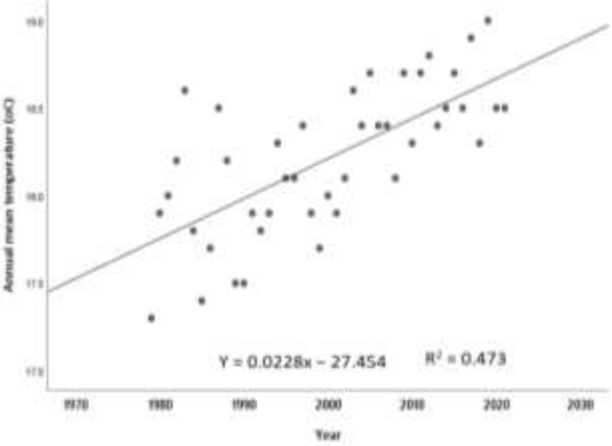

Figure 7. Annual mean temperature changes for Mount Meru, from 1979 to 2021. Linear regression with response variable (Y) and coefficient of determination (R^2).

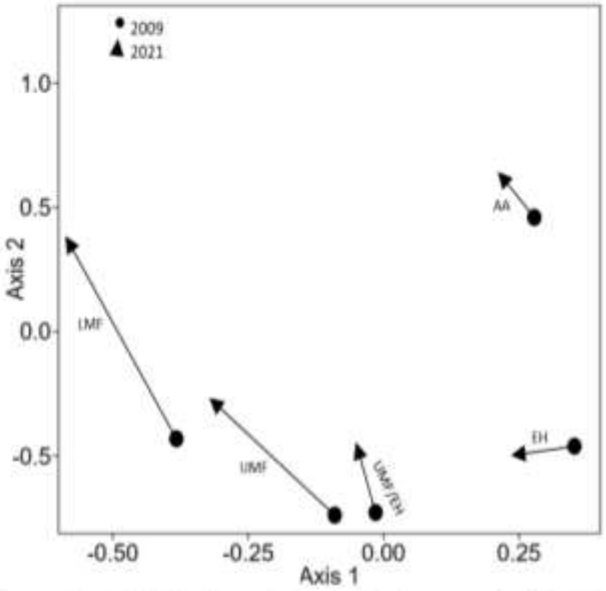

Figure 8. Elevational shifts in the community composition of small mammals on Mount Meru. Arrows indicate the degree of change in species composition between 2009 and 2021, based on the PCoA matrix. Axis 1 and Axis 2 refers to the PCoA 1 and PCoA 2 axis respectively. LMF (lower montane forest); UMF (upper montane forest); UMF/EH (upper montane forest/Ericaceous heathland); EH (ericaceous heathland); and AA (Afroalpine).

4. Discussion

4.1. Diversity and Distribution Patterns

The distribution of small mammals in the current study, generally, varied with elevation zones. We found the highest abundance and relatively lower evenness in the UMF, where *Praomys taitae* predominated. *Praomys taitae* was the most abundant species in our study and was highly confined to forest habitats. According to a previous study, *Praomys* is a forest-dwelling genus [37,38]. Previous studies from this study area [26] and others from Mount Kilimanjaro [17] have, also, reported a high abundance of *Praomys taitae* in the mountain forest habitats. The highest elevational site (AA) contributed the least number of individuals and species richness compared to other habitats. During our trapping in the AA, individuals that died in traps were frequently observed. Low temperatures and other harsh environmental factors affect the abundance of the species found at higher altitudinal levels [13]. At this highest elevation site, we recorded a daily minimum temperature as low as 2.3 °C (Appendix A Table A2). Thus, unfavourable weather conditions, presumably, contributed to the lower number of captures at high altitudes on Mount Meru. Our results support previous studies, showing that high altitudinal zones have comparatively lower species diversity and abundance [16,18].

Rhabdomys dilectus was the second most abundant rodent species in the study area, and was found at all sites, but in high numbers in the UMF/EH and above. Stanley et al. [17] and Stanley and Kihaule [26] reported a higher abundance of *Rhabdomys dilectus* from higher altitudes on Mount Kilimanjaro and Mount Meru, respectively. *Lophuromys verhageni*, an endemic species to Mount Meru, is found in the UMF/EH and above. *Lophuromys flavopunctatus*, in the same genus, has been reported to inhabit less favourable habitats at higher altitudes, including ericaceous heath and montane moorlands on Mount Elgon [19]. *Grammomys dolichurus* was captured in all sites, except the Afroalpine zone. Taylor [39] noted that *Grammomys dolichurus* is less specialised in its habitat requirements. *Mastomys natalensis* was restricted to lower–altitude savannas, whereas *Arvicanthis niloticus* was also, abundantly found in the savanna grassland, with a few individuals found in the LMF. The presence of these species in these sites was expected, given that several studies have confirmed their existence at lower elevations, with bushes or tall grasses [40,41]. Stanley [42], also, found a much greater abundance of *Mastomys natalensis*, at elevations below 900 m in the Udzungwa Scarp Forest Reserve. *Crocidura newmarki* was the most widespread endemic shrew species recorded in all vegetation zones, along the elevational gradients. Stanley and Kihaule [26] reported similar habitat occurrence of this species in this study area.

Our results suggest that the sampling effort used was appropriate for documenting small mammal species at different elevations on Mount Meru. By the third day of trapping, the total number of species reported had attained an asymptote at all elevations, except the UMF/EH (*Lemniscomys striatus* collected by the fourth day). Similarly, the estimated (Sest) and observed (Sobs) number of species was similar at almost every site, indicating a limited likelihood of capturing further new species. Thus, it would be tempting to consider that our sampling regime captured a reasonably comprehensive inventory of small mammal species in as few as four trapping days. Our studies may confirm the interpretations of Stanley and Kihaule [43], who recommended additional sampling effort to capture the complete lists of small mammals, since their species accumulation curves failed to achieve a plateau at every site in the study area. In fact, we documented six species that had not previously been recorded.

Unlike in the Udzungwa Mountains and Bwindi National Park, elevation was not significantly correlated with small mammal abundances and species diversity on Mount Meru. In the Udzungwa Mountains, the overall capture of small mammals and species richness of rodents was found to increase with an increase in elevation [21]. In Bwindi National Park, species richness decreased with elevation [44]. No effect of elevation on species richness or abundance was seen in our study, consistent with the report by Stanley and Kihaule [26]. However, it is important to note that, unlike the previous research, our study did not utilise additional pitfall buckets; hence, diversity indices and elevational data were generated for Sherman and Havahart. Our results showed a strong distribution pattern in species richness and abundance of small mammals, with an increase at the intermediate levels and a decrease towards the upper and lower altitudes. Thus, our findings support the hump–shaped distribution hypothesis, which has been observed for non–volant small mammals, across a wide range of altitudinal gradients worldwide [6,9]. We found species diversity to, distinctly, peak in the UMF/EH, a transition zone between upper montane forest and ericaceous heath. The occurrence of a great number of species in this zone provides more evidence for the hypothesis, that the highest species richness at a given altitude is the consequence of overlapping species range with different habitat requirements. On Mount Meru, we can observe this pattern, where vegetation heterogeneity increases and conditions are not too extreme [45,46].

4.2. Possible Changes in Species Composition between 2009 and 2021

Our findings provide evidence that along an elevational gradient on Mount Meru, small mammal species may have shifted their ranges upslope over the last 12 years, resulting in changes in species composition. Since all the species were captured at the highest elevation zone from which they were recorded in 2009, there was no evidence of downslope range shifts. Our analyses indicate that five out of nine species (55.6%) showed upward movement in their elevational range since 2009. This is smaller than that observed in Simien Mountains National Parks [9], where two–thirds (66.6%) of small mammal species have been observed to shift their elevational ranges upslope. The current increasing trend in temperature in Mount Meru may be having an ecological effect on the different habitat types along the elevation gradient and may be driving the observed shift in small mammal community patterns. Rising mean temperature, due to global warming, is predicted to shift various habitat types and ecosystems to higher latitudes and altitudes [8,47]. Since most small mammals are habitat specialists, the shift observed in our study is, most likely, a response to the 0.37 °C increase in the study region's mean average temperature, between the 2009 and 2021 surveys. Nevertheless, when we compare our findings with the 2009 results, there are other factors that should be taken into account, as follows.

First, although most of the sampling area falls within the protected Arusha National Park, human activities such as grazing and deforestation have intensified habitat degradation at the lower altitudes [23]. According to reports, about 60% of mountainous regions are exposed to intensive human pressure, mainly at lower elevations and mountain bases [48]. Therefore, we speculate that human activities may have, also, contributed to the upward elevational shifts in our study area.

Second, our survey used standard Sherman and Havahart traps, while the 2009 survey utilised Museum Special traps, Victor Rat traps, and additional pitfall buckets, to collect some species with low body weight. For example, the lower number of captured individuals for shrews in our survey, compared to 2009, could be related to an underestimation of their ability to be trapped by Sherman traps, due to their small size. As the trappability of species to bait varies, it would be important, also, to note the variations in the types of bait used in both surveys. In addition, considering the inconsistency in trapping seasons in the AA site between the two surveys would also be important, when comparing the 2009 and 2021 findings.

Finally, we expected that lower elevation zones (1700–2300 m) would experience a decrease in species richness over time. It is widely predicted that communities will shift upslope due to climate–related changes, and species richness will decline at lower elevations [3,49]. However, we found a greater number of small mammal species at low elevations over time. The higher species richness in our survey compared to 2009 could be due to two reasons. (i) The sufficiency of our sampling and the types of traps we used. For instance, the presence of *Cricetomys ansorgei* in our survey but not in 2009 is credited to the employment of Havahart traps in our trapping methods, to collect taxa with large body mass. (ii) We, clearly, do not have evidence of the occurrence of the six new species in the SA zone (1500–1700 m), which lies below the elevational range of the 2009 study. However, species that moved upslope from the montane forest zones were, likely, replaced by species from the SA zones, which are savanna habitats. This suggests that the community is shifting upslope due to lowland biotic attrition [50], whereby low and mid–elevation forests gain species from lower elevations. For example, *Arvicanthis niloticus* was not recorded in the 2009 survey, but we found it in the SA and LMF. In addition, Demeter and Hutterer [25] documented *Lemniscomys striatus* and *Graphiurus murinus* in lower elevations, including savanna habitats, whereas in our survey they were, instead, recorded at higher elevation zones, probably confirming that species have moved upward from savanna habitats to montane forest zones. This is supported by previous reports that upslope range shifts, due to climate change on tropical mountainsides, may be compensated by the influx of species currently found at lower elevations or by expansion from small nuclei left over from previous warming episodes [50].

Of the 10 small mammal taxa listed in 2009, *Otomys tropicalis* was not captured in 2021. In 2009, *Otomys tropicalis* was captured in the UMF/EH, EH, and AA elevational zones, which correspond to 2950 m, 3500 m, and 3650 m sites, respectively, in our study. It is very unlikely that their occurrence was underestimated by our sampling methods, since we included the elevation range surveyed in 2009, and our species accumulation curve indicated low probability of capturing new species with more sampling. Hence, this species may be absent or very rare. In addition, Demeter and Hutterer [25] recorded five specimens of *Otomys irroratus*, which was not recorded in 2021. It is widely understood that montane species are expected to experience further upward range shifts in the future, in response to recent temperature increases [51], and species that occur in low densities in narrow habitat bands are the most vulnerable [49,52]. In this manner, the *Otomys tropicalis* in our study area may become endangered, unless they are able to adapt quickly to changing conditions. Unlike lower elevation species, there is nowhere for higher elevation species to go [50,53]. In other words, a species cannot move upward beyond the top of a mountain [52]. Another important point to note here is that the EH belts had experienced a firebreak in 2015 [54]. It is, therefore, worth highlighting that rising temperatures over the past decade and vegetation changes, as a result of fire experience, may have resulted in the local extirpation of *Otomys* species on Mount Meru. However, the fact that our survey used only standard Sherman traps, while the 2009 survey employed different trap types, should not, also, be ruled out in light of the species's absence from record, as some reports mention that *Otomys* species are not easily trapped [55]. Therefore, further research is required to confirm the occurrence status of this species in the study area.

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Institutional Review Board Statement: The ethical clearance for the study was issued by the Tanzania Wildlife Research Institute and COSTECH (2021–008–NA–2020–238). This study was approved by Sokoine University of Agriculture (SUA/ADM/R.1/8/651 and SUA/PFC/D/2019/0021/05) for the use of animals in this study. The permission to work in the study area was sought from the Tanzania National Park Authority (AB.161/376/01).

Data Availability Statement: The data presented in this study are included with in this paper.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Individual captured small mammal species and sampling efforts in the 2009 and 2021 studies on Mount Meru.

Small Mammal Species	SA **	LMF		UMF		UMF/EH		EH		AA		TOTAL	
	2021	2009	2021	2009	2021	2009	2021	2009	2021	2009	2021	2009	2021
Rhabdomys dilectus	2	0	1	0	3	24	26	7	20	24	36	55	88
Otomys tropicalis	0	0	72	0	192	2	39	1	18	1	0	4	321
Praomys taitae	0	79	0	185	0	38	0	4	0	0	0	306	0
Montemys delectorum *	0	0	0	0	2	0	1	0	0	0	0	0	3
Mus triton	0	0	0	0	0	0	0	0	0	1	4	1	4
Mastomys natalensis	29	0	0	0	0	0	0	0	0	0	0	0	29
Lophuromys verhageni	0	0	0	18	0	9	12	30	37	2	5	59	54
Lemniscomys striatus	0	0	0	0	3	0	1	0	0	0	0	0	4
Graphiurus murinus	0	5	0	1	0	6	21	15	5	0	0	27	26
Grammomys dolichurus	6	3	3	4	5	2	4	4	3	0	0	13	21
Dendromus insignis	0	0	0	0	0	1	0	7	4	2	3	10	7
Dasymys incomtus	0	0	3	0	3	0	1	0	0	0	0	0	7
Cricetomys ansorgei	0	0	4	0	3	0	2	0	–	0	–	0	9
Arvicanthis niloticus	17	0	5	0	0	0	0	0	0	0	0	0	22
Crocidura newmarki	2	49	38	18	19	22	23	51	42	4	3	144	127
Crocidura allex	0	31	0	31	33	18	19	36	29	16	0	132	81
Species richness	5	5	7	6	9	9	11	10	8	6	5	10	15
Total number of captures	56	167	126	257	263	122	149	155	158	50	51	751	803
Total trap-effort	1200	1426	1200	1426	1200	1426	1200	1426	1140	1407	1140	7111	7080
Trap success	4.7	11.7	10.5	18	21.9	8.6	12.4	10.9	13.8	3.5	4.5	10.5	11.3

* As *Praomys delectorum* in previous studies (but see Nicolas et al., 2021); ** Not sampled in 2009.

