

**ECOLOGY OF RODENT SPECIES IN THE UKAGURU MOUNTAINS WITHIN
THE EASTERN ARC MOUNTAINS, TANZANIA**

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**A THESIS SUBMITTED IN FULFILMENT OF THE REQUIREMENTS FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY OF SOKOINE UNIVERSITY OF
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EXTENDED ABSTRACT

Rodents, one of the diverse groups of mammals, are important contributors to biodiversity and good ecological indicators of habitat disturbance and their assessment is an important component of the study of forest ecosystems. Forested mountains in East Africa, which are home to diverse flora and fauna with sizeable endemics, include the Eastern Arc mountains (EAM) region and collectively with its adjacent lowland coastal forests recognized as one of the top 25 biodiversity “hotspots” worldwide. As conservation of any landscape requires knowledge of the available resources in the area, it is critical to study the rodents of the EAM due to the high degree of endemism in these mountain ranges and the rapid degradation of the remaining montane forests. However, research on rodents in sub-Saharan Africa has focused on pest species, and data on non-pest species is rare, however, needed for the implementation of effective conservation measures. The Ukaguru Mountains within the EAM are of particular interests because the forests of this range have received little/no attention on rodents and are facing alarming rate of anthropogenic disturbances such as grazing, firewood collection, tree/pole cutting and clearance of forest for agriculture which may impact on the diversity, population structure and demography of rodents. This study, therefore, aimed at understanding the ecology of the rodents, population and demographic parameters of the dominant species in disturbed and undisturbed habitats of the Ukaguru Mountains.

There are two seasons in the landscape: wet and dry seasons; the wet season is October to May while the dry season is between June and September. Three methods were employed. In the first, the habitat association of the diversity and abundance of small mammals in the Ukaguru Mountains was assessed, by estimating the vegetation parameters using a Modified-Whittaker method and live-trapping of small mammals by

Capture-Mark-Recapture (CMR) technique for three consecutive nights per month in farmland, disturbed and intact forests from June 2018 to February 2020. Two 70 m x 70 m grids, 600 m apart, were set in each habitat; each grid consisted of seven parallel lines, 10 m apart, and seven trapping stations per line, also 10 m apart (a total of 49 trapping stations per grid). The two grids in the disturbed forest were in proximity (50 m) to human settlements and farmlands and were characterized by cattle grazing, illegal hunting, tree cutting and wood collection. The two grids in the intact forests were devoid of human activities and were farther than 3 km away from disturbed forests. With the second method, the data derived from the CMR trapping in the disturbed and intact forests, was used to investigate the impact of anthropogenic forest disturbance on the abundance, breeding patterns and sex ratios and two demographic parameters: survival and maturation rate of the dominant rodent species i.e. *Praomys delectorum*. With the third method, removal trapping technique was used in the survey for rodents trapped for 13 months to determine the dietary composition of rodents in the landscape. Fifty snap (kill) traps were set separately in farm/fallow lands and forest habitats and trapping of rodents was conducted for three consecutive nights per month. Micro-histological analysis of the stomach contents of rodents collected from various habitats was carried out to determine the food categories. Small mammals were identified to species levels using relevant keys and confirmed by sequencing the mitochondrial cytochrome b gene.

A total of 1196 individuals of small mammals comprising 13 species were captured from the CMR trapping in farmland, disturbed and intact forests; in the order of relative abundance, these are: *P. delectorum* (52.26%), *Mus triton* (21.07%), *Mastomys natalensis* (17.14%), *Mus minutoides* (2.93%), *Lophuromys kilonzo* (2.26%), *Crocidura hirta* (1.59%), *Beamys hindei* (1.59%), *Grammomys surdaster* (0.59%), *Graphiurus cf. raptor* (0.17%), *Lemniscomys rosalia* (0.17%), *Hylomyscus arcimontensis* (0.08%), *Pelomys*

fallax (0.08%) and *Xerus* sp. (0.08%). *Mastomys natalensis*, *Mus triton* and *Praomys delectorum* accounted for 90% of total captures. *Mus triton* and *Mastomys natalensis* were the most abundant in farmland with 46.75% and 42.77% of total captures respectively while *P. delectorum* accounted for 90% and 80% total captures in disturbed and intact forests respectively but the mean abundances in both habitats were not significantly different ($p = 0.72$). Species diversity and evenness in intact forest were much higher compared to disturbed forest. Principal component analysis (PCA) explained 87.70% of the variance with two factors. PCA 1 (67.47%) consists majorly of canopy cover, ground cover, shrubs and litter depth, with *P. delectorum*, *B. hindei* and *L. kilonzoi* loading positively. In the same component, herbs, *Mastomys natalensis* and *Mus triton* loaded negatively. Distance to human settlement contributed greatly to PCA 2 (20.23%) with *G. cf. raptor*, *L. kilonzoi* and *C. hirta* having greater than 0.5% loading. *Mastomys natalensis* and *Mus triton* associated with the herbaceous vegetation while *P. delectorum* correlated with litter depth and trees. The results suggest that vegetation and habitat disturbances are factors responsible for the observed diversity of small mammals in the Ukaguru Mountains.

Analysis on sex ratios, population structure and breeding parameters were carried out on the dominant species i.e. *P. delectorum* in the two forest types. The population density of *P. delectorum* varied temporally with peaks attained in the wet seasons in both disturbed and intact forests. Population structure showed few juveniles in most months and sub-adults accounted for the population increases in the wet seasons in all habitats, high number of adults from the late wet season to the end of the dry season in disturbed forest but a greater number of adults in the wet season in intact forest. The sex ratios showed highly significant number of males in intact forest compared to disturbed forest ($\chi^2 = 10.71$, $df = 1$, $p = 0.001$). The proportion of reproductively active individuals varied

temporally in both disturbed and intact forests while habitat disturbance showed no effect on the breeding activity of this species. Overall, these results suggest that rainfall and habitat disturbances as factors responsible for the varying sex ratios and population structure of *P. delectorum* in the landscape.

Furthermore, the effects of habitat disturbance on abundance as well as two demographic traits: survival and maturation of *P. delectorum* were investigated. Abundance was estimated using the Minimal Number of animals Alive and subjected to a generalized linear mixed model. Survival and maturation probabilities were estimated using multi-event capture-recapture models using the software E-SURGE. There was no variation in abundance or maturation between intact and disturbed forests, but habitat type did affect survival. However, this effect was sex-dependent since female survival was higher in disturbed forests while male survival remained similar across the two forest types potentially due to differences in predation pressure or food availability between the two habitats. These results highlight the need for continuous demographic monitoring of *P. delectorum* in the EAM given that the increasing human population surrounding the landscape is leading to higher deforestation rates, and expansion of the pine plantation in the forest reserve.

In the food analysis, *Mastomys natalensis*, *Lemniscomys rosalia* and *Mus triton*, seed/grain showed greater importance (> 35, > 55 and 60% respectively) whereas for *Lophuromys kilonzoi* (farm/fallow land), plant materials were more important (> 55%) than other categories. Seed/grains were more important (> 20%) in the diet of *P. delectorum*, while plant materials were more important (> 45 %) in the diet of forest-dwelling *L. kilonzoi*. Food diversity for rodents in farm/fallow land was relatively low compared to forest dwelling rodents. Niche overlap between *L. kilonzoi* and

P. delectorum was found to be relatively high. Given the interspersed nature of the forests with farmlands and their proximity, this may favour the establishment of farm generalists in the forests.

The findings of the present study are of concern in conservation of this landscape and necessitate urgent conservation actions in this EAM block to limit the effects of anthropogenic activities in the landscape. As the human population surrounding the Ukaguru Mountains and their encroaching activities increase, continuous exploitation of the forests of this landscape should be discouraged as this was shown to modify the habitats of the small mammals, reducing their diversity and evenness and affecting other demographic parameters.

DECLARATION

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

Olaoluwa John Ademola

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Date

The above declaration is confirmed by:

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(Main supervisor)

Date

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(Co-supervisor)

Date

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DEDICATION

I dedicate this work to my lovely wife and my late mother who passed away during this study.