Table A2. Climate data registered at each elevational site on Mount Meru in February–November 2021 during the small mammal survey. Totals presented as mean and standard deviation (Mean ± SD), range(R) and number of days measured (N). The rainfall samples are expressed as the number of days measured and number of days with rain (in parenthesis).

Elevation Zone	Daily Rainfall (mm)	Daily Minimum Temperature (°C)	Daily Maximum Temperature (°C)
SA			
Mean ± SD	0.1 ± 0.3	20.6 ± 5.8	20.9 ± 5.8
R	0–0.7	12.5–28.1	12.6–28.3
N	6(1)	6	6
LMF			
Mean ± SD	0	14.5 ± 1.5	15.6 ± 1.8
R	0	11.6–15.7	12.3–17.5
N	6(0)	6	6
UMF			
Mean ± SD	2.5 ± 1.4	14.7 ± 2.2	15.4 ± 2.8
R	0–4.1	13.3–18.9	13.6 ± 19.1
N	6(2)	6	6
UMF/EH			
Mean ± SD	2.2 ± 1.7	10 ± 0.34	12.5 ± 2.0
R	0–3.8	9.5–10.5	10.4–15.9
N	5(4)	5	5
EH			
Mean ± SD	3.3 ± 1.6	10.3 ± 0.2	12.8 ± 2.2
R	0–4.2	10.1–10.5	10.6–16.4
N	6(2)	6	6
AA			

Table A2. *Cont.*

Elevation Zone	Daily Rainfall (mm)	Daily Minimum Temperature (°C)	Daily Maximum Temperature (°C)
Mean ± SD	1.7 ± 1.9	5.5 ± 2.4	8 ± 1.3
R	0–3.8	2.3 ± 8.3	6.9–10.3
N	5(3)	5	5

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CHAPTER THREE

BREEDING AND DEMOGRAPHIC ASPECTS OF *MONTEMYS DELECTORUM*, AN EAST AFRICAN ENDEMIC RODENT

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Breeding and demographic aspects of *Montemys delectorum*, an East African endemic rodent

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Abstract

Montemys delectorum is the only member of the genus *Montemys* within the family Muridae, which is an endemic rodent of the Eastern Africa Highlands. It is a threatened species due to habitat loss, and its current conservation status is uncertain. We studied the breeding pattern and population size of *M. delectorum*, two of the most important factors in understanding the conservation status of a species. Capture–mark–release studies were conducted from February 2021 to June 2022 in open patchy forests and dense forest habitats. *Montemys delectorum* showed bimodal breeding seasonality; a low rate for the short interval between December and February and a pronounced rate for May–July, following the high rainfall in April. This shows that rainfall promotes vegetation availability, which stimulates breeding activity and adds offspring to the population, resulting in increased population abundance. The population of *M. delectorum* is not stable in this landscape, as indicated by the significant differences in population size between the two forest types, with a significantly greater population in the patchy open forest. This indicates that the patchy open forest should be considered an essential refuge for the species.

KEYWORDS
breeding, dense forest, *Montemys delectorum*, patchy open forest, seasonality

Résumé

Montemys delectorum est le seul membre du genre *Montemys* dans la famille des Muridae, qui est un rongeur endémique des hauts plateaux d'Afrique de l'Est. Il s'agit d'une espèce menacée en raison de la perte d'habitat et son statut de conservation actuel est incertain. Nous avons étudié le schéma de reproduction et la taille de la population de *M. delectorum*, deux des facteurs les plus importants pour comprendre le statut de conservation d'une espèce. Des études portant sur la capture, le marquage et le relâchement ont été menées de février 2021 à juin 2022 dans des habitats de forêts clairsemées et de forêts denses. *Montemys delectorum* a montré une saisonnalité de reproduction bimodale : un faible taux pendant le court intervalle entre décembre et février et un taux élevé pour la période mai-juillet, suite aux fortes précipitations d'avril. Cela montre que les précipitations favorisent la disponibilité de la végétation, ce qui stimule l'activité de reproduction et ajoute des petits à la population, ce qui entraîne augmentation de l'abondance de la population. La population de *M. delectorum* n'est pas stable dans ce paysage, comme l'indiquent les différences considérables dans la taille de la population entre les deux types de forêts, avec une population considérablement plus importante dans la forêt ouverte clairsemée. Cela indique que la forêt ouverte clairsemée devrait être considérée comme un refuge essentiel pour l'espèce.

1 | INTRODUCTION

Rodentia is the largest mammalian order (Burgin et al., 2018), with 463 species that are well represented in Sub-Saharan Africa (Monadjem et al., 2015). They are more elusive, inhabiting quiet corners of rainforests, mountains, deserts and rivers, and play a crucial role in ecosystems all over the world (Gazzard et al., 2023). Rodents are an invaluable link in the food chain; they serve as food for vertebrates as prey; and they regulate the population of insects and other invertebrates by acting as predators (Gazzard et al., 2023; Ojeda & Chazarreta, 2018). In addition, pruning vegetation, aerating soil and dispersing pollen, seeds and fungal spores (Geng et al., 2017; Wang & Ives, 2016) are among the ecological values of rodents. Burrowing species create subterranean habitats used by other animals, and other species act as engineers of entire ecosystems with their dams that help purify water systems and moderate floods and droughts (Gazzard et al., 2023; Lacher Jr et al., 2019). Due to their limited dispersal capacity and their high affinity for particular types of habitats (Cuypers et al., 2022), rodents are sensitive to environmental changes at smaller scales (Malcolm & Ray, 2000; Stirnemann et al., 2015). Hence, they are also excellent indicators of environmental change for landscape ecologists. Altogether, rodents are very important animals in nature, regardless of how we look at them, and they deserve to be recognised for their positive contribution. Despite their very important contribution to the proper functioning of ecosystems, most research on the ecology of rodents in Africa has been focused on pest species, which account for 5%–17% of the African rodent species (Massawe & Rwamugira, 2008; Monadjem et al., 2015; Mulungu, 2017), and data on non-pest species are limited. This research bias may have implications for the conservation of other non-pest rodent species in Africa.

The East African soft-furred mouse (*Montemys delectorum*, Thomas, 1910) is the only member of the genus *Montemys* in the family Muridae. It was formerly classified in the genus *Praomys* (i.e. *Praomys delectorum*), but was recently taxonomically revised (Nicolas et al., 2021). '*Montemys*' refers to the animal's natural habitat, which is a 'montane' forest, which refers to the 'high elevation' of the biome. The species was thought to be endemic to the East Arc Mountains (Cassola, 2016), but its current distribution extends to the northern Tanzania Mountains, including Mount Kilimanjaro (Mulungu et al., 2008; Thomas et al., 2022) and Mount Meru (Gebrezgiher et al., 2022, 2023). Our observations from the current study show that the distribution of *M. delectorum* needs to be corrected so that it is considered an endemic rodent of the Eastern Africa Highlands as opposed to the East Arc Mountains alone. However, this endemic vertebrate species is threatened throughout its range in the East African Highlands due to habitat loss caused by deforestation and the expansion of agricultural activities into its suitable habitats (Cassola, 2016).

East African Highlands such as Mount Kilimanjaro, Mount Kenya, Mount Elgon, the Eastern Arc Mountains and Mount Meru serve as potential refuges for a great array of rare and endemic vertebrates (Gebrezgiher et al., 2022; Mulungu et al., 2008; Stanley & Kihaule, 2016; Thomas et al., 2022). However, due to climate change and other human activities, the plight of montane species is increasing (Neate-Clegg et al., 2018; Rogora et al., 2018; Willig & Presley, 2016). Numerous species of rodents are struggling to survive in shrinking habitats and are further threatened by less-than-ideal habitats and a changing climate (Gazzard et al., 2023). For instance, Mount Meru (i.e. the topographic centrepiece of the Arusha National Park [ANAPA]) has experienced habitat disturbances due to fire outbreaks in the ericaceous habitats. Moreover, the degradation of habitats by human activities, including farming and grazing, has intensified in the last decades, particularly at the foot of the mountain (Maleko et al., 2012). This habitat and other climate-related changes affect the habitats and distribution of small mammals (Gebrezgiher et al., 2022). The effects on the population ecology of individual species also cannot be overstated. Despite the fact that *M. delectorum* is not on the IUCN Red List, as a forest specialist species, habitat change may cause a decline in population size. However, there is a lack of data on the basic ecology of this species in Africa and Tanzania in particular, which could help monitor its population.

Rodent populations in Sub-Saharan Africa often exhibit pronounced spatial–temporal variations in numbers and structure (Leirs et al., 1997; Makundi et al., 2005), which are influenced by innumerable factors. Rainfall appears to be the most important factor in the breeding patterns and population size of rodents through its effect on the initiation of reproduction, the length of the breeding season and the survival of offspring (Leirs et al., 1997; Lock & Wilson, 2017; Makundi et al., 2007, 2010; Meheretu et al., 2015). Since rainfall is seasonal, populations of many species of rodents also show strong seasonality in breeding patterns. The central issue is that seasonal rodent breeding is stimulated by vegetation following seasonal rains and that reproductive output is affected by the quality and quantity of plant biomass. Rodent abundance is also determined by habitat landscapes and the patchiness of the forests (Gitzen & West, 2002). Patchy forests are characterised by an open canopy and gaps in

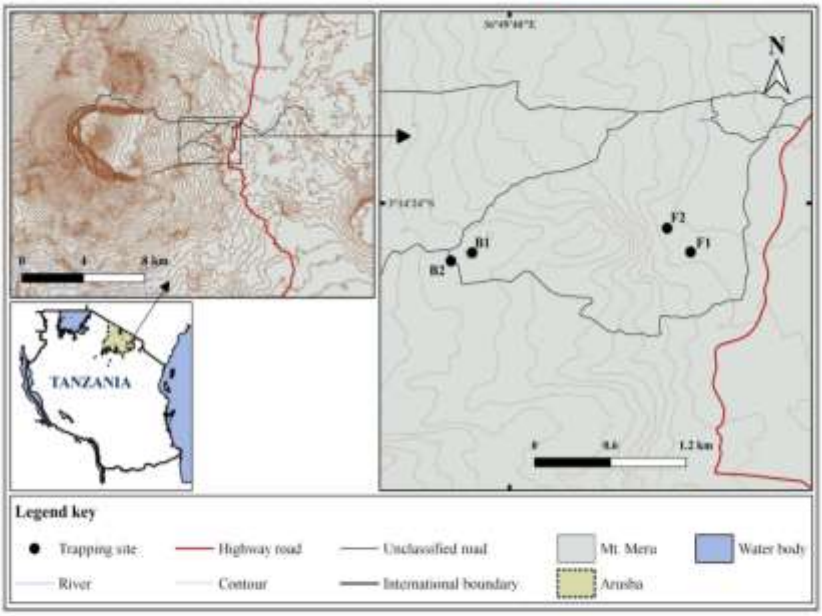


FIGURE 1 Map of the study area and trapping locations (B1 and B2—grids in patchy open forest, F1 and F2—grids in dense forest).

the forest that can be caused by natural events, such as mature trees falling and natural topography. These open natural features enhance habitat diversity by allowing light to improve the growth and availability of underground cover compared to dense forests with a closed canopy (Girvetz & Greco, 2007; Gitzen & West, 2002; Goodsell et al., 2007). Furthermore, altitude and mosaic landscape type (swamp, near the river, position to sunlight) are known to influence rodent population size (Richard et al., 2022), but their relative contributions and effects may vary among species. Most studies on African rodent demographic aspects have focused on pest species (Mayamba et al., 2019; Meheretu et al., 2015; Mulungu et al., 2013), while ecology studies on non-pest montane species, including *M. delectorum*, are scarce. The aim of the study was therefore to determine the breeding patterns and demographic aspects of *M. delectorum* which are vital factors in understanding the conservation status of a species (IUCN, 2001). The study specifically answered the following questions: (i) Does breeding activity of *M. delectorum* differ between habitat and season? (ii) Does the population abundance of *M. delectorum* vary between habitats and seasons? (iii) Does the breeding and population pattern of *M. delectorum* follow the rainfall pattern?

2 | MATERIALS AND METHODS

2.1 | Study sites

The study was carried out in the Mount Meru Forest Reserve (1400–4566 m; 3° 14′ 48″ and 36° 44′ 54″), the topographic centrepiece of Arusha National Park, located in the Arusha region of Tanzania (Figure 1). The rainy season runs from November to May, and June–October are the driest months. Mount Meru is distinguished by its vegetation zones, which include grasslands and deciduous open woodlands at lower elevations, followed by montane forests between 1700 and 3000 m. Higher up, evergreen ericaceous scrub forms the transition to afro-alpine vegetation (for details, see Bussmann, 2006; Gebrezgiher et al., 2022; Neduvoto et al., 2012).

The trapping sites (Figure 1) were located in a montane forest zone in the southeast and northeast parts of the mountain at a distance of about 10 km. The average annual rainfall at the sites during 2021 and 2022 was about 1283 mm. The trapping grids in the northeast were established in the dense forest (F1 and F2) at an altitude of 1750 m, primarily dominated by *Diospyros abyssinica* and *Nuxia congesta* with a high canopy and low light penetration to the ground. At these sites, there were few shrubs on the ground, which included *Cheilanthes farinosa* and *Pteridium aquilinum*. Wild animals such as baboons and leopards were common around the trapping site. Habitat degradation by human activities, such as grazing and agricultural activities at the foot of the National Park, is common. The trapping grids in the southeast were established in the patchy open forest (B1 and B2) (Figure 1) of Tululusia Hill, an isolated landscape with a view of Mount Kilimanjaro that receives direct sunlight throughout the day. It is distinguished by heterogeneous habitats surrounded by swampy areas. The patchy open forest is dominated by the following tree species: *P. aquilinum*, *Cheilanthes farinosa*, *Kniphofia thomsonii*, *Hagenia abyssinica*, *Oxalis* spp., *Plantago palmata*, *Oldenlandia monanthos*, *Rubia cordifolia*, *Adenocarpus* spp., *Crotalaria* spp., *Cyperus* spp., *Peucedanum* spp. and Iridaceae, ferns, moss, lichen and liverworts covered by moss-draped bushes and epiphytes. Big, patchy trees such as *Ficus* and *Rhamnus* were also common.

2.2 | Animal trapping and sample analysis

Capture–mark–release technique was employed to trap rodents from February 2021 to June 2022. Four 70×70m grids were established, two in the dense montane forest (F1 and F2) and two in the patchy open forest (B1 and B2). The grids were 500m apart to prevent rodents from moving between grids. Forty-nine Sherman live traps were set in each grid, consisting of seven parallel lines 10m apart and seven trapping stations per line, also 10m apart. One Sherman LFA live trap (H.B. Sherman Traps Inc.) was placed at each trapping station. Trapping was conducted for three consecutive nights every month. Traps were baited with peanut butter mixed with maize bran and inspected at 7:00–8:00h in the morning. The trapping station, sex, weight and age of the animal were recorded. The captured individuals were grouped into two age classes: juveniles and adults. Male individuals were classified as juveniles and adults based on the type of fur and reproductive status, which is based on the position of the testes, whether scrotal or abdominal. For females, the vaginal condition (open or closed), nipple condition (small, lactating or recently lactating) and the presence or absence of palpable embryos and types of fur were recorded. Captured animals were released at the location of capture.

2.3 | Data analysis

Given that *M. delectorum* was the most abundant species in all four fields, we decided to analyse the data for this species only. The Minimum Number Alive (MNA) technique was used to estimate population size (MNKA; Krebs, 1966). It has been applied by many studies (Ademola et al., 2021; Gentile et al., 2000; Granjon et al., 2005) as an appropriate method for population determination on the basis of the number of animals that are known to exist within and around the grids. This method uses the capture history of each individual to establish those who were alive in all the trapping sessions between the first and last time of capture. Based on the general pattern of breeding activity observed, we split the rodents' breeding season into three 'seasons' as follows: wet season (November–May), early dry season (June and July) and dry season (August–October). To test for differences in abundance between habitats and seasons, an analysis of variance was used after checking for normality. In this paper, breeding was analysed as the number of reproductively active females in the population. We excluded reproductively active males from the analysis because one male is able to breed with several females and, therefore, males are not a limiting factor (Meheretu et al., 2015).

3 | RESULTS

3.1 | Captured animals and demographic aspects

Overall, seven species of small mammals (*M. delectorum*, *Grammomys surdaster*, *Lophuromys verhageni*, *Rhabdomys dilectus*, *Graphiurus* cf. *raptor*, *Crocidura newmarki* and *Crocidura montis*) were recorded in the study grids; while all seven species were captured in the patchy open montane forest (B1, B2), only two of the seven, *M. delectorum* and *Grammomys surdaster*, were captured in the dense montane forests (F1, F2). *Montemys delectorum* was the dominant species in all grids, accounting for about 84% and 94% of the total captures in the patchy open forest and dense forest respectively.

The result indicates a greater number of *M. delectorum* individuals were found in the patchy open forest than in the dense forest ($F=8.1$, $df=1$; $p=0.0001$). The MNA differed between habitats and seasons (Figure 2a), but did not vary between grids within habitats (Figure 2b). Population abundances were generally higher from the mid of the rainy season to the early dry season, but a rapid decline occurred towards the end of the dry season. The pattern of variation in abundance of *M. delectorum* in the patchy open forest habitats exhibited fairly distinct phases, in May and June and a dramatic drop in September and August. In the patchy open forest, though individuals were present in all months, there were significant variations ($F=9.6$, $p=0.015$) between seasons. In the dense forest, the fluctuations were relatively lower than in the patchy open forest, with a higher MNA in December; however, zero catches were common in all seasons, and the MNA did not differ statistically between seasons ($F=2.24$, $p=0.23$).

3.2 | Breeding patterns

Our results showed that *M. delectorum* is a seasonally breeding species. Breeding commenced in the middle of the wet season and continued through the early dry season (June and July). *Montemys delectorum* showed two breeding periods: a low rate for the short

FIGURE 2 Minimum Number Alive (MNA): (a) between habitat types; (b) between grids (B1 and B2—patchy open forest, F1, F2—dense forest).

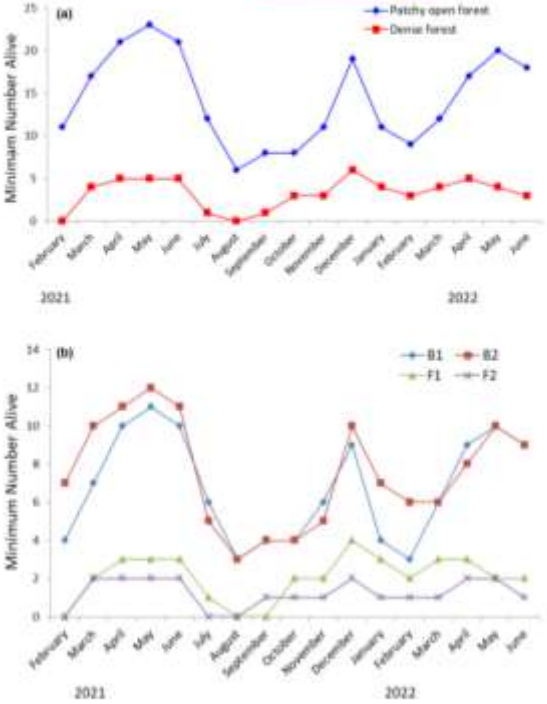
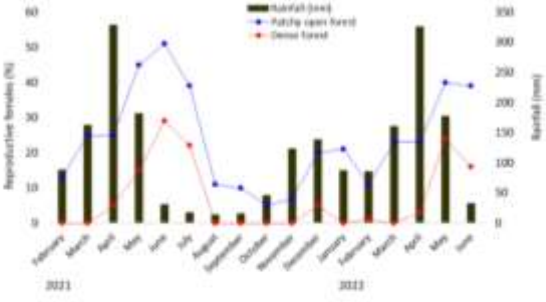


FIGURE 3 Proportion of reproductively active females between habitats and months.



interval between December and February and a pronounced rate from May to July. The highest abundance of reproductively active females in both forest habitats was in May and June, followed by the high rainfall in April. Moreover, a greater numbers of sexually active females were observed in the patchy open forest than in the dense forest (Figure 3). In the patchy open forest, the breeding activity of

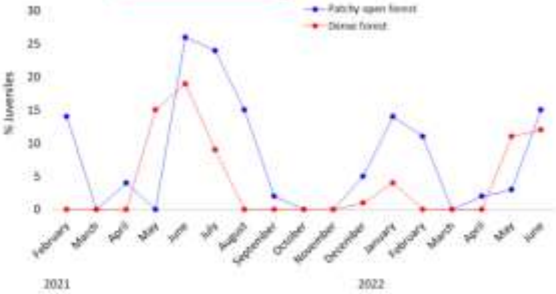


FIGURE 4 Percentage of juveniles in the population.

female *M. delectorum* was extended and occurred in all months, but only a small proportion of the animals were sexually active towards the end of the driest months (August–October). The number of reproductively active females in both habitats peaked in June, following months of high rainfall. Our results also show that the number of juveniles captured was greater in June compared to the other months in both habitats (Figure 4).

4 | DISCUSSION

Montemys delectorum was the most abundant small mammal species in the study area (Gebrezgiher et al., 2022; Stanley & Kihaule, 2016). This species has been recorded in high densities in forest habitats throughout East Africa and is known to be a forest specialist (Ademola et al., 2021; Cassola, 2016; Thomas et al., 2022). It is, therefore, not surprising that it was the dominant species in both montane forest sites in the Mount Meru forest reserve. The higher abundance of *M. delectorum* in the patchy open forest sites, which are located at a higher elevation compared to the dense forest at a lower elevation in our study, might indicate that the patchy open forest sites had abundant food resources for this species. Moreover, studies show that elevation determines the distribution of different species (Brown, 2001). Moreover, Richard et al. (2022) and Gebrezgiher et al. (2022) reported the elevational distribution of the current study's species, with higher preferences at relatively higher elevations. However, by itself, elevation above sea level means nothing to a species (Brown, 2001). The correlated environmental variables, such as vegetation structure, that change rapidly over short distances generate and maintain patterns of abundance. As elevation increases, the forest canopy decreases (Dillon & Conway, 2021), which may increase light availability, resulting in higher underground covers that support a greater number of individuals. This was evident in our study, which revealed that the higher altitude forest (i.e. the patchy open forest at 2100 m) supported more *M. delectorum* individuals than the lower altitude forest (i.e. the dense forest at 1750 m). The dominance of *M. delectorum* in the patchy open forest sites in our study contradicts the idea that *M. delectorum* is a weak competitor among other rodent species, resulting in a lower abundance in sites with higher species diversity (Makundi et al., 2003).

In this study, the population of *M. delectorum* fluctuated temporally, consistent with previous studies reported for other rodent species in Tanzania (Makundi et al., 2007) and Ethiopia (Meheretu et al., 2015). Abundance peaked from the mid-rainy season to the early dry season, indicating that rainfall is an important environmental factor in the population abundance of a species, in particular its effects on plant growth. Vegetation is not only used as a food source that triggers reproduction and adds newborns to the population, but it is also used as a cover to protect the animals from predators, implying that the population changes of the rodent are driven by changes in food resources and vegetation cover (Makundi et al., 2007; Previtali et al., 2009). The vegetation in the patchy open forest was dominated by ferns, moss, epiphytes and grasses, whose growth is determined seasonally, drying out during the dry season and quickly growing in the wet season. The relatively lower abundances of *M. delectorum* in the dense forest suggest that the tree canopy may limit the availability of resources for the rodents on the ground, resulting in decreased sexual activity, juvenile recruitment and individual survival. Our capture history data in the dense forest indicated a lower number of recaptured individuals throughout the study, which might point to a high rate of emigration, mortality or both. The animals are more vulnerable to predation when there is less vegetation cover. Signs of predatory incidents, such as trap disturbances and broken traps, were frequently observed in the dense forest.

Our results showed that the breeding patterns of *M. delectorum* were seasonal, having commenced in the wet season and continuing through the early dry season. This is a typical case of bimodal breeding seasonality with two breeding periods: a low rate for the short interval between December and February and a pronounced rate for May–July. The highest abundance of reproductively active females in May and June appeared following the high rainfall in April. These findings are consistent with previous studies on African rodents (Meheretu et al., 2015), which showed a delayed population increase after the peak month of rainfall. Rainfall is known to affect the breeding activity of small mammals by increasing plant productivity and bringing quantity and quality food for reproductive females, but the role of rainfall in bringing quality vegetation cover for shelter and protection from a potential predator is as important as food. Less vegetation cover makes the animal more vulnerable to predators, which can directly or indirectly affect its breeding activity. Predators not only kill reproductively active individuals and their offspring but also allow prey to increase time spent on vigilance and decrease feeding time, or stay longer in refuges in response to predator cues (Lima & Bednekoff, 1999). This may result in malnutrition, affecting the reproduction potential of the species. Moreover, predator-induced maternal stress lowers reproduction and compromises the offspring's health condition (Sheriff et al., 2011). Therefore, a higher number of reproductive individuals and juveniles following the long rainy season in our study are likely associated with vegetation availability driven by rainfall. Generally, the proximate factor leading to the onset of reproduction is access to growing vegetation, which is similar to what many studies have found for other rodent species (Mayamba et al., 2019; Meheretu et al., 2015; Mulungu et al., 2013). On the other way, the lower proportion of reproductively active females and newborns in the dense forest sites may be attributed to the lower availability of food and ground cover due to forest canopy, which allowed animals to migrate in search of food and or left them exposed to direct and indirect effects of predation. Furthermore, it is clear from this study that the higher number of juveniles during the breeding season is due to the higher number of females.

5 | CONCLUSION

The breeding pattern of *M. delectorum* in our study was seasonal. Typically, there are two breeding periods: a low rate for the short interval between December and February and a pronounced rate for May–July, following the high rainfall of April. The breeding seasonality and population size observed in this study confirm the observations made elsewhere in Africa, which support the hypothesis that rainfall events promote primary productivity, which stimulates breeding activity and adds new offspring to the population, resulting in increased population abundance. The population of *M. delectorum* is not stable in this landscape, as indicated by the significant differences in population size between the two forest types. A significantly greater population in the patchy open forest implies that the patchy open forest should be considered an essential refuge for the species. In addition, the limited vegetation availability for food and shelter against potential predators may also be to blame for the lower number of reproductively active individuals and population size in the dense forest. Finally, this study is short term and focused on a few population parameters; it lacks information on other vital population parameters such as survival, movement pattern and recruitment. Therefore, continuous demographic monitoring of these parameters of *M. delectorum* is vital to better understanding its current conservation status.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

All of the data for the study are included within the paper.

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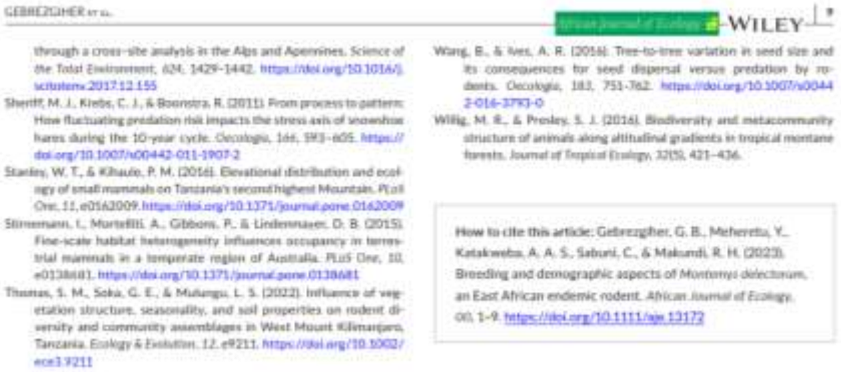

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CHAPTER FOUR

ARTHROPOD ECTOPARASITES OF TWO RODENT SPECIES OCCURRING IN VARIED ELEVATIONS ON TANZANIA’S SECOND HIGHEST MOUNTAIN

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Arthropod Ectoparasites of Two Rodent Species Occurring in Varied Elevations on Tanzania's Second Highest Mountain

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Simple Summary: The interaction of small mammals in the ecosystem is not limited to humans and other wildlife; it also includes organisms that inhibit their bodies, so-called "parasites". Arthropod ectoparasites are a diverse and well-adapted group of invertebrates that live on the body surfaces of their hosts, typically vertebrates but rarely other invertebrates. Ectoparasites such as fleas and some mite species are of veterinary and medical importance because they are associated with the transmission of zoonotic diseases. The study determined factors influencing ectoparasite infestation on two rodent species on Mount Meru, one of Tanzania's most popular research and ecotourism sites. Host sex, species, and environmental temperature predicted ectoparasite infestation patterns in the two rodent species. We expected host density to predict parasite prevalences and abundances, because hosts in higher densities should have more parasites due to increased contact between individuals. However, temperature, not host density, affected ectoparasite distribution. Since temperatures decrease with elevation, parasite prevalences and abundances were lower at higher elevations, highlighting that cold conditions at higher elevations limit reproduction and development—this shows that higher elevation zones are ideal for conservation.