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LIST OF ABBREVIATIONS AND SYMBOLS

%	Percent
ANOVA	Analysis of Variance
ca.	circa (=about)
CMR	Capture-Mark-Recapture
df	Degrees of freedom
DENSITY	Software for estimating population density
EAM	Eastern Arc Mountains
E-SURGE	A software application for fitting multievent models
IUCN	International Union for Conservation of Nature
No.	Number
Np	number of parameters
AICc	corrected Akaike's Information Criterion
$\Delta AICc$	Difference in AICc
GLMM	Generalized Linear Mixed Model
GOF	Goodness-of-fit
ha	Hectare
km	Kilometre
m	Metre
MNA	Minimum Number of animals Alive
M(h)	Model of Heterogeneity (Jackknife estimator)
MARK	Software for Capture-Mark-Recapture data
U-CARE	Utilities for CAPture-REcapture software
P	Probability
PAST	PAleontological STatistics

Q-GIS	Quantum Geological Information System software
SE	Standard Error
SUA	Sokoine University of Agriculture
χ^2	Chi-square

CHAPTER ONE

1.0 GENERAL INTRODUCTION

1.1 Small Mammals

Terrestrial small mammals are mammals (< 500 g) that include rodents and shrews grouped together for practical convenience of research methodology and not as a taxonomic group (Hoffmann *et al.*, 2010). Rodents are a dominant group of mammals representing 42% of all mammalian species and occur in a wide range of natural habitats, agricultural landscapes, rural and urban areas (Aplin *et al.*, 2003). They are represented in sub-Saharan Africa with 463 species adapted to heterogeneous environments and extant in all habitats (Monadjem *et al.*, 2015). In Africa, 5 – 17 % of the rodent species are pests (Monadjem *et al.*, 2015; Mulungu, 2017; Swanepoel *et al.*, 2017) impacting negatively on agriculture, stored products and are reservoirs/hosts of zoonotic diseases (Gratz, 1997; Aplin *et al.*, 2003; Meerburg *et al.*, 2009; Mulungu, 2017). However, rodents and other small mammals in general, provide important ecosystem services as they are sources of food for predators (ophidian, avian and mammalian), regulate insect populations and modify the soil (structure, organic content and mineral cycling) which affects plant growth (Hayward and Phillipson, 1979). They consume and disperse seed (Hayward and Phillipson, 1979); for instance, in forest ecosystems, rodents are effective in seed dispersal by hoarding of seeds in caches which is a coping strategy for fluctuating seed supply (Corlett and Hughes, 2015). Therefore, small mammals are important contributors to biodiversity and good ecological indicators of habitat disturbance (Linzey and Kesner, 1997; Kisingo *et al.*, 2005; Avenant and Cavallini, 2007; Avenant *et al.*, 2008); hence their assessment is an important component of the study of terrestrial ecosystems.

1.2 Eastern Arc Mountains and their Small Mammals

Forested mountains in East Africa, which are home to diverse flora and fauna with sizeable endemics (Carleton and Stanley, 2012), include the Eastern Arc mountains (EAM) region and collectively with its adjacent lowland coastal forests recognized as one of the top 25 biodiversity “hotspots” worldwide (Myers *et al.*, 2000). The EAM has 13 identifiable and separate mountain blocks of which one (Taita) is in Kenya while 12 (North Pare, South Pare, West Usambara, East Usambara, Nguu, Nguru, Uluguru, Ukaguru, Rubeho, Malundwe, Udzungwa, Mahenge) are in Tanzania (Burgess *et al.*, 1998; Burgess *et al.*, 2007; Rovero *et al.*, 2014). This mountain range, which is home to at least 136 and 75 species of vertebrates that are endemic and near-endemic respectively, is facing an alarming rate of anthropogenic disturbances (Burgess *et al.*, 1998; Rovero *et al.*, 2014). The rapidly expanding human population surrounding the mountains results in greater pressures on the natural forests and their vertebrate fauna. Major threat facing the EAM include: fire, agricultural encroachment, grazing, pole/timber cutting, firewood collection, charcoal burning, mining, hunting and collection of medicinal plants (Forestry and Beekeeping Division, 2005).

Most fauna studies in the EAM have generally focused on large vertebrates with few studies focused on small mammals (Stanley and Goodman, 2011). While an extensive survey of small mammals lasting 3 years took place in East and West Usambara, other surveys in other EAM blocks have been for a short period of time. For example, Stanley *et al.* (1998) carried out a survey of small mammals in six sites of the EAM for a period of 3 months while Lema and Magige (2018) recently surveyed the North Pare for 2 months. Small mammal studies conducted in the EAM show that *Praomys delectorum* is a dominant species in the forests of the EAM (Stanley *et al.*, 1998; Makundi *et al.*, 2003, 2006; Stanley and Goodman, 2011; Ralaizafisoloarivony *et al.*, 2014; Lema and Magige,

2018) while in the surrounding agricultural settings/fallow lands, *Mastomys natalensis* predominates (Makundi *et al.*, 2003; Ralaizafisoloarivony *et al.*, 2014; Lema and Magige, 2018). In the EAM, small mammals belonging to the following genera have been reported: *Lophuromys*, *Mus*, *Beamys*, *Dendromus*, *Otomys*, *Aethomys*, *Hylomyscus*, *Grammomys*, *Graphiurus*, *Arvicanthis*, *Crocidura*, *Myosorex* and *Sylvisorex* (Stanley *et al.*, 1998; Makundi *et al.*, 2003, 2006; Stanley and Goodman, 2011; Ralaizafisoloarivony *et al.*, 2014; Lema and Magige, 2018).

1.3 Factors determining Rodent Species Diversity and Abundance

Small mammal diversity is influenced by factors that include climate and its variability, habitat heterogeneity, history of the colonization and evolution, energy, competition, predation and disturbance (Currie, 2010). However, small mammals strongly associate with vegetation parameters (Andrews and Brien, 2000; Tews *et al.*, 2004) that serve as sources of food and cover (Ecke *et al.*, 2001). Habitat characteristics majorly accounted for the variation in small mammal abundance and diversity in southern California (Aviv and Douglas, 2020), arid Andean foothills Argentina (Novillo *et al.*, 2017), African savannas (Loggins *et al.*, 2019), tropical Australian forests (Williams *et al.*, 2002). Habitat disturbances from anthropogenic activities alter vegetation structure and composition (Wimberly and Spies, 2001; Wimberly and Ohmann, 2004; Men *et al.*, 2015) which affects small mammal abundance (Ochoa, 2000; Lambert *et al.*, 2003, 2005, 2006; Gitonga *et al.*, 2016) and species diversity and evenness (Kasangaki *et al.*, 2003; Mortelliti and Boitani, 2006; Men *et al.*, 2015; Lema and Magige, 2018).

1.4 Demographic Characteristics of Rodents and Associated Factors

Rodents show considerable fluctuations in population size at different times of the year and such dynamics are the result of underlying demographic parameters (Oli and Dobson,

1999). Environmental influences on population dynamics operate through their effects on the demographic parameters (Dobson and Oli, 2001); hence, linking population fluctuations with the underlying demographic parameters is crucial for a clearer understanding of population dynamics (Lima *et al.*, 2001a, 2001b, 2003; Benthem *et al.*, 2017). The environmental factors influencing demographic parameters include habitat quality (cover and food), predation pressure, temperature, humidity and rainfall (Batzli, 1986; Getz *et al.*, 2006; Lin and Batzli, 2001). However, in tropical rodents, rainfall is the most fundamental factor regulating demographic processes and population dynamics as primary productivity (food availability) is dependent on rains (Delany, 1972; Neal, 1981; Bronson, 1985; Bronson and Perrigo, 1987; Leirs *et al.*, 1989; Neal and Alibhai, 1991; Leirs *et al.*, 1994; Lima *et al.*, 2001b; Makundi *et al.*, 2006; Massawe *et al.*, 2007, 2012; Mason-Romo *et al.*, 2018). Due to the greater water availability and improved food quality and quantity that come with the rains, demographic parameters and ultimately population dynamics of rodents have been linked with rainfall pattern (Field, 1975; Taylor and Green, 1976; Christian, 1979; Batzli, 1986; Sicard *et al.*, 1993; Degen *et al.*, 2004; Jackson and van Aarde, 2004). Also, it is believed that a non-estrogenic chemical, 6-methoxy-2-benzoxazolinone (6-MBOA), found in sprouting vegetation (Berger *et al.*, 1977, 1981) is able to stimulate breeding in tropical rodents (Alibhai, 1986; Linn, 1991) though evidence for this is not widespread.