Abstract: Climate change causes organisms, including species that act as parasite reservoirs and vectors, to shift their distribution to higher altitudes, affecting wildlife infestation patterns. We studied how ectoparasite distributions varied with altitude using two rodent species, *Montemys delectorum* and *Rhabdomys dilectus*, at different elevations (1500–3500 m). The ectoparasites infesting the two rodent species were influenced by the host sex, species, and temperature. We expected host density to predict parasite infestation patterns, because hosts in higher densities should have more parasites due to increased contact between individuals. However, temperature, not host density, affected ectoparasite distribution. Since temperatures decrease with elevation, parasite prevalences and abundances were lower at higher elevations, highlighting that the cold conditions at higher elevations limit reproduction and development—this shows that higher elevation zones are ideal for conservation. The rodents and ectoparasite species described in this study have been reported as vectors of diseases of medical and veterinary importance, necessitating precautions. Moreover, Mount Meru is a refuge for a number of endemic and threatened species on the IUCN Red List. Thus, the parasitic infection can also be an additional risk to these critical species as well as biodiversity in general. Therefore, our study lays the groundwork for future wildlife disease surveillance and biodiversity conservation management actions. The study found a previously uncharacterized mite

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species in the Mesostigmata group that was previously known to be a parasite of honeybees. Further investigations may shed light into the role of this mite species on Mount Meru.

Keywords: *Montemys delectorum*; *Rhabdomys dilectus*; *Varroa* mite; PCR; fleas; Mount Meru

1. Introduction

The interaction of small mammals in the ecosystem is not limited to humans and other wildlife; it also includes organisms that inhibit their bodies, so-called "parasites". This implies that the host serves as a habitat for the parasite, providing it with food, space to live, and mating opportunities, regardless of whether they reside inside or outside the body of the host [1,2]. Arthropod ectoparasites are a diverse and well-adapted group of invertebrates, ranging from obligatory to facultative, and permanent to intermittent; they live on the body surfaces of their hosts, particularly vertebrates [2]. Some arthropod ectoparasites are also known to parasitize invertebrates. For instance, the *Varroa* spp. (Mesostigmata mite) is a known parasite of honeybees [3–7]. Ectoparasites can harm hosts by feeding on their tissues and causing dermatitis, and some of them are vectors of pathogenic and life-threatening diseases. As an example, plague is a flea-borne zoonosis of mammalian hosts that causes significant human mortality throughout the world, including Africa [8–11]. Parasite infections impair host fitness, because the development of antiparasitic defenses needs resources which are depleted from those needed for life-history processes [12]. Parasites slow host growth, survival, and fecundity, which have the potential to reduce host density [13]. High ectoparasite loads, for example, resulted in lower reproduction and overwinter survival in yellow-bellied marmots (*Marmota flaviventer*) in the Italian Alps [12], hare populations (*Lepus* spp.) in the Scottish mountains [14], and red grouse (*Lagopus lagopus scoticus*) in England, which may affect host fitness and make population dynamics unstable. However, the risk of parasitic infection transmission varies with the movement and dispersal behavior of the host species across a landscape, which may alter their parasite community and increase transmission to other species [15].

The distribution of parasites among host individuals is uneven, due to host- and parasite-related characteristics and environmental factors that affect host exposure and susceptibility to parasites [16]. Host-related factors include, but are not limited to, age, body size, sex, and breeding status [17]. Parasite load may vary between age groups. Adults provide greater dietary resources for parasites than juveniles [18,19], and have a prolonged period of exposure to parasites. Additionally, parasitism may be sex-biased, with males being more heavily parasitized than females, which could be due to their larger body sizes [20], as well as their greater mobility and social contact patterns [21] in males. Parasite infection is also often higher in breeding individuals than in non-breeding individuals because reproduction is linked with increased body contact, food acquisition to meet increased nutritional and energetic demands, a change in physiology, and thus increased vulnerability to parasites [22]. However, other factors, including reduced mobility of females during pregnancy and lactation to take care of juveniles, may reduce the risk of encountering ectoparasites [23].

Parasites are not only dependent on their host, but also on favorable environmental conditions for transmission and infestation. Environmental factors that have an important regulating role in the distribution and developmental success of parasites in mammals include precipitation [24], temperature [25,26], and elevation [27,28]. Parasite distributions are anticipated to shift northward and to higher altitudes, as a result of climate change [29]. In fact, rising temperatures associated with climate change are increasing parasite abundance over time [30–33]. These distribution changes may lead to new host–parasite encounters, forcing host populations to deal with parasites with which they have not co-evolved, which could eventually result in local host population extinctions [34].

Steep mountain ranges provide a natural experimental background for studying how species distribution varies across climatic gradients [35]. Altitudinal gradients reflect substantial changes in precipitation, temperature, humidity, soil, and vegetation, with extreme environmental conditions strongly influencing the physiology and survival rate of organisms [36]. These variations have been demonstrated to affect faunal distribution across different altitudes in different geographic regions worldwide [36–41]. For example, small mammals' distribution along elevation has been extensively studied throughout the world, and often shows a hump-shaped distribution pattern in which species richness and abundance peak at the mid-level elevations where the conditions are not too extreme (i.e., hot or cold) [37–39]. Studies indicate that the spatial and numerical distribution of the host population determines the distribution patterns of their parasites [42]. Thus, hosts in high densities contain a greater parasite load than hosts in low densities, because of the increased contact between individuals, making contagious parasite transmission easier [42,43]. Accordingly, we hypothesized that ectoparasite distributions follow the distribution patterns of their hosts; ectoparasites should peak at the mid-elevation. Yet, the assumption regarding parasite distribution along elevational gradients is still being debated. On the other hand, the number of feather mites in birds [44] and fleas in rodents [45] has been shown to decline as elevation increases.

This study determined the distribution of arthropod ectoparasites on the East African soft-furred mouse (*Montemys delectorum*) and the mesic four-striped grass rat (*Rhabdomys dilectus*) at different elevations on Mount Meru, the centerpiece of Arusha National Park, a popular ecotourism destination in Tanzania. *Rhabdomys* has traditionally been seen as a single species, *Rhabdomys pumilio*. However, karyotype and mtDNA evidence suggests that it includes a second species, *Rhabdomys dilectus*, which is found all over Africa [46]. *M. delectorum* is the only member of the genus *Montemys* within the family Muridae. It was formerly classified in the genus *Praomys* (i.e., *Praomys delectorum*), and was recently taxonomically revised [47]. *M. delectorum* is an endemic mammal to the East African Highlands. It is a threatened species throughout its range due to habitat loss, and its IUCN conservation status is uncertain [48]. We examined which traits of the host (sex, species, density) and environmental factors (elevation, temperature) determined the prevalence and abundance of arthropod ectoparasite vectors, which is important to understand the patterns of parasitic infectious disease. We also tested the hypothesis that ectoparasite distribution follows the distribution patterns of their host. The distribution pattern of rodents and shrews on Mount Meru is greater at intermediate elevation levels [39,41]; hence, if host density predicts the occurrence of the ectoparasites, we particularly expected rodent individuals at the middle elevations to suffer a high risk of being infested. Furthermore, the two rodent species have been identified as hosts of ectoparasites, including as potential vectors and reservoirs of pathogens [49]. Given the 65% increase in zoonotic outbreaks in Africa over the past decade [50], recognizing the patterns of parasite distribution among wildlife hosts is of major importance. Our study contributes to a better understanding of the ecology of host-ectoparasite relationships along elevational gradients, which is important not only for identifying potential ectoparasite vectors, but also for designing and implementing vector-borne disease management programs for wildlife conservation and human health.

2. Materials and Methods

2.1. Study Area and Trapping Sites

Mount Meru is located in northeastern Tanzania at 3°14′48″ and 36°44′54″, about 35 km northeast of the town of Arusha (Figure 1). The topography rises from the Momela Lakes, lying at 1400 m above sea level, to the summit at 4566 m. The rainy season extends from November to May with relatively lower rain in January and February. June through October is characterized as the dry and cold season. Annual atmospheric temperatures range between 15 °C and 34 °C [51]. Details of the vegetation types of the sites from which the rodents were trapped are outlined in Gebrezgiher et al. [39] and Bussmann [52], and all trapping locations were within Arusha National Park (Figure 1). The study was conducted between February 2021 and June 2022. The sampling sites were across five elevations from 1500 to 3500 m as follows:

(1) Elevation 1500 m (3°13′20.766″ S, 36°52′50.076″ E)—This trapping site was located at the base of Mount Meru, and vegetation cover ranges from grassland, thicket, and bushland to woodland. *Caesalpinia decapetala, Croton macrostachyus, Jacaranda mimosifolia, Ocimum gratissimum, Solanum incanum, Aerva lanata, Lantana trifoliata*, and tussock grasses are among the notable plant species. Patches of Acacia trees are also prevalent.

(2) Elevation 2000 m (3°14′33.102″ S, 36°49′15.528″ E)—This site was situated in a lower montane forest, with a dense canopy of trees of various species, including *Diospyros abyssinica, Olea hochstetteri, Rhamnus prinoides*, and *Ficus thonningii*.

(3) Elevation 2500 m (3° 14′ 32.892″ S, 36° 47′ 25.644″ E)—This site was in the upper montane forest dominated by *Juniperus procera* and *Podocarpus gracilior*. Herbaceous plants, various lianas, and shrubs formed a thick understory, and the trees were often covered with epiphytes.

(4) Elevation 2950 m (3°13′28.724″ S, 36°47′7.782″ E) —This site was characterized as a transitional zone between habitats of higher montane forest and ericaceous heath.

(5) Elevation 3500 m (3°13′6.192″ S, 36°46′24.042″ E)—This highest trapping site was located in the ericaceous heathland habitats dominated by Erica spp.

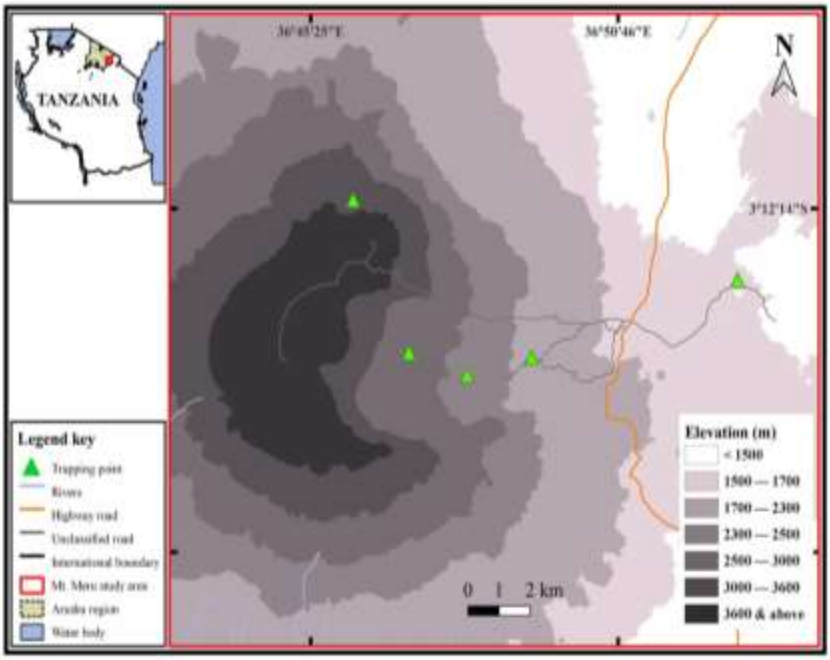

Figure 1. Geographic locations of trapping sites on Mount Meru.

2.2. Rodent Trapping

Sherman is a foldable metal trap designed to capture live animals. Four trap lines were established at a distance of 30 to 50 m, each with 50 traps separated by 10 m. Sites received six days of trapping with a total of 200 traps. All traps were equipped with bait (peanut butter mixed with maize flour and avocado) and placed in the shade to avoid being too hot. Traps were inspected and re-baited (i.e., if the bait was found eaten by insects) every morning between 07:00 and 08:00 h. Each Sherman trap that captured an animal was replaced with a new one (i.e., previously washed). Each individual trapped rodent was first placed in a cotton bag and humanely anesthetized using diethyl ether (LOBA CHEMIEPVT. LTD.) on cotton wool, then placed in a bucket with a lid. Standard external body measurements (body, tail, hindfoot, and left ear), sex, and weight of the trapped hosts were recorded. Species identification followed Happold and Kingdon [53], and sex identification followed Hoffmann et al. [54]. The rodent species identification was confirmed using molecular (Cytochrome b) techniques.

2.3. Ectoparasite Collection and Identification

The ectoparasites were combed out of the rodents, using a small shoe-like brush, into a clean, wide, and long aluminum pan. A different brush was used for each host individual to make sure ectoparasites were not spread from one to another through sharing a brush. The softer body parts of the rodents, such as the belly, ear, and tail regions, were further examined. The ectoparasites were collected with fine brushes, and each host was separately counted and preserved in a labeled Eppendorf tube (Inqaba Biotec East Africa Ltd., Nairobi, Kenya) containing 70% ethanol. Each ectoparasite was identified morphologically using a compound microscope, with the aid of available dichotomous taxonomic keys [55–57]. Existing procedures were employed for the microscopic examination of specimens [58,59]. The specimens were temporarily mounted in glycerol, covered with a cover slip, and viewed under a compound microscope. Moreover, to allow internal structures to be clearly visible, and for external features to be more distinct, the specimens were cleared in a 10% KOH solution, boiled for 10 min for fleas, and maintained for 24 h for mite specimens. The alkaline solution was neutralized with 10% acetic acid for 30 min. After dehydrating the specimens using a series of ethanol washes (70%, 80%, and 100%), each for 1 h, they were transferred to clove oil overnight to rehydrate prior to mounting. Dibutyl phthalate-polystyrene-xylene (DPX) was used to mount the flea specimen on a microscope slide [59]. The flea and mite species identification was further confirmed using molecular techniques.

2.4. Molecular Identification of Fleas and Mites

DNA was extracted from the whole body of individual fleas (16 samples) and mites (4 samples) using the Quick-DNA™ Miniprep Plus Kit (Zymo Research), according to the manufacturer's instructions. The purity and concentration of the DNA was determined using a Nano spectrophotometer at 260 and 280 nm wavelengths.

To identify the fleas, the cytochrome oxidase subunit II (cox2) gene was amplified using the following primer sequences: forward primer (F-Leu: TCTAATATGGCAGATTAGTGC) and reverse primer (R-Lys: GAGACCAGTACTTGCTTTCAGTCATC) [60]. PCR amplification was performed using AccuPower® PCR PreMix from Bioneer (Bioneer Corporation, Daejeon, Republic of Korea). The PCR reaction mixture for the fleas consisted of 2 µL of template DNA, 0.5 µL of forward primer, 0.5 µL of reverse primer, and 17 µL of nuclease free water in a micro-tube containing AccuPower® PCR PreMix concentrate, making a total reaction volume of 20 µL. Cycling conditions consisted of an initial denaturation at 95 °C for 5 min followed by 40 cycles of 94 °C for 40 s, 56 °C for 45 s, and 72 °C for 45 s. A final extension at 72 °C for 5 min was performed to complete the extension.

For the mites, the cytochrome oxidase subunit I (cox1) gene was amplified using primer sequences as follows: forward primer (cox1-F: GTTTTGGGATATCTCTCATAC) and reverse primer (cox1-R: GAGCAACAACATAATAAGTAT) [61]. A total of 20 µL of PCR reaction mixture consisted of 2 µL of extracted DNA, 1 µL of forward primer, 1 µL of reverse primer, and 16µL of nuclease-free water in a micro-tube containing AccuPower® PCR PreMix concentrate. Cycling conditions consisted of initial denaturation at 95 °C for 5 min followed by 40 cycles of 95 °C for 40 s, 47 °C for 40 s, and 72 °C for 30 s. A final extension at 72 °C for 5 min was performed to complete the extension.

Once the PCR reaction was carried out, a 1.5% agarose gel was prepared by dissolving 1.5 g of agarose into 100 mL of sodium borate buffer and heated until the agarose had dissolved completely, and was stained with 4 µL of EZ-Vision® In-Gel Solution. A volume of 4 µL of each sample was loaded into each well of the gel, and 4 µL of DNA ladder was loaded into the first well in order to indicate the size of any fragments. The voltage was set to 100 V, and electrophoresis was allowed to run for 40 min. The image of the DNA fragments was captured using Bio-Rad's Gel Doc™ EZ Imaging System. Nine amplicons, five for fleas (2–3 per species) and four for mites, were sequenced at Macrogen Europe (Amsterdam, The Netherlands). The raw sequence data were cleaned, edited, and assembled using Geneious Prime version 2022.1.1 software [62] to obtain consensus sequences. The obtained nucleotide sequences were aligned with other ectoparasite reference sequences available in the GenBank database. A maximum likelihood phylogenetic tree was constructed with the robustness of 1000 bootstraps, using the T92/+G+1 substitution model with an AICc value of 5008.13 implemented in MEGA 11 [63]. Four nucleotide sequences for mites (accession number: OP776142, OP798020, OP798021, and OP798022) and five for fleas (accession number: OP857545, OP857546, OP857547, OP857548, and OP857549) were submitted to the GenBank.

2.5. Data Analysis

Quantitative descriptors of the ectoparasite species on each host species were calculated in accordance with [64]. P—Prevalence (proportion of infested host individuals) was estimated using the formula ($P = Re/Rt * 100\%$), where Re = number of individual rodent species infested with one or more ectoparasite species and Rt = total number of examined hosts. D—Ecological index of dominance was estimated using the formula ($D = Es/Et * 100$), where Es = number of ectoparasites of a given species collected from the rodents and Et = total number of ectoparasite species collected from the rodents; it refers the degree to which a species is more numerous than other species in an ecological community. MA—Mean Abundance of the ectoparasites was estimated using the formula ($MA = Ea/Ht$), where Ea = number of ectoparasites of a given species collected from the rodent species, and Ht = total number of hosts examined for that particular parasite species. Statistics are presented as mean ± SE with bias corrections.

We employed multiple regression models to determine the effects of the independent variables (temperature, elevation, host sex, host species, and host density) on the response variables, ectoparasite infestation (prevalence and abundance). Because of the small sample size, which resulted in zero ectoparasite or low rodent host counts at some of the sites, analysis was made of the combined ectoparasites (fleas and mites) and host species. As a result, no species-specific ectoparasite or rodent models were fitted. To avoid bias due to the smaller sample size, we excluded the data of the 1500 m site ($N = 6$ hosts) from the regression model. Host density was described as the number of captures per trap and per night, as described in Stanko et al. [65]. The distribution of ectoparasite abundance is usually patchy, with many hosts having low parasitic loads and only a few having high parasite loads, resulting in an excess zero in the data [66]. Thus, to account for dispersion and bias due to excess zero, we employed zero-inflated negative binomial (ZINB) regression models with a log link function to assess the effects on mean ectoparasite abundance. Since 41.2% of the host population had no ectoparasites present, we, therefore, used generalized linear models with a binomial distribution (infested or not infested) linked to a logit function. A host infested at least by one ectoparasite was represented by "1," and the host not infested was represented by "0." The probability of being infested was referred to as the prevalence. Since elevation negatively correlates with temperature, we employed them in different models to avoid confounding effects. The best-fitting model among candidate models was selected on the basis of Akaike's information criterion corrected for small sample sizes (AICc) [67]. The model with a lower ΔAICc value was selected as a best-fit model. The summary of parameter estimates for the fitting model is presented as estimates, SE, and 95% confidence intervals; the confidence interval which includes zero is not significant. The "lme4" and "pscl" packages in R ver. 4.2.2 [68] were used for binomial and ZINB models, respectively.

3. Results

3.1. Morphological and Molecular Identification Results of Fleas and Mites

Samples of mounted vouchers of flea and mite species are provided in Figure 2a,b. BLAST search results revealed three ectoparasite species: *Ctenophthalmus calcatus cabirus* (n = 3), *Dinopsyllus ellobius* (n = 2), and *Varroa rindereri* (n = 4). The comparison of *C. calcatus cabirus* in our study with sequences obtained from *Lemniscomys striatus* from Rwanda (MH142447.1) revealed 95.19–97.89% identity of similarity in the BLAST. The phylogenetic tree for fleas (Figure 3A) was rooted using *Tunga trimamillata* as the outgroup species. *C. calcatus cabirus* (OP857547, OP857548 and OP857549) of this study shared different lineages with the reference (MH142447.1) obtained from GenBank. The percent BLAST similarity between *D. ellobius* (OP857545 and OP857546) sequences in our study and the closest match in the GenBank (EU335993.1) was 95.75%. The two *D. ellobius* sequences were clustered together, but were distantly grouped with *D. ellobius* from the references (EU335993.1). The flea, *Xenopsylla cheopis*, was not sequenced because there were not enough samples for molecular analysis; it was identified only morphologically. On the other hand, the mite species identification result in this study was ambiguous; it was identified morphologically as a *Laelaps* species (Mesostigmata). However, the cox1 gene sequence results of all four mite samples (OP776142, OP798020, OP798021, and OP798022) provided the highest-scoring BLAST hit to a sequence from the species *V. rindereri* (Order Mesostigmata) in the GenBank (AF107261.2), with an 83.24% identity of similarity. Morphologically, *Laelaps* possess a flask-shaped ventral genital shield that is distinct from the sternal plate, whereas in *Varroa* the genital shield is large, with deep lateral and angular projections that are fused with the sternal plate. Metapodal shields are greatly enlarged and broadly triangular in *Varroa* but small and inconspicuous in *Laelaps* (Figure 2b). The phylogenetic tree for mites (Figure 3B) was rooted using *Laelaps* as the out-group. The *V. rindereri* sequences in this study share different lineages with *V. rindereri* from the reference sequences (AF107261.2).

3.2. Quantitative Descriptors of Ectoparasite Infestation

A total of 398 rodents (335 of *Montemys delectorum* and 63 of *Rhabdomys dilectus*) were examined for flea and mite infestation (Table 1). Overall, a total of 266 mites and 99 flea individuals were recovered from the two host rodents. About 58.8% of the hosts (234/398) were infested by at least one ectoparasite. Probabilities of ectoparasite infestation of 63% and 37% were observed in *M. delectorum* and *R. dilectus*, respectively. In *M. delectorum*, 95% males and 41% females were infested, whereas in *R. dilectus*, 48.3% males and 30% females were parasitized by at least one ectoparasite (Figure 4a). The mites were recorded most frequently, accounting for 81.85% of the total ectoparasite ecological index of dominance, and contributing to 50.68% of the infestation in the total host population. Of the fleas, *D. ellobius* was the most abundant flea species, accounting for 7.11% of the total ectoparasite dominance index (Table 2). On *M. delectorum*, there were 8.8 ± 5.01 fleas and 41.6 ± 21.66 mites, whereas on *R. dilectus*, there were 3 ± 1.5 fleas and 11.6 ± 7.17 mites (Figure 4b,c). *R. dilectus* was parasitized by all the flea and mite species, whereas *M. delectorum* was infested by *D. ellobius* and mites only. In both rodent species, the mite and *D. ellobius* contributed the most to the overall parasite infestation (Figure 5). The prevalence of ectoparasites declined with increasing elevation for both host species, with the lowest record at 3500 m (Figure 6). However, the low prevalence at 1500 m (Table 1) was due to the smaller sample size of rodent hosts examined for *M. delectorum* (n = 2) and *R. dilectus* (n = 4). The flea *X. cheopis* was recorded only at 1500 m on *R. dilectus*, whereas the other ectoparasite species were found at multiple elevations (Table 1).

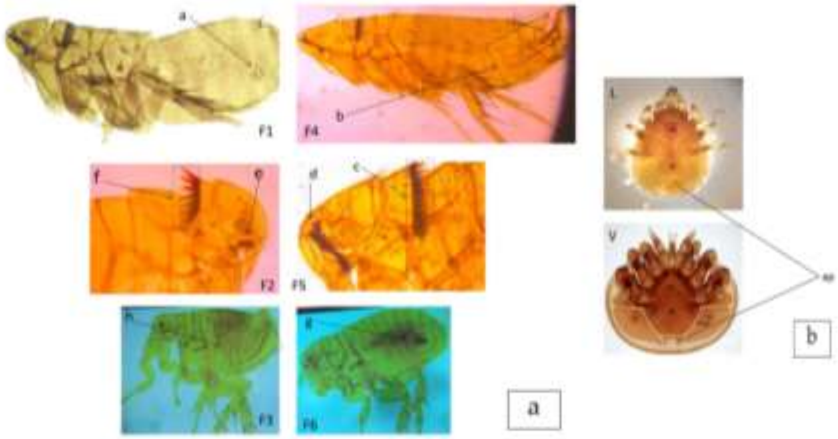

Figure 2. (**a**) Mounted vouchers of flea species: F1—*Dinopsyllus ellobius* (female, a—spermatheica); F2—*Ctenophthalmus calceatus cabirus* (front part; e—genal ctenidia with three spines, f—Pronotal ctenidia); F3—*Xenopsylla cheopis* (male; h—clasper); F4—*Dinopsyllus ellobius* (male, b—clasper); F5—*Dinopsyllus ellobius* (front part; c—Pronotal ctenidia, d—genal ctenidia); F6— *Xenopsylla cheopis* (male; h—clasper). (**b**) Ventral view of *Laelaps* mite (L) and *Varroa* mite (V) [69]. *Varroa* (V): Sternal plate (sp) fused with genital shield (gs); genital shield is large with lateral deep and angular projections; metapodal shields (mps) greatly enlarged and broadly triangular. *Laelaps* (L): Genital shield is flask-shaped and distinctive from the sternal plate. Both mites possess one post anal setae in the anal plate (ap).

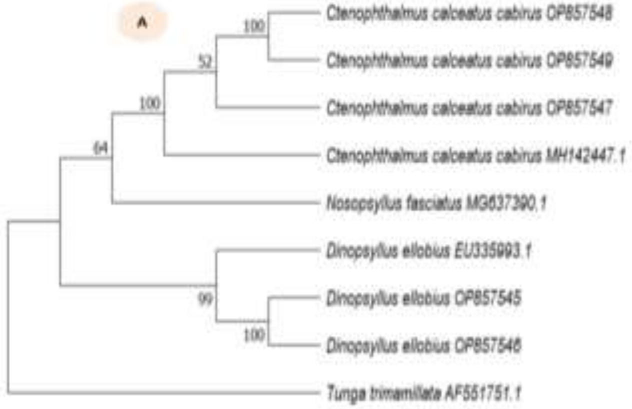

Figure 3. *Cont.*

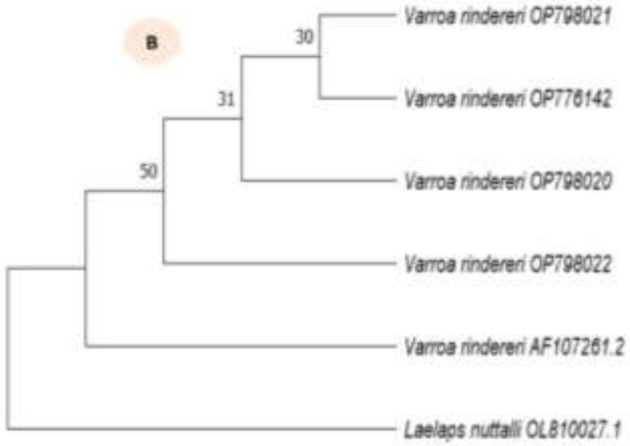

Figure 3. Phylogenetic tree for fleas (**A**) and mites (**B**) using cox2 and cox1 genes, respectively. The evolutionary history was inferred using the maximum likelihood method with bootstrap tests (1000 replicates). The percentage of trees in which the associated taxa clustered together is shown next to the branches. The phylogenetic tree was constructed using the sequences from this study, as well as other reference sequences from GenBank. *Tunga* and *Laelaps* were used as outgroup species for fleas and mites, respectively.

Table 1. Flea and mite species infecting *M. delectorum* and *R. dilectus* at different elevation zones on Mount Meru. N and n are the numbers of hosts examined and infested, respectively. Count and mean abundance of the fleas and mites are provided in brackets.

Host (Infested/ Examined)	**Ectoparasite Taxa**	**1500 m N = 6 n = 3**	**2000 m N = 83 n = 57**	**2500 m N = 201 n = 130**	**2950 m N = 70 n = 29**	**3500 m N = 38 n = 15**	**Total N = 398 n = 234**
Montemys delectorum (211/335)	*Xenopsylla cheopis*	0	0	0	0	0	0
	Dinopsyllus ellobius	0	22(0.28)	20(0.21)	2(0.05)	0	44
	Ctenophthalmus calceatus cabirus	0	0	0	0	0	0
	Mite	0	52(0.67)	121(0.62)	24(0.56)	11(0.60)	208
	Total	0	74(0.95)	141(0.72)	26(0.64)	11(0.60)	252
Rhabdomys dilectus (23/63)	*Xenopsylla cheopis*	2(0.05)	0	0	0	0	2
	Dinopsyllus ellobius	0	0	2(0.40)	5(0.19)	0	7
	Ctenophthalmus calceatus cabirus	0	0	1(0.20)	4(0.15)	1(0.05)	6
	Mite	3(0.75)	0	0	37(1.37)	18 (0.82)	58
	Total	5(1.25)	0	3(0.6)	46(1.70)	19(0.86)	73
	Overall ectoparasites (MA ± SE)	0.16 ± 0.10	0.29 ± 0.17	0.19 ± 0.12	0.16 ± 0.08	0.12 ± 0.09	

MA = mean abundance.