Anthropogenic forest disturbances may have impact on sex ratios, breeding patterns and population dynamics of rodents (Makundi *et al.*, 2006) as these man-made disturbances may modify the environmental factors that these rodents depend on. Previous studies have demonstrated that tropical rodents in disturbed habitats are exposed to lower predation pressures (Lambert *et al.*, 2003) and greater food resources (Ochoa, 2000) and interaction of both may impact positively on their population size and demographic

processes (Lambert *et al.*, 2006). For example, populations of *Praomys jacksoni* in cultivated lands showed an extended breeding season than those in forest. The extended breeding season of populations in the cultivated area was attributed to the continuous supply of food from the growing crops (Happold, 1974; Rahm, 1970). The sex ratios of rodent species trapped can vary with habitats and seasons due to the differences in activities between sexes, changing behavior patterns or differing sex mortalities (Delany, 1972; Smith and Avenant, 2004; Mlyashimbi *et al.*, 2020) which could be modified by anthropogenic disturbances in their habitats. Likewise, as the age structure of a population changes temporally depending on the breeding seasonality and survival rate (Delany, 1972; Happold and Happold, 1989), any effect of anthropogenic disturbances on the breeding seasonality and survival rate will definitely result in change in the population structure.

1.5 Dietary Composition of Rodents

In rodents, resource partitioning is partly attributed to variation in diet (Iwuala *et al.*, 1980; Pinotti *et al.*, 2011); hence, rodent diet assessments can provide insights into mechanism of coexistence even among them (Sato *et al.*, 2018). By feeding on seeds, tropical rodents are agents of seed dispersal significantly contributing to seedling recruitment in forest ecosystems (Brewer and Rejmánek, 1999). Thus, ecological studies on rodent diets is vital in forest management. However, most of the studies on diets of rodents in sub-Saharan Africa have focused on the pestiferous species that are of economic impact such as *Mastomys natalensis* (Oguge, 1995; Mulungu *et al.*, 2011a, 2011b; Mlyashimbi *et al.*, 2018) while information on diets of other species are scarce despite the role they play in ecosystems. Previously, the diet of the Natal multimammate mouse, *M. natalensis* and *Gerbilliscus vicinus* from fallow habitats in Central Tanzania has been reported (Mulungu *et al.*, 2011b). The authors showed that grain and vegetative

materials were the most consumed food categories for these rodent species in different magnitude where *M. natalensis* ate more seeds while *G. vicinus* ate more plant materials, and thereby coexisting.

1.6 Justification of the Study

As conservation of any landscape requires knowledge of the available resources in the area, it is critical to survey the habitats of the EAM due to the high degree of endemism in these mountain ranges and the rapid degradation of the remaining montane forests of Tanzania (Stanley *et al.*, 1998). Research on rodents in sub-Saharan Africa has been focused on pest species, and data on non-pest species is rare, however needed for the implementation of effective conservation measures (Swanepoel *et al.*, 2017). The Ukaguru Mountains are of particular interests because some of the forests of this range have received little attention and might support additional species of interest (Rovero *et al.*, 2014). The surveys carried out in the Ukaguru Mountains has concentrated on plants, amphibians, reptiles and birds (Evans *et al.*, 1992). At least three strictly endemic and 14 Eastern Arc endemic vertebrate species are found in the Ukaguru Mountains (Rovero *et al.*, 2014). The forests also contain plants species that are either strictly endemic or of restricted distribution (Lovett and Pócs, 1993). Extensive surveys in this less known area may discover even more new species and range records in the EAM (Rovero *et al.*, 2014). Pertinently, little or no information exists on the rodents and small mammals in general of Ukaguru Mountains as this landscape has not attracted the same degree of attention in terms of small mammal research compared to the other EAM blocks (Stanley *et al.*, 1998; Rovero *et al.*, 2014; Lema and Magige, 2018).

Also, the Ukaguru Mountains are facing alarming rate of forest clearance which impacts on diversity and structure of the fauna species including small mammals. Human threats

to the forests include grazing, firewood collection, tree/pole cutting, illegal hunting and clearance of forest for agriculture and pine plantation (Forestry and Beekeeping Division, 2005; Gwegime *et al.*, 2014). Given the dependence of many species on forest habitats, the change or removal of that habitat will result in the loss of some or all of those species from an area depending on the intensity and extent of the disturbance and the requirements of the species (Doggart and Loserian, 2007).

While several authors have investigated the small mammal abundance and diversity in other Eastern Arc mountain blocks (Stanley *et al.*, 1998; Makundi *et al.*, 2003; Stanley and Goodman, 2011; Stanley *et al.*, 2011; Ralaizafisoloarivony *et al.*, 2014; Lema and Magige, 2018), information about the habitat associations of the EAM small mammal species is very scarce. Investigating these habitat associations is of great importance given the alarming rate of anthropogenic disturbances in the EAM and will elucidate the complex responses of small mammals seen after habitat perturbations (Lambert *et al.*, 2006). In addition, considering that anthropogenic habitat disturbances may alter the spatial distribution of small mammals, structure of their population and demographic parameters (Makundi *et al.*, 2006), the Ukaguru Mountains, with the level of anthropogenic disturbances taking place, provides a good model to study the impact of these disturbances on the population structure and demographic parameters of small mammals in the Eastern Arc Mountains.

Despite the fact that rodent interactions are possible between forests and interspersing farm/fallow lands (Makundi *et al.*, 2003), studies on diet ecology of rodents dwelling in forest/forests interspersed with farms are sparse in East Africa. Most of the studies on diets of rodents in sub-Saharan Africa have focused on the pestiferous species that are of economic impact such as *M. natalensis* (Oguge, 1995; Mulungu *et al.*, 2011a, 2011b;

Mlyashimbi *et al.*, 2018) while information on diets of other species are scarce despite the role they play in ecosystems. Diet assessment can provide insights into mechanism of coexistence among rodents, impact of their foraging habits on community structure and breeding and management (Delany, 1971, 1972; Iwuala *et al.*, 1980; Litvaitis, 2000; Sato *et al.*, 2018; Taylor and Green, 1976). This necessitates the studying of the diets of the rodents of the Ukaguru Mountains as these have not been previously studied.

This study provides information on the impact of anthropogenic disturbances on the small mammal abundance, diversity and demographic traits in the Ukaguru Mountains. Also, the dietary preferences and niche overlap of rodents in the landscape is elucidated in this study. Put together, the knowledge derived from this work, will be useful to optimize the current conservation and management strategies of the small mammals and be valuable in the conservation of the forests of this landscape.

1.7 Objectives

1.7.1 Overall objective

This study aimed at understanding the community ecology of the rodent species in the different habitats of the Ukaguru Mountains.

1.7.2 Specific objectives

The specific objectives of this study were to:

- i. assess the small mammal abundance and species diversity and their habitat associations in both intact forests and disturbed habitats in the Ukaguru EAM;
- ii. investigate the impact of anthropogenic activities on the sex ratios, population dynamics and reproduction of the dominant rodent species;
- iii. determine the effects of anthropogenic forest disturbance on the population density, survival and maturation rate of the dominant rodent species;

- iv. assess the dietary composition and niche overlap of rodent species.

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CHAPTER TWO

HABITAT ASSOCIATION OF SMALL MAMMAL ABUNDANCE AND DIVERSITY IN THE CENTRAL WING OF THE EASTERN ARC MOUNTAINS, EAST AFRICA.