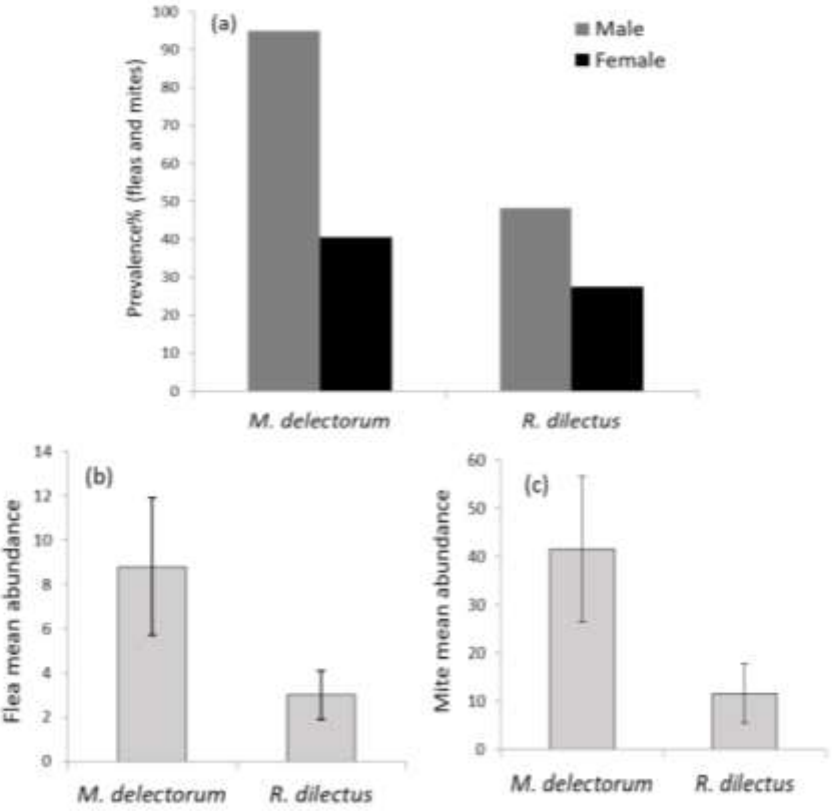

Figure 4. Ectoparasite infestation on *M. delectorum* and *R. dilectus*: (**a**) prevalence (%) between host sexes; (**b**) flea mean abundance with SE bar; (**c**) mite mean abundance with SE bar.

Table 2. Flea and mite infestation probability (%P) and ecological dominance index (%D) on *M. delectorum* and *R. dilectus* rodents.

Ectoparasite Taxa	%P	%D
Xenopsylla cheopis	0.25	0.62
Dinopsyllus ellobius	7.11	15.69
Ctenophthalmus calceatus cabirus	0.76	1.85
Over all fleas	8.12	18.15
Mites	50.68	81.85

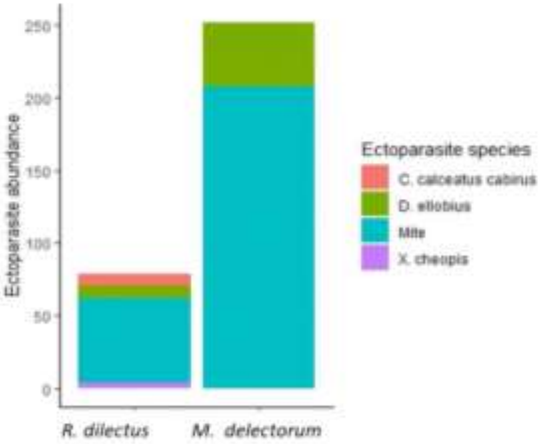

Figure 5. Relative contributions of flea and mite species infesting *M. delectorum* and *R. dilectus* on Mount Meru, Tanzania.

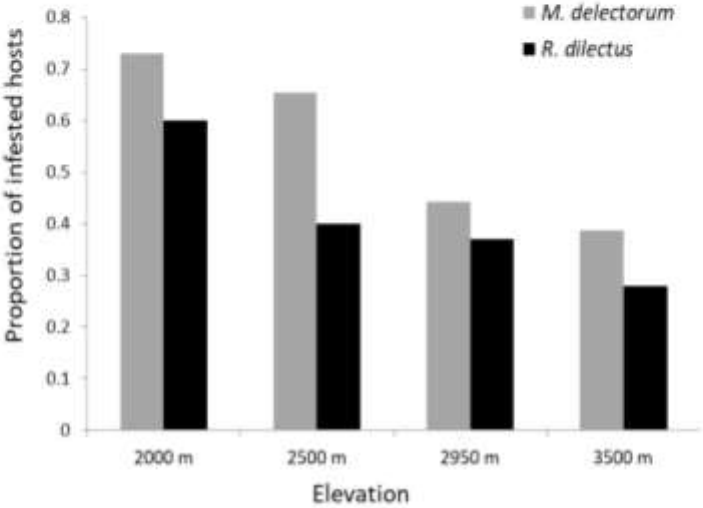

Figure 6. Ectoparasite prevalence of *M. delectorum* and *R. dilectus* in relation to elevation on Mount Meru.

3.3. Assessment of Parameters Influencing Ectoparasite Occurrence

The results of the study show that host species, sex, and temperature best predict ectoparasite prevalence and mean abundance (Tables 3, S1 and S2). M. delectorum had a higher prevalence (1.22 ± 0.30) than R. dilectus, and male individuals had a greater prevalence (2.56 ± 0.28) than female individuals. Similarly, the parasites' mean abundance was greater in M. delectorum (0.42 ± 0.14) and in males (0.93 ± 0.12).

Table 3. Summary of best model describing the ectoparasite abundance (zero-inflated negative binomial) and prevalence (binomial and logitlink function) of the rodents *M. delectorum* and *R. dilectus* on Mount Meru, Tanzania. For categorical variables, the reference level is reported in parentheses.

Variables	Estimate	SE	95% LCL	95% UCL
Prevalence				
Host species (Md)	1.22	0.30	0.32	5.21
Host sex (Male)	2.56	0.28	0.39	4.69
Temperature (°C)	0.50	0.12	0.28	3.44
Abundance				
Host species (Md)	0.42	0.14	0.04	8.06
Host sex (Male)	0.93	0.12	0.13	9.17
Temperature (°C)	2.10	0.99	1.16	4.48

Md = *M. delectorum*; SE = standard error; LCL = lower confidence interval; UCL = upper confidence interval.

4. Discussion

This study investigated the distribution of arthropod ectoparasites on *Rhabdomys dilectus* (mesic four-striped grass rat) and *Montemys delectorum* (East African soft-furred mouse), which are the two most abundant species, with a wide range of distribution on Mount Meru [39,41]. Mount Meru has experienced habitat disturbances due to a fire outbreak in the ericaceous habitats; deforestation; road construction along the National Park; and eco-tourism activities including clearing of land for vehicle parking and camping. Moreover, the degradation of habitats by human activities, including farming and grazing, has intensified in the last decades, particularly at the base of the mountain [51]. The habitat degradation and temperature increases due to climate change have been reported to cause an upward shift in the distribution of rodent and shrew species, including endemic and threatened species on the IUCN Red List [39]. However, parasites can also be a danger to threatened species because many threatened mammal populations are fragmented and small, and have low levels of genetic diversity [70,71]. These conditions can enhance host susceptibility and exposure to parasitic infections [72]; moreover, parasitic infections could be another factor that contributes to an increased probability of stochastic extinction [73,74]. Therefore, the parasite burden observed in this study, especially for the endemic *M. delectorum* (with 63% parasite prevalence), needs attention and improved conservation management.

Rodents on Mount Meru were infested more with mites than fleas, consistent with previous studies elsewhere [75,76]. In contrast, despite the fact that fleas are the most dominant group of ectoparasites for small mammals [77], we collected far fewer fleas than mites. The most likely explanation is that fleas spend more time in the nests of their host than on their bodies, lowering the likelihood of their collection [77]. Moreover, the fact that mites are more host generalists than fleas [78] may have also contributed to their greater abundance.

The mites in this study were identified as *Laelaps* species, using morphological cues; they did, however, provide the highest-scoring BLAST hit to a sequence from the species *Varroa rindereri* using the cox1 gene. Surprisingly, the mite species was discovered in honeybees in 1998 (accession no: AF107261.2) [3]. *Varroa* was previously known as the "Laelappid-like mite", and belonged to the family Laelapidea before being separated into the Varroadea family [79]. Thus, the low percent identity value (83.24%) between the DNA sequences suggests that our mites belong to a previously uncharacterized species in the Mesostigmata group. To the best of our knowledge, this is the first study on the molecular identification of rodent mites in Tanzania. Thus, the quite limited sequenced data for Mesostigmata mites and fleas from Tanzania available in GenBank made it difficult to compare our DNA sequence. We only sequenced small samples to confirm the species; thus, further study using different "target genes" is needed to resolve the ambiguity of the mite species identification, and to detail the molecular characteristics of the ectoparasites. Finally, it might also be worth questioning: "Can the same mite species parasitize rodents and honeybees?"

While there remains much to be learned, our study provided an overview of the key factors that determine the distribution of ectoparasites on the two rodent species; host species, sex, and temperature are predictive variables. Host species influenced parasite prevalence and ectoparasite abundance. This is due to the fact that different species have different resistances (i.e., the capacity of the host to reduce parasite establishment) and tolerance (i.e., the competence of the host to resist a given parasite load and sustain fitness while under infestation) [80]. Moreover, the infestation of the animal may be determined by different factors, such as the color and type of the host's fur. The greater prevalence and abundance of ectoparasites on *M. delectorum* than on *R. dilectus* may partly be associated with its soft fur, which potentially allows ectoparasites to penetrate easily. However, the greater ectoparasite species diversity (four species) in *R. dilectus* could be due to the striped, white-grey color of the rodent, which could be easily detectable by the ectoparasites, as some species are known to use the host's color to find their host. Though it may depend on the host–parasite taxon, this can support previous findings that found plumage color affected the infestation of lice on *Columba livia* [81]. Moreover, our study showed that sex was among the predictors of ectoparasite load, with the burden of parasites biased towards male individuals. Similar findings were reported in previous studies on different taxa: rodents [82,83], geckos (*Quedenfeldtia trachyblepharus*) [84], and grey squirrel species [85]. Different factors may contribute to these sex-based variations. Larger male hosts in mammal species [86] provide a wider range of niches for parasites, and can thus support a greater number of parasites [87,88]. In addition, male hosts often have higher energetic requirements, necessitating longer distances travelled in the quest of food, increasing their chances of encountering ectoparasites [89]. Furthermore, due to the physiological differences between males and females, the immunosuppressive properties of testosterone tend to diminish the body's immunity, causing a substantial decline in male immune fitness [90].

We expected that parasite infestation would be affected by the density of the host; this is due to the idea that hosts in high densities should contain more parasite species than hosts in low densities because of the increased contact between individuals [42]. However, we did not see the influence of host density in this study, and it was not a predictor variable in the parasite distribution, which was in line with the findings of Singleton [91], which reported no association between host density and parasite infestation rate in *Mus musculus*. Thus, other abiotic factors such as temperature, humidity, host burrow structures, and soil type may determine the distribution of the parasite [92].

It is commonly reported that elevation determines organisms' distribution. However, by itself, elevation above sea level means nothing to a species [93]. The correlated environmental variables that change rapidly over short distances generate and maintain the patterns of abundance and distribution [37,38,93]. Generally, the most obvious change predictor with increasing elevation is linear decrease in temperature [94]. Our study showed that temperature significantly influenced the occurrence of ectoparasites, supporting the idea that temperature is considered to be the most important factor changing elevational distribution of species [24,93]. The lower ectoparasite prevalence and mean abundance at 3500 m, in the site where a daily minimum temperature was 2.7–4.6 °C, implies that the cold conditions of the highlands impose thermoregulatory constraints on ectoparasites, and have a direct effect on their physiology and survival rate. This justifies the fact that as temperature is inversely linked to elevation; warmer temperatures at lower elevations provide more favorable conditions for parasite development than at higher elevations.

Another reason for the lower infestation at higher elevations would be due to the cold weather; there is less movement of the hosts, hence reduced contact with other individuals and a lower probability of being infested. Though our study is not species-specific, the findings do corroborate prior studies of parasitic mites on lizards [95], feather mites on birds [44], and fleas on rodents [45].

Disease ecologists and conservation biologists argue that parasites are increasing in abundance through time [31]. Parasite outbreaks are predicted to be a result of habitat change, biodiversity loss, and rising temperatures related to climate change [31–33]. Previous studies provided evidence that Mount Meru has shown an increase in mean annual temperature, particularly in the last decade where a 0.37 °C rise in mean annual temperature was recorded [39]. This may provide a platform for parasites to increase in abundance through time. However, for the vast majority of wildlife parasite species, the hypothesis that parasites are increasing in abundance over time remains entirely untested [31]. Our study may provide historical data as a baseline against which to compare contemporary parasite burdens over time.

Some of the ectoparasites and rodents reported in this study have been identified as having medical and veterinary importance [49]. The fleas, *X. cheopis*, *C. calceatus*, and *Dinopsyllus spp.*, for instance, are confirmed efficient vectors of bubonic plague in Tanzania, and have been recovered from rodents involved in plague outbreaks [49]. Bubonic plague is a rodent-borne infectious disease caused by the bacterium *Yersinia pestis*. It affects both humans and animals, and is primarily transmitted by flea bites that jump from rodents to humans [9]. In addition, *C. calceatus* has also been reported as a transmitter of bartonellosis in Rwanda [96]. Bartonellosis is another rodent-borne disease caused by Gram-negative bacteria in the genus *Bartonella*. It affects both humans and wild and domestic animals, and is spread to humans by fleas or contact with flea-infested animals [97]. Moreover, some mites, such as *Laelaps* spp., are vectors for zoonoses such as Q fever and rickettsialpox [98], and Chigger mites for scrub typhus [99]. Moreover, the mite, *Varroa destructor*, is a vector of the deformed wing virus (DWV), a bee-pathogenic RNA virus that causes honeybee (*Apis mellifera)* colony losses worldwide [6]. Therefore, more research on zoonotic pathogens is needed to ascertain the risk of zoonosis. Mount Meru is the centerpiece of the Arusha National Park, and is a popular ecotourism destination. It is home to diverse endemic and threatened species. Mount Meru attracts a large number of tourists and researchers, due to its rich biodiversity and numerous trails for nature enthusiasts to explore. On the other hand, animals in the park interact with these parties, who in turn are likely to interact with the local community. Moreover, wildlife, including rodents, cross the park boundaries and enter human dwellings, coming into direct or indirect contact with people and livestock along the edge of the park. All of these interactions increase the likelihood of anthroponotic and zoonotic pathogen transmission, altering the threat of disease to both animals and humans [49]. As human–wildlife interactions increase, the importance of surveillance for zoonotic diseases cannot be overstated. Given the 63% increase in zoonotic outbreaks in Africa over the last decade [50], recognizing the patterns of parasite distribution among wildlife hosts is of major importance. Our study contributes to a better understanding of the ecology of host–ectoparasite relationships along elevational gradients; this is important in this region, not only for identifying potential ectoparasite vectors, but also for designing and implementing vector-borne disease management programs for wildlife conservation and human health. Moreover, no information is available regarding the role of arthropod ectoparasites in the transmission of zoonotic infectious agents. This study may lay the groundwork for screening rodent hosts and their ectoparasites for potential zoonotic pathogens on Mount Meru.

5. Conclusions

The elevational distribution of ectoparasites infesting *Montemys delectorum* and *Rhabdomys dilectus* was influenced by the host traits (species and sex), in combination with environmental factors such as temperature. The host sex and species influenced the prevalence and abundances of ectoparasites, such that it was higher for males than females and for *M. delectorum* than *R. dilectus*. Our findings did not support our hypothesis that host density predicts the prevalence and abundances of ectoparasites in the two rodent species, but rather that temperature was the best predictor. Since temperatures decrease with elevation, parasite prevalence and mean abundance were lower at higher elevations, highlighting the idea that cold conditions at higher elevations limit reproduction and development—this shows higher elevation zones are ideal for conservation. This may have an impact in light of climate change, since organisms shift their distribution towards higher altitudes. This could also affect species that act as parasite reservoirs and vectors, altering wildlife and livestock infestation patterns. Furthermore, the rodents and ectoparasite species described in this study have been reported to be vectors of diseases of medical and veterinary importance, necessitating precautions. Moreover, Mount Meru is a refuge for a number of endemic and threatened species on the IUCN Red List. Thus, parasitic infection can also be an additional risk to these critical species and biodiversity in general. Therefore, our study lays the groundwork for future wildlife disease surveillance and biodiversity conservation management plans. In addition, the flea and mite species identification using cytochrome oxidase genes in this study at least partly helps to fill the scarcity of sequence data for ectoparasites of African rodents in GenBank. We found a previously uncharacterized mite species in the Mesostigmata group that was previously known to be a parasite of honeybees. Further investigations may shed light into the role of this mite species on Mount Meru.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/biology12030394/s1, Table S1: AICc models for ectoparasite prevalence; Table S2: AICc models for abundance of ectoparasites.

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Data Availability Statement: All of the data for the study are provided in the paper and Supplementary Materials.

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CHAPTER FIVE

5.0 GENERAL DISCUSSION

The current study generally aimed to investigate the ecological dynamics and distribution patterns of small mammals and their arthropod ectoparasites across different elevations of Mount Meru, Tanzania. Specifically, the following research objectives were determined: changes in the elevational distribution of small mammals over temporal spans, breeding patterns and population abundance of the dominant small mammal species, and the elevational distribution of arthropod ectoparasites infesting the two dominant small mammal species. In a broader sense, this PhD study explains how the diversity and distribution of the small mammals and their arthropod ectoparasites would likely respond to the future changing ecological dynamics of Mount Meru. Additionally, how would this response be explained in the long term? And how would it present challenges for the conservation of biodiversity and safeguarding human well-being?

Mount Meru is among the biodiversity hotspots of Tanzania, where its fauna comprises many rare and endemic species (Demeter and Hutterer, 1986), with many parts of the mountain remaining unassessed and many more species yet to be identified. Demeter and Hutterer (1986) provided scattered reports of a few small mammal species from the lower altitudes of Mount Meru and its environs. In 2009, Stanley and Kihaule (2016) documented a total of 10 small mammal species, covering some of the vegetation zones along the elevation gradients. Yet, the real wealth of small mammal species in the area has not been fully assessed due to a paucity of studies to cover all the major vegetation types. Conservationists concerned that a number of small mammal species are threatened due to severe habitat loss before being adequately documented (Gordon *et al.,* 2012). Accordingly, the current study extensively sampled the majority of the vegetation types, increasing the number of species to 15, two of which are endemic to the area. This study certainly increases the unearthing of hidden mammalian diversity in the Meru ecosystem as well as the country.

Moreover, this study shows that the predominant small mammal species on Mount Meru is the soft-furred mouse (*Montemys delectorum*). This finding contradicts previous evidence provided by Cassola (2016), who declared that *Montemys delectorum* is exclusively found in the East Arc Mountains. Our observations from this study, however, demonstrate that the current range distribution of the species extends to the Northern Tanzanian Mountains, which include Kilimanjaro and Meru (Mulungu *et al*., 2008; Thomas *et al*., 2022). One may argue that the species has expanded from the adjacent mountains, such as Northern Pare, or that its distribution has not been adequately assessed. Though more sampling is required, the species distribution information needs to be corrected to include its distribution in Mount Meru and Kilimanjaro and be considered an endemic species to the Eastern Africa Highlands rather than just the East Arc Mountains. It is also noted that this species was formerly classified in the genus *Praomys* (i.e., *Praomys delectorum*), but Nicolas *et al*. (2021) taxonomically revised it to *Montemys delectorum.* This study calls for updated information on the taxonomy and geographical distribution range of this and other species so as to enhance biological diversity conservation efforts.

This study also determined the elevational distribution pattern of small mammal species, specifically rodents and shrews, at Mount Meru, revealing peaks at intermediate altitudes and decreasing trends towards upper and lower altitudes. The results lend credence to the hypothesis of mid-elevational peaks, frequently known as "Hump-shaped patterns", where species richness is higher at the intermediate altitudes (Brown, 2001), highlighting the need for conservation concern in the mid-elevation of the mountain ecosystem. The current finding is generally in support of previous surveys from a wide range of altitudinal gradients worldwide (Chen *et al*., 2020; Craig *et al*., 2020). Although the mechanisms that shape the distribution patterns of biodiversity are still the subject of considerable debate (Dunn *et al*., 2007), relationships between species and elevation differ for taxon and zoogeographical location (Rahbek, 2005). Some of the explanations regarding why the concentration of species occurring at intermediate altitudes in the Meru Mountains may exemplify a theory put forth by Brown that species richness may be amplified at a given elevation when three conditions are met: 1) species having different habitat requirements overlap in their distributions; 2) this occurs where vegetation heterogeneity increases and conditions are not too extreme, resulting in the most productive point in the gradient; and 3) species are being pushed higher from the lower altitudes to the middle altitudes to escape ever-increasing temperatures in the face of climate or habitat change (Brown 2001).

Moreover, the findings demonstrated that along an elevational gradient on Mount Meru, about 56% of the small mammal species recorded may have shifted their ranges upslope over the last decade, resulting in changes in species composition. The degree of change in species composition in this study is relatively small compared with the resurveys conducted by Craig *et a*l., 2020, after 88 years in Ethiopia, and Rowe *et al*., 2010, after a century in the United States. The relatively smaller change in species composition in this study could probably be due to the short interval of reassessment. The upslope movement typically indicates species that are jeopardized in their habitat owing to different causes usually migrate and seek refuge in a new location. Several studies have reported that montane small mammal species are facing challenges maintaining their existence due to habitat loss (Gazzard *et al*., 2023), attributed to climate change, ecological disturbances, and other impacts caused by human activity (Neate-Clegg *et al*., 2018; Rogora *et a*l., 2018; Gazzard *et al*., 2023). Studies simplified how species respond to these environmental and climate changes in the tropics, as well as how community composition may change: lowland species become extinct if they lack nearby opportunities to escape from too-warm conditions, whereas foothill species migrate upslope

(Colwell *et al*., 2008; Korner *et al*., 2009; Spehn, 2011). The high-elevation species move towards summit regions, whereas the summit species with no possibility to escape upslope suffer from increasing competition from immigrants from lower elevations. Some highland taxa can escape short distances by taking advantage of microhabitat diversity in rugged terrain, resulting in changing community mosaics at a given elevation. Species already living near the top of elevational gradients face a threat due to a lack of alternative habitats, unless they have disjunct populations elsewhere on higher mountains or at cooler latitudes (Brown, 2001; Colwell *et al*., 2008; Korner *et al*., 2009). So, gaining insight into the distribution patterns of montane species across elevational gradients over time holds significant value for biodiversity conservation efforts as well as for predicting species' responses to forthcoming environmental changes and facilitating effective conservation strategies to maintain the species. This study is notable for the comprehensive insight it provides into the specific and general patterns of mammalian elevational distribution, which contributes to the existing literature on the elevational distribution of mammals along mountain slopes, particularly on African mountainsides, where limited evidence is available. As small mammals have limited dispersal capacity and high affinity for specific habitats, they are highly susceptible to environmental changes on a smaller scale (Cuypers *et al*., 2022). This work may shed light on their elevational distribution and ecology, which are critical for forecasting their response to future environmental changes, as well as biodiversity conservation planning and management.

This study has further demonstrated that the breeding seasonality of *Montemys delectorum* is bimodal, which is consistent with previous observations made in Africa, revealing that rodent breeding commenced in the wet season and continued through to the early dry season (Makundi *et al*., 2007; Yonas *et al.,* 2015). This supports to the notion that rainfall patterns promote vegetation productivity for food, provide better nesting sites, and cover against potential predators, which in turn stimulates breeding activity and adds new offspring to the population, ultimately leading to an increased population abundance (Previtali *et a*l., 2009). Seasonal breeding leads to seasonal fluctuations in population abundance, signifying that higher population abundance occurs during the breeding season and vice versa. The considerable variation in population abundance between the two forest habitats, with a greater population in the patchy open forest, also indicates the population in this landscape is unstable. It would appear to suggest that the patchy open forest is a better refuge for the species, in line with previous studies (Forman and Godron, 1981; Walke et al., 2003; Gitzen and West, 2002; Goodsel et al., 2007). On the other hand, many authors have linked fluctuations in the abundance of a rodent zoonotic pathogen reservoir population with temporal variation in the number of new disease cases (Olsson *et al*., 2003; Rose *et a*l., 2003; Davis and Calvet, 2005). And a growing number of studies have found that higher primary productivity of a landscape can be linked to high numbers of rodent-borne zoonoses cases (Franke *et al*., 2002), leading some to trophic cascade hypothesis. This hypothesis suggests that higher primary production leads to increased rodent population abundance, which may enhance human-animal contact and potentially increase the risks of zoonosis in the reservoir population and community (Gage and Kosoy, 2005). However, evidence for this hypothesis is limited (Brown and Ernest, 2002).

This study also examines the arthropod ectoparasite infestations of two rodent species, *Montemys delectorum* and *Rhabdomys dilectus,* with a wide distribution across the elevation gradient. The results of the study revealed that some rodent species and ectoparasites, including fleas and mites, found on Mount Meru have been linked to medicinal and veterinary significance in earlier research conducted elsewhere (Makundi *et al*., 2015; Yonas *et a*l., 2011). The fleas, *X. cheopis*, *C. calceatus, and Dinopsyllus* spp., for example, are confirmed efficient vectors of bubonic plague in Tanzania and have been found in rodents involved in plague outbreaks (Makundi *et al*., 2015). In addition, it has been mentioned that *C. calceatus* is linked with the transmission of bartonellosis in Rwanda (Nziza *et al*., 2019). Although the identification of mite species is ambiguous—*Laelaps* or *Varroa*—certain *Laelaps* species are known to serve as vectors for zoonoses like rickettsial pox and Q fever (Diaz, 2010). Similarly, *Varroa* spp. is known to transmit a bee-pathogenic RNA virus known as the deformed wing virus (DWV), which is responsible for honeybee (*Apis mellifera*) colony losses world-wide (Gisder and Genersch, 2021).

The controversial point in this study that required further investigation was the identification of the mites. Using morphological traits, the mites were identified as *Laelaps* species; however, using the cox1 gene, they provided the highest-scoring BLAST hit to a sequence from *Varroa rindereri*. *Varroa rindereri* was surprisingly discovered in honeybees in 1998 (Anderson and Trueman, 2000). *Varroa* was previously known as the Laelappid-like mite, and belonged to the family Laelapidea before being separated into the Varroadea family (Delfinado and Baker, 1974). Probably the low percent identity value (83.24%) between the DNA sequences suggests that the mites found in Mount Meru rodents belong to a previously uncharacterized species in the Mesostigmata group. According to the information available so far, this is the first molecular identification of small mammal mites in Tanzania. Thus, the quite limited sequenced data for Mesostigmata mites and fleas from Tanzania available in GenBank made it difficult to compare the DNA sequence from this study. Only small samples were sequenced to confirm the species; so, further study using different target genes is needed to resolve the ambiguity of the mite species identification and to detail the molecular characteristics of the ectoparasites. Finally, it might also be worthwhile to ask if *Varroa* species could possibly parasitize rodents. This appears to be a topic that warrants more study in the fields of biology and ecology related to mites and confirms their role in zoonotic diseases.

Furthermore, the nature and frequency of human contact on Mount Meru with wildlife, small mammals inclusive, in the ecosystem seem to be rising as a result of research activities, ecotourism, human encroachment on wildlife habitats because of grazing from the lower altitudes, and other activities that bring people and wildlife into close proximity or direct contact. Wildlife, including rodents, move across the Arusha National Park boundary, venturing into areas used by humans, and thus come into direct or indirect contact with people along the park margin and their livestock. Conversely, animals in the park interact with the field assistants and tourists, who later interact with the local community. All such interactions are known to have the potential to increase the possibility of zoonotic pathogen transmission, thereby affecting the overall health of animals and humans (Gilardi *et al*., 2015). Moreover, according to the WHO (2022) report, Africa is facing an increasing risk of zoonotic disease epidemics, with outbreaks increasing by 63% from 2012 to 2022, compared to the preceding decade, of which 75% originate from wildlife (Jones *et al*., 2008). Due to the fact that Tanzania is among the handful of countries in Africa where active foci of zoonotic diseases, like plague, still persist, this preliminary study may lay the groundwork for screening rodent hosts and their ectoparasites for potential zoonotic pathogens on Mount Meru and its environs.

The two rodent species included in this study had an overall ectoparasite prevalence of 58.8%, which is higher than the prevalence results of other small mammal species reported in Uganda (Mawanda *et al.,* 2020) but lower than the values reported in Ethiopia by Yonas *et al*. (2011). This might be related to the fact that parasite infestations differ between geographical regions and taxa. Yet, several studies on other species have found that parasitic infection results in lower reproduction and overwinter survival in yellow-bellied marmots (Zanet *et al.,* 2017) and hare populations (Newey *et al*., 2007). These studies may support the fact that parasites can regulate their host populations depending on the characteristics of the host-parasite relationship (Harris and Dunn, 2010; Schmid-Hempel, 2021). Parasites can deteriorate host fitness by draining resources, consuming and reducing host energy, causing physical harm, and increasing mortality (Hakkarainen *et al*., 2007; Wolf *et al*., 2018), which can lead to reduced host density and potentially affect ecosystem function. Moreover, increased exposure and a larger accumulation of additional parasite infestations in hosts heighten the likelihood of transmission to other members of the community (Solak *et al*., 2020). Particularly, the potential impacts of parasites become apparent when a newly emerging disease causes devastating losses to the population of conservation concern (Pedersen and Fenton, 2015). Understanding the diversity and abundance of ectoparasite species provides valuable insights into the ecological functions they play in the regulation of their host populations and communities (Wei *et al*., 2010; Kasso, 2023). Owing to the considerable biological diversity of Mount Meru, which includes endemic and threatened species listed on the IUCN Red List (Stanley and Kihaule, 2016), such as *Crocidura newmarki*, *Lophuromys verhageni*, and *Montemys delectorum*, the level of parasite infestation reported by this study may also pose a concern. This can be supported by the fact that many threatened mammal populations are fragmented, small, and have low levels of genetic diversity (Altizer *et al*., 2003), which can increase host susceptibility and exposure to parasitic diseases (Lyles and Dobson, 1993).