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**HABITAT ASSOCIATION OF SMALL MAMMAL ABUNDANCE AND
DIVERSITY IN THE CENTRAL WING OF THE EASTERN ARC MOUNTAINS,
EAST AFRICA.**

Abstract

The habitat association of the diversity and abundance of small mammals in the Ukaguru Mountains within the Eastern Arc Mountains, Tanzania, was assessed by estimating the vegetation parameters and live-trapping of small mammals for three consecutive nights per month for 21 months in farmland, disturbed and intact forests. A total of 1196 individuals of small mammals comprising 13 species were captured. *Mastomys natalensis*, *Mus triton* and *Praomys delectorum* accounted for 90% of total captures in the landscape. *Mus triton* and *Mastomys natalensis* were the most abundant in farmland with 46.75% and 42.77% of total captures respectively and associated with the herbaceous vegetation while *P. delectorum* correlated with litter depth and trees and accounted for 90% and 80% total captures in disturbed and intact forests respectively but the mean abundances in both habitats were not significantly different ($p = 0.72$). Species diversity and evenness in intact forest were much higher compared to disturbed forest. Principal component analysis (PCA) explained 87.70% of the variance with two factors. The study suggests vegetation and habitat disturbances are factors responsible for the observed diversities of small mammals in the Ukaguru Mountains.

Keywords: Rodents, *Crocidura*, habitat disturbance, vegetation structure, conservation

2.1 Introduction

Terrestrial small mammals are small sized mammals that include rodents and shrews grouped together for practical convenience of research methodology and not as a taxonomic group (Hoffmann *et al.*, 2010). Rodents are a dominant group of mammals representing 42% of all mammalian species and occur in a wide range of natural habitats, agricultural landscapes, rural and urban areas. They impact negatively on agriculture by causing damage and losses of crops in field and storage resulting in reduction of the quantity and value of crops. Globally, rodents are reservoirs of zoonotic diseases. However, not all rodent species are pests; for example in Africa, only 5 – 17 % of rodent species are pests (Monadjem *et al.*, 2015; Mulungu, 2017; Swanepoel *et al.*, 2017). Rodents and small mammals in general provide food for avian, ophidian and mammalian predators while they also consume of seeds and other plant materials (Hayward and Phillipson, 1979; Kisingo *et al.*, 2005). Therefore, small mammals are important contributors to biodiversity and good ecological indicators of habitat disturbance (Linzey and Kesner, 1997; Kisingo *et al.*, 2005; Avenant and Cavallini, 2007; Avenant *et al.*, 2008).

Small mammal diversity is influenced by factors that include climate and its variability, habitat heterogeneity, history of the colonization and evolution, energy, competition, predation, and disturbance (Currie, 2010). However, small mammals strongly associate with vegetation parameters (Andrews and Brien, 2000; Tews *et al.*, 2004) that serve as sources of food and cover (Ecke *et al.*, 2001). Habitat characteristics majorly accounted for the variation in small mammal abundance and diversity in southern California (Aviv and Douglas, 2020), arid Andean foothills Argentina (Novillo *et al.*, 2017), African savannas (Loggins *et al.*, 2019), tropical Australian forests (Williams *et al.*, 2002). Forested mountains in East Africa, which are home to diverse flora and fauna with

sizeable endemics (Carleton and Stanley, 2012), include the Eastern Arc mountains (EAM) region and collectively with its adjacent lowland coastal forests recognized as one of the top 25 biodiversity “hotspots” worldwide (Myers *et al.*, 2000). The EAM has 13 identifiable and separate mountain blocks of which one (Taita) is in Kenya while twelve (North Pare, South Pare, West Usambara, East Usambara, Nguu, Nguru, Uluguru, Ukaguru, Rubeho, Malundwe, Udzungwa, Mahenge) are in Tanzania (Burgess *et al.*, 1998; Burgess *et al.*, 2007; Rovero *et al.*, 2014). Ninety-six and 71 species of vertebrates are endemic and near-endemic respectively to the EAM (Burgess *et al.*, 2007). Recently, this has been updated to 136 endemic and 75 regionally endemic (Rovero *et al.*, 2014). In particular, the Ukaguru Mountains (central wing) have not attracted the same degree of attention as other EAM blocks (Lema and Magige, 2018; Rovero *et al.*, 2014; Stanley *et al.*, 1998). The Ukaguru Mountains are of particular interests because some of the forests of this range are biologically unexplored and might support additional species of interest (Rovero *et al.*, 2014). At least three strictly endemic and 14 Eastern Arc endemic vertebrate species are found in the Ukaguru Mountains (Rovero *et al.*, 2014). The forests also contain plants species that are either strictly endemic or of restricted distribution (Lovett and Pócs, 1993). Extensive surveys in this less known area may discover even more new species and range records in the EAM (Rovero *et al.*, 2014). Also, the Ukaguru Mountains are facing alarming rate of forest clearance which impacts on diversity and structure of the fauna species including small mammals. Human threats to the forests include grazing, firewood collection and tree/pole cutting (Gwegime *et al.*, 2014). Given the dependence of many species on forest habitats, the change or removal of that habitat will result in the loss of some or all of those species from an area depending on the intensity and extent of the disturbance and the requirements of the species (Doggart and Loserian, 2007). Habitat disturbances from anthropogenic activities alter vegetation structure and composition (Men *et al.*, 2015; Wimberly and Ohmann, 2004; Wimberly

and Spies, 2001) which affects small mammal abundance (Ochoa 2000; Lambert *et al.*, 2003, 2005, 2006; Gitonga *et al.*, 2016) and species diversity and evenness (Kasangaki *et al.*, 2003; Mortelliti and Boitani, 2006; Men *et al.*, 2015; Lema and Magige 2018). Although several authors have investigated the small mammal abundance and diversity in other Eastern Arc mountain blocks (Stanley *et al.*, 1998; Makundi *et al.*, 2003; Stanley and Goodman, 2011; Stanley *et al.*, 2011; Ralaizafisoloarivony *et al.*, 2014; Lema and Magige, 2018), information about the habitat associations of the EAM small mammal species is very scarce. Investigating these habitat associations is of great importance given the alarming rate of anthropogenic disturbances in the EAM and will elucidate the complex responses of small mammals seen after habitat perturbations (Lambert *et al.*, 2006). Also, in comparison to other EAM blocks, little or no information exists on the small mammals in the Ukaguru Mountains. Therefore, this study is aimed at providing information on the small mammal abundance and species diversity and their habitat associations in both intact forests and disturbed habitats in the Ukaguru Mountains.

2.2 Materials and Methods

2.2.1 Study area

This study was carried out in the Ukaguru Mountains within the EAM, Tanzania. The Ukaguru Mountains are located in Gairo District, Morogoro, Tanzania (36° 57'00'' – 38° 00' 00'' East and 06° 25' 00'' – 06° 57' 00'' South; Fig. 2.1). They comprise six catchment forest reserves which are Ikwamba (889 ha), Mamboto (149 ha), Mamboya (204 ha), Mamiwa Kisara-North (8 203 ha), Mamiwa-Kisara South (6 266.4 ha), and Uponera (375 ha). Mamiwa-Kisara forest is the most important forest in the Ukaguru Mountains in terms of its biodiversity values providing habitat for three Ukaguru-endemic vertebrate species and one Ukaguru-endemic plant species (Gwegime *et al.*, 2014). There is also a large softwood plantation in the mountains that occupies an

additional 3 600 ha. The elevation of this landscape extends up to 2 250 m above sea level. The estimated annual rainfall is 1 400 mm (Gwegime *et al.*, 2014). The dry season is between June and September, with maximum temperatures of 21°C recorded in January and minimum temperatures of 17°C in July (Gwegime *et al.*, 2014).

Generally, the vegetation type is montane and sub-montane forest. The montane forest is mainly characterised by the following tree species: *Polyscias fulva*, *Schefflera lukwangulensis*, *Garcinia volkensii*, *Ocotea usambarensis* and *Cussonia spicata*. Others are *Dombeya burgessiae*, *Clerodendrum* sp., *Macaranga capensis* and *Albizia gummifera*. The sub-montane forest is characterized by *Myrianthus holstii*, *Albizia gummifera*, *Allanblackia stuhlmannii* and *Bersama abyssinica*. (Gwegime *et al.*, 2014). The human population surrounding the forest is at least 75 720 people and land outside the forest reserves is generally farmland (EAMCEF, 2021). Crops commonly cultivated include: maize (*Zea mays*), beans (*Phaseolus lunatus*), Irish potatoes (*Solanum tuberosum*) and common pea (*Pisum sativum*).

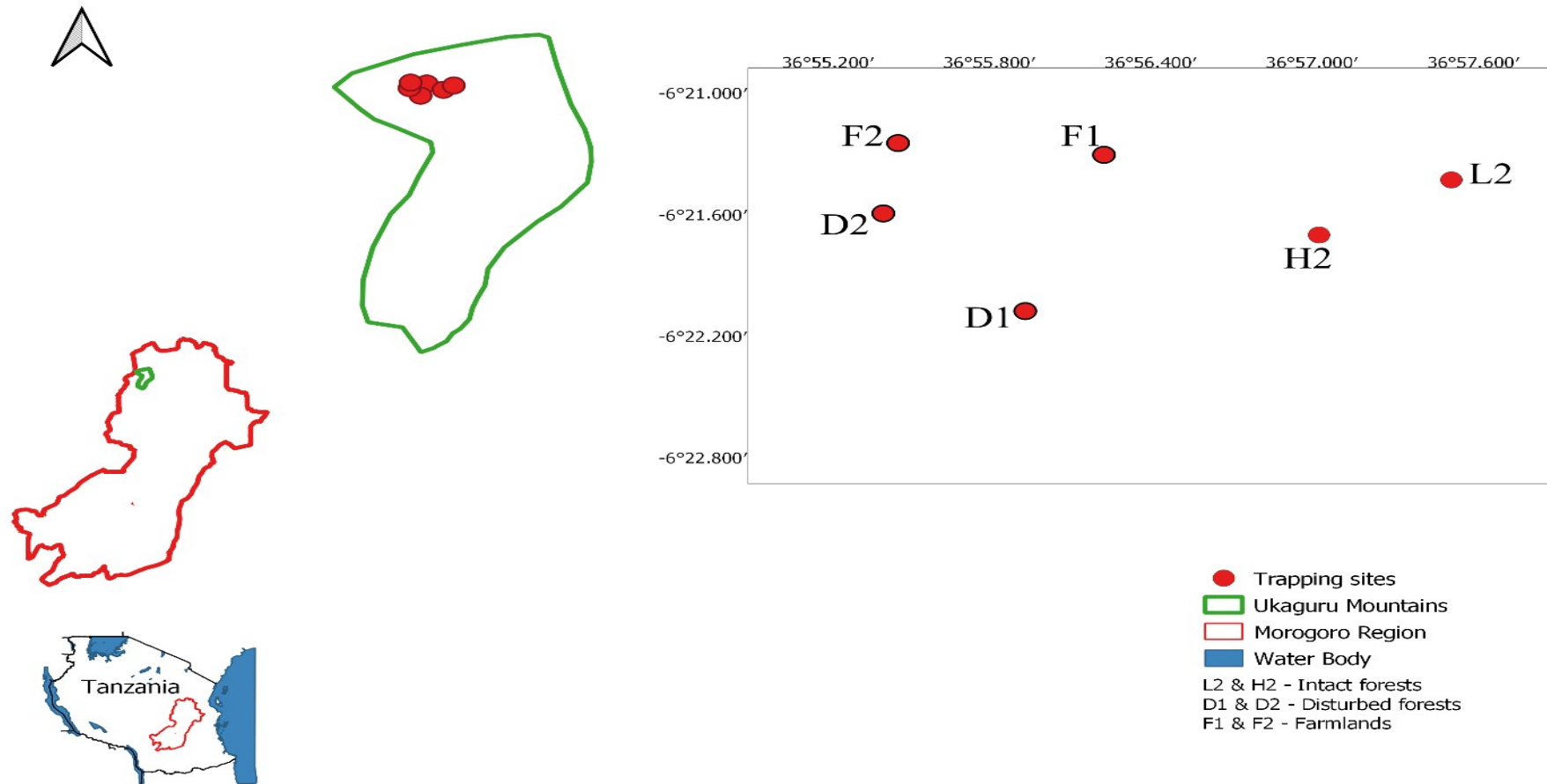


Figure 2.1: Study area and the coordinates of the trapping sites in the Ukaguru Mountains, Tanzania (map is not to scale).

2.2.2 Habitat characterisation

A nested quadrat approach which is a Modified-Whittaker method was employed (Stohlgren *et al.*, 1995). Six plots, each 50 m x 20 m (1 000 m² or 0.1 hectares) demarcated within the 70m x 70m permanent grids for small mammal studies, were used to record the trees. Each tree encountered within the plot was identified to species level, its diameter at breast height (DBH) measured and its height estimated. For shrubs, six nested plots, each of size 5.0 m x 2.0 m one in each of the 50 m x 20 m main plots were used. For grasses and herbs 24 nested plots each of size 1.0 m x 1.0 m and four of them were established within each of the 50 m x 20 m main plots. All grasses, herbs and shrubs were identified. In addition, their percentage cover within the plot was estimated using a scale of 0 – 100% cover.

The percentage cover was used as an indirect measure of the performance of the species found within the plot. In this case, a single species covering the entire plot was given a score of 100%. The litter depth (cm) was measured in each grid using a standard measuring ruler. According to Avsar and Ayyildiz (2010), canopy cover was determined with the per cent of a forest area occupied by the vertical projections of tree crowns.

2.2.3 Trapping

Capture-Mark-Recapture (CMR) trapping technique was used to investigate small mammal composition and abundance from June 2018 to February 2020. Six 70 x 70m grids were set, two in intact sites (H2 and L2, 600 m apart), two in disturbed sites (D1 and D2, 600 m apart) and two in farmlands (F1 and F2, 600 m apart). Disturbed forest sites were in proximity (50 m) to human settlements and farmlands and characterized by cattle grazing, illegal hunting, tree cutting and wood collection while intact forests were devoid of human activities and were greater than 3 km from disturbed forests (Table 2.1).

The farmlands were under the cultivation of mainly maize. Each grid consisted of seven parallel lines 10 m apart and seven trapping stations per line, also 10 m apart (a total of 49 trapping stations per grid). One Sherman LFA live trap (H.B Sherman Traps Inc., Tallahassee, FL) was placed at each trapping station. Trapping of rodents was conducted for three consecutive nights every month. Traps were baited with peanut butter mixed with maize bran and inspected in the morning. Toe clipping (which does not affect the movement or survival of the animal) using number codes generated from CMR software *MARK* was employed in individual identification (Borremans *et al.*, 2015). Captured animals were identified to species levels using relevant keys (Happold, 2013; Monadjem *et al.*, 2015) and species confirmation was done by sequencing the mitochondrial cytochrome b gene (see Appendix 2.1).

2.2.4 Data analysis

Species richness, abundance, diversity, evenness and habitat associations were estimated from the data of the CMR grids. Species richness was by direct enumeration for each of the habitats. Abundance was presented as total number caught and the relative percentage of each species relative to other species within each habitat. The relative percentage was calculated by dividing the number of captured individuals of each species by the total number of captured individuals of all species of that habitat and multiplied by 100. It was decided to check if forest disturbance had any effect on the most abundant (*Praomys delectorum*) in the landscape. To achieve this, the minimum number alive (MNA) for *Praomys delectorum* was calculated and its comparisons between disturbed and intact forests was carried out using one-way analysis of variance (ANOVA) – as very few animals were captured in L2, this was dropped in the analysis (see Appendix 2.2).

The Shannon-Wiener index of diversity (H') (Shannon and Weaver, 1949) was used to calculate the diversity of species. It is a heterogeneity measure that considers the degree of evenness in species abundances (Magurran, 2004).