The distribution of ectoparasites in this study was explained by sex, species type, and environmental temperature, consistent with previous studies (Matthee *et al.,* 2010; Scantlebury, 2010; Comas, 2020), which revealed parasite distribution is determined by the combination of host traits as well as host microhabitats. The parasitism level of infestation in this study was sex-biased, with males tending to be more heavily parasitized than females. This sex-based variation could be due to different factors: This may be a direct consequence of sexual dimorphism in body size because most mammalian males have larger body sizes than females (Shilereyo *et al*., 2022; Kowalski *et al*., 2015), which provides a wider range of niches for parasites and can thus support a greater number of parasites (Young *et al.,* 2015). In addition, male hosts often have higher energetic requirements, necessitating longer distances traveled in the quest for food, increasing their chances of encountering ectoparasites (Postawa and Nagy, 2016). Furthermore, due to the physiological differences between males and females, the immunosuppressive properties of testosterone tend to diminish the body's immunity, causing a substantial decline in male immune fitness (Krasnov *et al*., 2021). Moreover, the infestation of *Montemys delectorum* was greater than that of *Rhabdomys dilectus,* which supports studies carried out elsewhere by Shilereyo *et al.* (2022), mentioning that host species are determinants of infestation so that different species have different resistances (i.e., the capacity of the host to reduce parasite establishment) and tolerances (i.e., the competence of the host to resist a given parasite load and sustain fitness while under infestation) (Medzhitov *et al*., 2012). Moreover, the infestation of the animal may be determined by the type of the host's fur. The greater prevalence and abundance of ectoparasites on *Montemys delectorum* may partly be associated with its soft fur, which potentially allows ectoparasites to penetrate easily.

The investigation also supports previous findings that revealed ectoparasite distribution is determined not only by host traits but also by the climatic conditions and landscape of the environment where the host and its ectoparasites reside (Young *et al.,* 2015). It is frequently reported that elevation determines organisms' distribution, which potentially extends to their arthropod ectoparasites. However, by itself, elevation above sea level means nothing to a species (Lomolino *et al*., 2001). The correlated environmental variables that change rapidly over short distances generate and maintain patterns of abundance and distribution (McCain, 2003; Brown, 2001; Lomolino *et al*., 2001). Generally, the most obvious change predictor with increasing elevation is the linear decrease in temperature (Zamora-Vilchis *et al*., 2012). The lower ectoparasite prevalence and mean abundance at higher elevations in Mount Meru imply that the cold conditions of the highlands impose thermoregulatory constraints on ectoparasites and have a direct effect on their physiology and survival rate. This justifies the fact that temperature is inversely linked to elevation; warmer temperatures at lower elevations provide more favorable conditions for parasite development than at higher elevations, highlighting the idea that cold conditions at higher elevations limit reproduction and development. This may demonstrate that higher elevation zones are ideal for conservation. In the light of climate change, many mountain organisms, including small mammals, shift their distribution frequently to higher altitudes, which may have an impact on species that serve as parasite reservoirs and vectors, altering wildlife and livestock infestation patterns. The study contributes knowledge to enhance understanding of spatial parasite-host dynamics, which is crucial for biodiversity conservation and zoonoses management.

In the general sense, elevational gradients influence small mammal distribution, potentially extending to the parasites they host. The shifting in the distribution of small mammals and their interaction with ectoparasites on Mount Meru is a microcosm of the broader challenges facing mountain ecosystems around the world. These insights go beyond the immediate context of Mount Meru and suggest that we need to consider the long-term consequences of ecological dynamics on biodiversity conservation. As climate change and habitat loss continue to shape mountain landscapes, our understanding of these complex relationships becomes critical. Its impact is not limited to species interactions but also touches the field of human well-being. The conservation of biodiversity is intrinsically linked to our own well-being, as biodiversity and human societies are intricately intertwined; the well-being of humans depends on the well-being of all other species in the environment. As we struggle with these complexities, the lessons of this research resonate as a call to appropriate conservation action in the Meru Mountains.

CHAPTER SIX

6.0 GENERAL CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

Gaining insight into the distribution patterns of montane species across elevational gradients holds significant value for biodiversity conservation efforts as well as for predicting species' responses to forthcoming environmental changes and facilitating effective conservation strategies to maintain them. The current study sheds new light on the ecology and distribution of small mammals and the arthropod ectoparasites they host in Mount Meru. The small mammal species found in the various habitat types of the mountain landscape was well documented. It is worth noting that *Crocidura newmarki* (Near Threatened species under IUCN Red List specific criteria) and *Lophuromys verhageni* are both endemic species to the mountain. The predominant small mammal in our captures in this landscape is *Montemys delectorum*, a species whose conservation status is a matter of concern because of the ongoing habitat loss across Africa. The study also revealed that the small mammal species found in the mountain have experienced an upward shift in their range along the elevational gradients in the past decade, which is likely attributed to climate change, fire incidences, and human pressure. Although *Otomys tropicalis* was reported from Mount Meru in the 2009 study, its presence in the current study remains uncertain. Furthermore, the study looks at the breeding patterns and population abundance of *Montomys delectrom*, revealing a seasonal breeding pattern in which rainfall emerged as the primary influencing factor. Since there is a significantly higher population in the patchy open forest than in a dense forest, it is clear that the population abundance in the study region is unstable.

The rodents and ectoparasites described in this study have been receiving significant attention for their role in the transmission of life-threatening medical and veterinary diseases throughout Africa, including Tanzania. Furthermore, this is the first study to use molecular techniques to identify flea and mite species in Tanzanian small mammals. We found a previously uncharacterized new mite species in the Mesostigmata group. The study also revealed that the elevational distribution of rodent arthropod ectoparasites was influenced by host traits such as species and sex in combination with environmental temperature. The prevalence and mean abundance of ectoparasites was found to be higher at lower elevations, indicating that the reproductive and developmental rates of these parasites are influenced by the warmer conditions typically experienced at lower altitudes.

I would close the conclusion by explaining how the diversity and distribution of the small mammals and their arthropod ectoparasites would likely respond to the future changing ecological dynamics of Mount Meru, in a broader sense. Additionally, how would this response be explained in the long term? And how would it present challenges for the conservation of biodiversity and safeguarding human well-being in the face of climate change?

In a broader sense, shifting in the distribution of small mammals and their ectoparasites on Mount Meru is a microcosm of broader challenges facing mountain ecosystems around the world. These insights go beyond the immediate context of Mount Meru and suggest that we need to consider the long-term consequences of ecological dynamics on biodiversity conservation. As climate change and habitat loss continue to shape mountain landscapes, our understanding of these complex relationships becomes critical. Its impact is not limited to species interactions, but also touches the field of human well-being. The conservation of biodiversity is intrinsically linked to our own well-being, as biodiversity and human societies are intricately intertwined. As we struggle with these complexities, the lessons of this research resonate as a call to appropriate conservation action in Mount Meru.

6.2 Recommendations

Understanding the distribution patterns of montane species along elevational gradients is of great importance for biodiversity conservation initiatives. It also aids in predicting how these species will respond to future environmental changes and enables the development of effective conservation strategies to preserve them. Given the significant importance of the Mount Meru ecosystems in terms of its rich biodiversity, the shift in the distribution of small mammals and their ectoparasites, along with the presence of species that hold medical and veterinary importance, raises a great concern for biodiversity conservation and human well-being. Therefore, the following recommendations are proposed to address the gaps identified by the findings of this study:

The upslope shifts in small mammals’ distribution in Mount Meru, likely caused by changes in climate, uncontrolled fire incidences, and human activities, call for proactive conservation measures. Enhanced conservation of the ecosystem would not only safeguard rare, threatened, and endemic wildlife, but also offer a potential refuge for lower-elevation species responding to rising global temperatures. Moreover, regularly monitor program for small mammals’ distribution is highly advised to gauge the potential impact of environmental and ecological changes on their diversity and distribution in the future. Furthermore, further studies are necessary to clarify the uncertainty regarding the presence of *Otomys tropicalis* in Mount Meru because the loss of one species from a certain habitat has a far-reaching impact on biodiversity.

The demographic study of *Montemys delectorum* conducted in this research is limited in scope, focusing on a few population parameters. Expanding this research to include movement patterns, survival rates, and recruitment would offer a more comprehensive understanding of the species' conservation status.

While the study concentrated on the demographic aspects of the dominant species, *Montemys delectorum*, it is equally important to gather demographic characteristics for the other small mammals, especially those designated as endemic or threatened by the IUCN Red List species, such as the Newmark's shrew *Crocidura newmarki*.

The presence of medically and veterinary important rodents and ectoparasites, as well as their interaction with humans and domestic animals, at the lower altitude of the mountain calls for heightened attention because warmer climatic conditions speed up parasite reproduction and development while encouraging host small mammals to move upslope, potentially spreading infection to other wildlife. Thus, a better management plan is needed to protect threatened and endemic species, overall biodiversity, and the well-being of humans within and surrounding the mountain.

The identification of mite species previously known to infest honeybees on a rodents based on DNA analysis requires further detailed study. This will help answer the question, Is it plausible for these mite species to engage in parasitic relationships with both rodents and honeybees? which can expand our understanding of parasite ecology and confirm their role in zoonotic disease.

This preliminary study serves as a foundation for further in-depth study into the rodent host-ectoparasite interactions. Screening hosts and ectoparasites for potential zoonotic pathogens is vital to enhances our understanding of zoonotic pathogen dynamics, informs conservation strategies, and helps strike a balance between protecting biodiversity and safeguarding human health.

While the study concentrated on fleas and mites in the two dominant small mammal species, a comprehensive assessment of all small mammal species in the study area for ectoparasites, including ticks, is recommended. Ticks play a crucial role in the transmission of human and livestock diseases.

Opportunistic species of rodents reported, such as *Mastomys natalensis* and *Arvicanthis niloticus*, quickly colonize areas following disturbance, overgrazing, and cultivation. Therefore, conducting a comprehensive community survey and impact assessment of households near Mount Meru is strongly advised to mitigate potential zoonotic disease risks, evaluate the threat posed by these rodent species to farmers, and implement effective pest management strategies accordingly.

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APPENDICES

Appendix 1: Individual captured small mammal species and sampling efforts in the 2009 and 2021 studies on Mount Meru.

Small Mammal	SA [ns]	LMF		UMF		UMF/EH		EH		AA		TOTAL	
Species	**2021**	**2009**	**2021**	**2009**	**2021**	**2009**	**2021**	**2009**	**2021**	**2009**	**2021**	**2009**	**2021**
Rhabdomys dilectus	2	0	1	0	3	24	26	7	20	24	36	55	88
Otomys tropicali	0	0	0	0	0	2	0	1	0	1	0	4	0
Praomys taitae	0	79	72	185	192	38	39	4	18	0	0	306	321
Montemys delectorum [@]	0	0	0	0	2	0	1	0	0	0	0	0	3
Mus triton	0	0	0	0	0	0	0	0	0	1	4	1	4
Mastomys natalensis	29	0	0	0	0	0	0	0	0	0	0	0	29
Lophuromys verhageni	0	0	0	18	0	9	12	30	37	2	5	59	54
Lemniscomys striatus	0	0	0	0	3	0	1	0	0	0	0	0	4
Graphiurus murinus	0	5	0	1	0	6	21	15	5	0	0	27	26
Grammomys dolichurus	6	3	3	4	5	2	4	4	3	0	0	13	21
Dendromus insignis	0	0	0	0	0	1	0	7	4	2	3	10	7
Dasymys incomtus	0	0	3	0	3	0	1	0	0	0	0	0	7
Cricetomys ansorgei	0	0	4	0	3	0	2	0	–	0	–	0	9
Arvicanthis niloticus	17	0	5	0	0	0	0	0	0	0	0	0	22
Crocidura newmarki	2	49	38	18	19	22	23	51	42	4	3	144	127
Crocidura allex	0	31	0	31	33	18	19	36	29	16	0	132	81
Species richness	5	5	7	6	9	9	11	10	8	6	5	10	15
Total number of captures	56	167	126	257	263	122	149	155	158	50	51	751	803
Total trap-effort	1200	1426	1200	1426	1200	1426	1200	1426	1140	1407	1140	7111	7080
Trap success	4.7	11.7	10.5	18	21.9	8.6	12.4	10.9	13.8	3.5	4.5	10.5	11.3

[@] *As Praomys delectorum* in previous studies (but see Nicolas *et al*., 2021); [ns] Not sampled in 2009.

Appendix 2: **Climate data registered at each elevational site on Mount Meru in February–November 2021 during the small mammal survey. Totals presented as mean and standard deviation (Mean ± SD), range(R) and number of days measured (N). The rainfall samples are expressed as the number of days measured and number of days with rain (in parenthesis).**

Elevation Zone	Daily Rainfall (mm)	Daily Minimum Temperature (°C)	Daily Maximum Temperature (°C)
SA			
Mean ± SD	0.1 ± 0.3	20.6 ± 5.8	20.9 ± 5.8
R	0–0.7	12.5–28.1	12.6–28.3
N	6(1)	6	6
LMF			
Mean ± SD	0	14.5 ± 1.5	15.6 ± 1.8
R	0	11.6–15.7	12.3–17.5
N	6(0)	6	6
UMF			
Mean ± SD	2.5 ± 1.4	14.7 ± 2.2	15.4 ± 2.8
R	0–4.1	13.3–18.9	13.6 ± 19.1
N	6(2)	6	6
UMF/EH			
Mean ± SD	2.2 ± 1.7	10 ± 0.34	12.5 ± 2.0
R	0–3.8	9.5–10.5	10.4–15.9
N	5(4)	5	5
EH			
Mean ± SD	3.3 ± 1.6	10.3 ± 0.2	12.8 ± 2.2
R	0–4.2	10.1–10.5	10.6–16.4
N	6(2)	6	6
AA			
Mean ± SD	1.7 ± 1.9	5.5 ± 2.4	8 ± 1.3
R	0–3.8	2.3 ± 8.3	6.9–10.3
N	5(3)	5	5