$H' = - \sum p_i \ln p_i$ (P_i is the proportion of individuals found in the i th species). Diversity indices between habitats were compared by t-test using the *PAleontological STatistics* software (PAST) (Hammer *et al.*, 2001). Species evenness (E) was estimated:

$E = H'/H_{\max}$ ($H_{\max} = \ln(S)$, S is the number of species) (Pielou, 1975).

Similarity among trapping grids was compared using the Bray-Curtis similarity index (Bray and Curtis, 1957) and a similarity dendrogram for the six grids was constructed. Species association with habitat features (distance to human settlements (m), litter depth (cm), canopy cover (%), ground cover (%), herbs, shrubs and trees) was plotted using principal component analysis (PCA) using the correlation matrix and the Varimax rotation method; components were significant for eigenvalues ≥ 1 and coefficients of factor loadings ≥ 0.25 were considered significant (*Hylomyscus arcimontensis*, *Lemniscomys rosalia*, *Pelomys fallax* and *Xerus* sp were captured only in one grid and not used in the PCA).

2.2.5 Ethical considerations

This research was approved by the Sokoine University of Agriculture, Tanzania (reference: SUA/DPRTC/PFC/D/2017/0010/11) and Tanzania Forest Service Agency (TFS). Animal handling followed the guidelines of the American Society of Mammalogists (ASM) for the use of wild mammals in research and education (Sikes and Animal Care and Use Committee of the American Society of Mammalogists 2016).

2.3 Results

2.3.1 Species abundance, diversity and evenness

A total of 1196 individuals of small mammals comprising 13 species were captured from June 2018 to February 2020 (Table 2.2). Of these, *Mastomys natalensis*, *Mus triton* and *Praomys delectorum* accounted for ca. 90% of total captures in the landscape. By habitat, *M. triton* and *M. natalensis* were the most abundant in farmland with 223 (46.75%) and 204 (42.77%) individuals respectively (Table 2.2). *Praomys delectorum* accounted for 90% and 80% total captures (Table 2.2) in disturbed and intact forests respectively, though mean abundance was not significantly different ($F_{2,58} = 0.34$, $P = 0.72$). Both farmlands and disturbed forest recorded 8 species separately while species richness in intact forests was 7 (Table 2.2). *Crocidura hirta* was recorded in all habitats; *M. natalensis* and *M. triton* in disturbed forests and farmlands. *Graphiurus cf. raptor* was recorded in intact forests but not in disturbed forests. *Grammomys surdaster* was captured only in disturbed forest. Shannon diversity index was lowest in disturbed forest (Fig. 2.2) and both intact forest and farmlands showed significantly higher species diversity than disturbed forest ($p < 0.05$).

Also, the diversity index was significantly different between intact forest and farmland. Individuals of the species in disturbed forests were less equitably distributed compared to those in intact forest and farmland (Fig. 2.2).

2.3.2 Habitat association

In the disturbed forests, the vegetation was associated with a higher number of herbs and less canopy cover (Table 2.1). Combining habitat features and small mammal species and abundance, two clusters were generated using the Bray-Curtis similarity index (one for the farm and one for both disturbed and intact forests with both branching off) with

Pearson cophenetic correlation of 0.97 (Fig. 2.3). The two grids in each habitat type (intact forest, disturbed forest and farmland) had mutual Bray-Curtis similarity of not less than 70% (Fig. 2.3).

Principal component analysis explained 87.70% of the variance with two factors (Table 2.3). PCA 1 (67.47%) consists majorly of canopy cover, ground cover, shrubs and litter depth, with *P. delectorum*, *Beamys hindei* and *Lophuromys kilonzo*i loading positively. In the same component, herbs, *Mastomys natalensis*, *Mus triton*, *Mus minutoides* and *G. surdaster* loaded negatively. Distance to human settlement contributed greatly to PCA 2 (20.23%) with *G. cf. raptor*, *L. kilonzo*i and *C. hirta* having greater than 0.5% loading. We show graphically in a plot the association between the species and the vegetation variables with the small mammal species correlating with certain habitat features (Fig. 2.4). *Mastomys natalensis*, *Mus triton*, *Mus minutoides* and *G. surdaster* associated with the herbaceous vegetation while litter depth and trees associated with *P. delectorum* (Fig. 2.4; see Appendix 2.3). *Beamys hindei* associated with canopy cover and shrubs (Fig. 2.4; Appendix 2.3). *Graphiurus cf. raptor* and *L. kilonzo*i correlated with greater distance from human settlement in addition to other forest features (Fig. 2.4; Appendix 2.3).

Table 2.1: Vegetation characteristics of the trapping grids in the Ukaguru Mountains, Tanzania

Characteristics	F1	F2	Grid D1	D2	L2	H2
General vegetation type	Farm land with maize, banana, pumpkin, Irish potatoes	Farm land with maize, banana, pumpkin, Irish potatoes, yams, peas and beans	Forest disturbed by grazing, hunting, tree cutting	Forest disturbed by grazing, hunting, tree cutting	Forest relatively undisturbed	Forest relatively undisturbed
Distance to human settlements (m)	30	70	50	50	800	800
Depth of litter (cm)	N/A	N/A	10	20	5	10
Canopy cover (%)	N/A	N/A	65	55	85	85
Ground cover (%)	30	30	50	50	50	50
Herbs	22	26	10	11	10	7
Shrubs	1	0	7	7	7	8
Trees	0	1	7	15	8	9
Tree DBH Range (cm)	N/A	N/A	10 – 40	15 - 35	15 - 40	15 - 50
Tree DBH Mean (cm)	N/A	N/A	30	30	25	20
Tree Stem Density (Nha ⁻¹)	N/A	N/A	75	70	75	75
Tree Dominant Height (m)	N/A	N/A	30	25	30	30

F1 and F2 – Farmlands; D1 and D2 – Disturbed forests; L2 and H2 – Intact forests; *DBH – Diameter at breast height; Nha⁻¹ – number per hectare

Table 2.2: Small mammal abundance in the Ukaguru Mountains, Tanzania

Species	Number and percentage of individual animals captured			Total
	Intact forest	Disturbed forest	Farmland	
<i>Beamys hindei</i> (Thomas, 1909)	13 (4.83)	6 (1.33)	0 (0.00)	19 (1.59)
<i>Crocidura hirta</i> (Peters, 1852)	12 (4.46)	2 (0.44)	5 (1.05)	19 (1.59)
<i>Grammomys surdaster</i> (Thomas and Wroughton, 1908)	0 (0.00)	1 (0.22)	6 (1.26)	7 (0.59)
<i>Graphiurus cf. raptor</i>	2 (0.74)	0 (0.00)	0 (0.00)	2 (0.17)
<i>Hylomyscus arcimontensis</i> (Carleton and Stanley, 2005)	1 (0.37)	0 (0.00)	0 (0.00)	1 (0.08)
<i>Lemniscomys rosalia</i> (Thomas, 1904)	0 (0.00)	0 (0.00)	2 (0.42)	2 (0.17)
<i>Lophuromys kilonzoi</i> (Verheyen <i>et al.</i> , 2007)	25 (9.29)	2 (0.44)	0 (0.00)	27 (2.26)
<i>Mastomys natalensis</i> (Smith, 1834)	0 (0.00)	1 (0.22)	204 (42.77)	205 (17.14)
<i>Mus minutoides</i> (Smith, 1834)	0 (0.00)	0 (0.00)	35 (7.34)	35 (2.93)
<i>Mus triton</i> (Thomas, 1909)	1 (0.37)	28 (6.22)	223 (46.75)	252 (21.07)
<i>Pelomys fallax</i> (Peters, 1852)	0 (0.00)	0 (0.00)	1 (0.21)	1 (0.08)
<i>Praomys delectorum</i> (Thomas, 1910)	215 (79.93)	409 (90.89)	1 (0.21)	625 (52.26)
<i>Xerus</i> sp.	0 (0.00)	1 (0.22)	0 (0.00)	1 (0.08)
Total	269	450	477	1196

Values in brackets – percentage contribution of each of the species within habitat

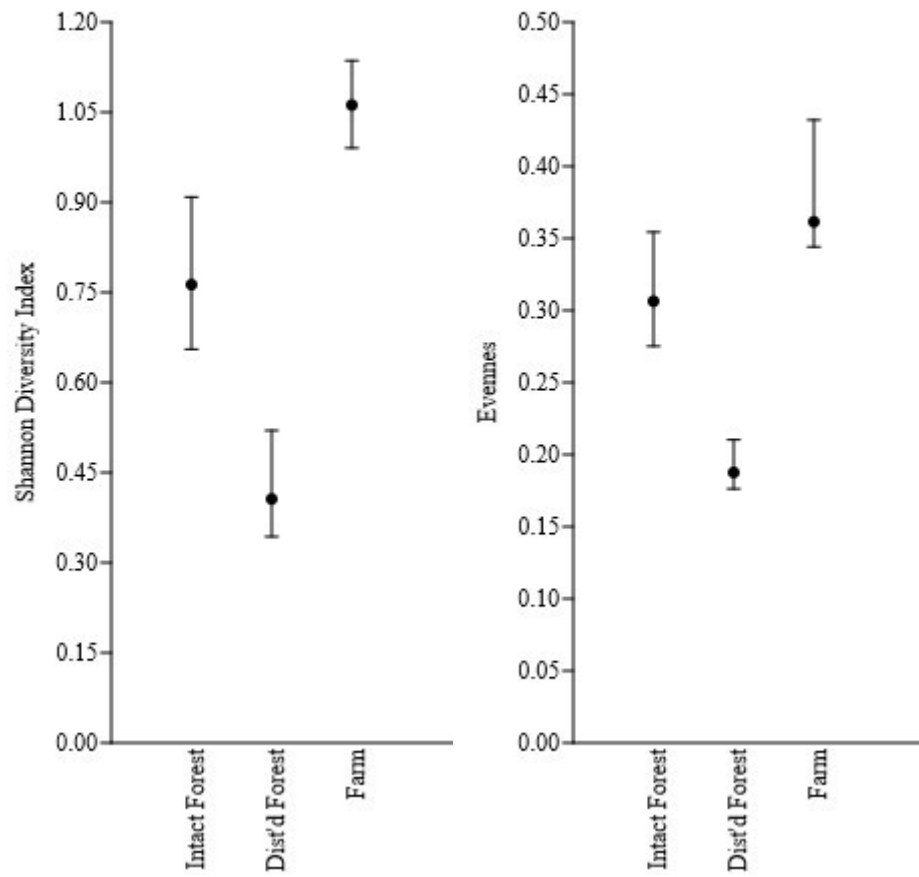


Figure 2.2: Shannon diversity index and evenness for the small mammal species in various habitats in the Ukaguru Mountains, Tanzania

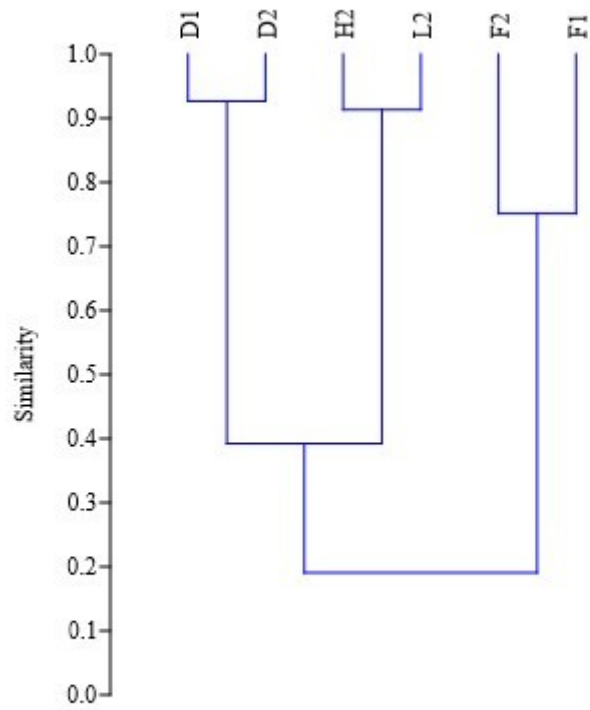


Figure 2.3: Bray-Curtis similarity indices of the different habitats in Ukaguru Mountains, Tanzania (D1 & D2 – Disturbed forest; L2 & H2 – Intact forest; F1 & F2 – Farmland)

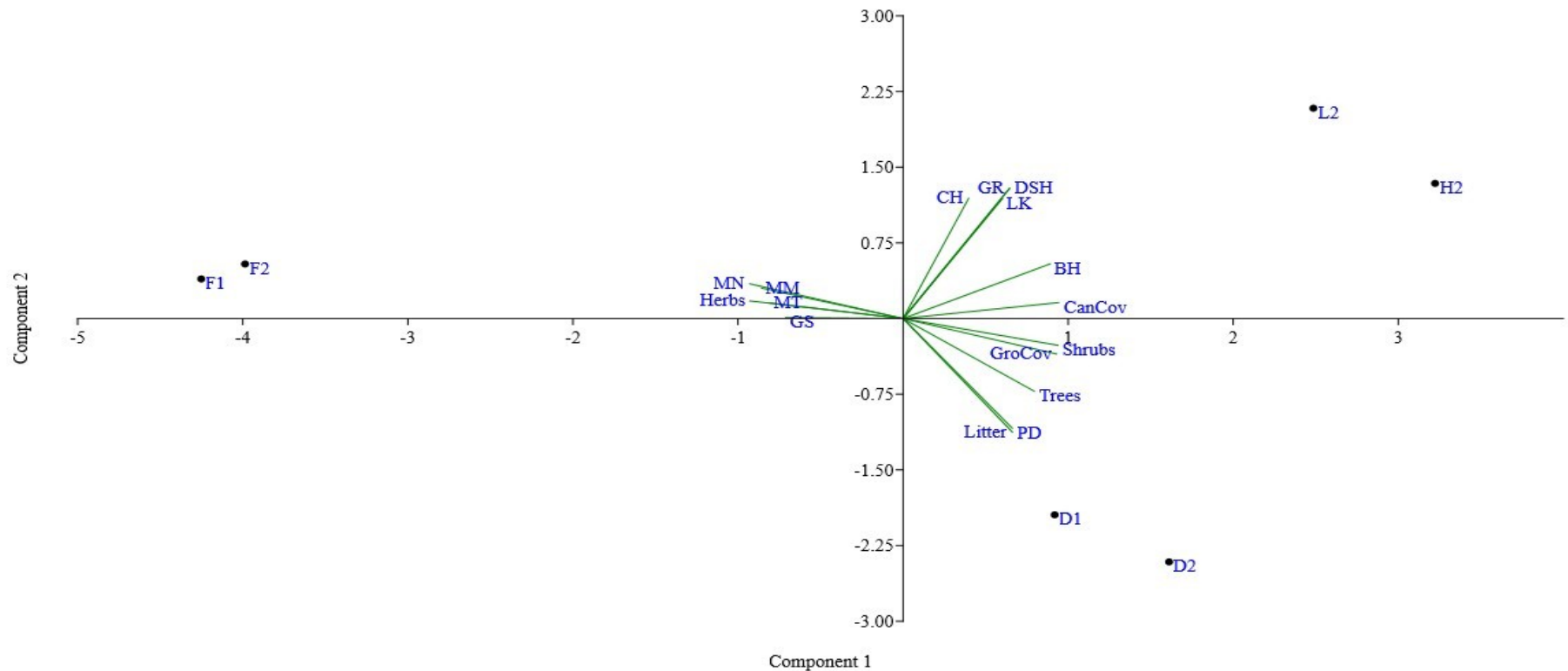


Figure 2.4: Association of small mammal species with the habitat types and vegetation parameters on the first two axes of a principal component analysis. Components 1 and 2 account for 87 % of the variance (L2 & H2 – intact forests; D1 & D2 – disturbed forests; F1 & F2 – Farmlands; Litter – Litter depth; GroCov – ground cover; CanCov – canopy cover; DSH – Distance to human settlement; PD – *Praomys delectorum*; BH – *Beamys hindei*; LK – *Lophuromys kilonzo*; GR – *Graphiurus cf. raptor*; CH – *Crocidura hirta*; MN – *Mastomys natalensis*; MT – *Mus triton*; MM – *Mus minutoides*; GS – *Grammomys surdaster*).

Table 2.3: Rotated component loadings from the principal component analysis of vegetation parameters and small mammal species

Variable	Correlations	
	PC 1	PC 2
Distance to settlements	0.20	0.98
Litter depth	0.92	-0.19
Canopy cover	0.80	0.59
Ground cover	0.94	0.33
Herbs	-0.88	-0.42
Shrubs	0.92	0.38
Trees	0.92	0.08
<i>Beamys hindei</i>	0.64	0.75
<i>Crocidura hirta</i>	-0.00	0.80
<i>Grammomys surdaster</i>	-0.64	-0.38
<i>Graphiurus cf. raptor</i>	0.20	0.98
<i>Lophuromys kilonzoi</i>	0.19	0.91
<i>Mastomys natalensis</i>	-0.93	-0.33
<i>Mus minutoides</i>	-0.86	-0.32
<i>Mus triton</i>	-0.77	-0.36
<i>Praomys delectorum</i>	0.91	-0.18

Varimax rotation method was used. Coefficients of factor loadings ≥ 0.5 and most abundant species are in bold

2.4 Discussion

In the current study the distribution of small mammals varied with habitats with *P. delectorum* dominating in both disturbed and intact forests while *Mastomys natalensis* and *Mus triton* predominating in agricultural settings. Previous surveys indicated *P. delectorum* as one of the dominant species in other EAM blocks (Stanley *et al.*, 1998; Makundi *et al.*, 2003, 2006). There was no significant differences in the mean abundance of *P. delectorum* between disturbed and intact forests which is similar to the findings of Mortelliti and Boitani (2006) who observed no significant differences in captures of *Praomys jacksoni* in disturbed and undisturbed forests in Kenya. This is contrary to the reports that posit that members of the genus *Praomys* are more abundant in disturbed habitats than unperturbed habitats (Gitonga *et al.*, 2015, 2016; Monadjem *et al.*, 2015). A likely explanation for this deviation observed in our study could be the shorter duration wherein the populations of *P. delectorum* were observed in those studies which might have only revealed opportunistic density increases/overflow into disturbed habitats during peaks in breeding, or patchiness of the habitats building up greater densities in disturbed habitats as a result of migration from undisturbed habitats (Van Horne, 1983).

The present investigation revealed differences in species richness between disturbed and intact forests, being higher in the former. Similarly, rodent species richness was reported to be greater in disturbed forests than in undisturbed forests in Kibale forest, Uganda (Isabirye-Basuta and Kasenene, 1987). Although, forest disturbance results in a richer rodent fauna, it does not necessarily eliminate any of the typical species (Delany, 1971; Isabirye-Basuta and Kasenene, 1987). Greater species richness in disturbed forest can be attributed to the proximity to the road, human settlements and cultivated lands (Mortelliti and Boitani, 2006). Such closeness favours the entrance and subsequent establishment of non-forest species, thus increasing rodent species richness (Mortelliti and Boitani, 2006).

Species diversity in intact forest and farmland in the current study was significantly different from disturbed forests which could be attributed to changes in vegetation and human disturbance (Men *et al.*, 2015). Also, intact forest showed greater species evenness than those from disturbed habitats. This is in consonance with the findings of Mortelliti and Boitani (2006) who reported lower evenness in disturbed forest which could have been due to the less variability of microhabitats in this habitat type. However, herbaceous vegetation is greater in disturbed forest compared to intact forest and may provide substantially more food for small mammals in the former compared to unperturbed forests (Greenberg *et al.*, 2011). A higher species richness in disturbed forests compared to intact forest is as a result of the exploitation of these habitats by non-forest rodents such as *Mastomys natalensis*, *G. surdaster* and *Mus triton*; though this is often at the peril of forest-adapted species (Fitzgibbon *et al.*, 1995; Mulungu *et al.*, 2008). The high species richness and diversity observed in farmland could be attributed to abundant resources available in this habitat. Agricultural settings provide highly variable microhabitats, abundant food and shelter which support the coexistence of diverse small mammal species and their prolific breeding and survival (Caro, 2001; Kasangaki *et al.*, 2003; Mulungu *et al.*, 2014).

The association of small mammal abundance and species diversity with vegetation structure has been widely studied (Rosenzweig, 1973; Price, 1978; Williams *et al.*, 2002; Tews *et al.*, 2004; Fricke *et al.*, 2009; Thompson and Gese, 2012; Ralaizafisolariovony *et al.*, 2014; Loggins *et al.*, 2019; Aviv and Douglas, 2020). Our results showed some dissimilarity in both small mammal community and vegetation parameters between the habitats as revealed by the Bray-Curtis index. Similarly, Mulungu *et al.* (2008) while investigating variation of diversity of small mammals on Mount Kilimanjaro, Tanzania reported greater dissimilarity between different vegetation types with areas with closely

related vegetation showing no marked variation in species composition. Availability of food and shelter might have influenced the distribution of small mammals across the different habitats (Greenberg *et al.*, 2011; Ostfeld *et al.*, 1985; Taylor and Green, 1976).

The small mammal-habitat association analysis revealed that though *P. delectorum* clustered with trees and associated variables, this species was strongly associated with litter depth which is in agreement with previous findings that reported that this species forages on the ground in leaf litter (Happold, 2013) and build their nests from vegetable materials (Monadjem *et al.*, 2015). *Beamys hindei*, a forest specialist, associated with canopy cover and shrubs which is in agreement with Fitzgibbon *et al.* (1995) that reported the abundant occurrence of *B. hindei* in habitats with dense shrub layer and closely spaced canopy trees in Arabuko-Sokoke Forest, Kenya. In our study, the percentage species composition of *B. hindei* was greater in intact forest compared to disturbed forests. Sabuni *et al.* (2015) reported the occurrence of *B. hindei* in unperturbed coastal forests in Saadani National Park, Tanzania but failed to record this species in adjacent forests whose vegetation structure had been altered due to anthropogenic activities. Also, Stanley and Goodman (2011) reported the occurrence of *B. hindei* in undisturbed and only slightly disturbed forests in East Usambara, Tanzania. *Lophuromys* spp are known to occur in both disturbed and undisturbed habitats (Monadjem *et al.*, 2015), in agreement with the findings of this study where *L. kilonzo*i was trapped in intact and disturbed forests. Makundi *et al.* (2015) reported relatively abundant captures of *Lophuromys* spp in moist closed canopy forests in northern Tanzania. *Lophuromys kilonzo*i was previously described mostly from forest or fallow land in Usambara Mountains and Uluguru mountains, Tanzania (Monadjem *et al.*, 2015; Verheyen *et al.*, 2007). Our study shows that *Mastomys natalensis*, *Mus triton* and *Mus minutoides* associate with herbaceous vegetation. *Mastomys natalensis* has a wide distribution and tolerate diverse habitats

including disturbed areas such as agricultural settings as it have been previously reported in high abundance in these areas (Happold, 2013; Lema and Magige, 2018; Mayamba *et al.*, 2019; Monadjem *et al.*, 2015; Mulungu *et al.*, 2014). *Mastomys natalensis* can easily colonize disturbed areas such as crop fields and disturbed forests owing to the abundant resources that these areas provide. *Mus triton* was reported in cultivated fields in eastern Democratic Republic of Congo (Kaleme *et al.*, 2007) and grasslands on the Zomba Plateau, Malawi (Happold and Happold, 1989). While Happold and Happold (1989) failed to trap *M. triton* in forest habitats on the Zomba Plateau, Malawi, in the Bale mountains, Ethiopia they are restricted to the forests (Happold, 2013; Yalden, 1988). A sizeable number of *M. triton* were trapped in disturbed forests in this study in agreement with Mulungu *et al.* (2008) who reported the occurrence of *M. triton* in disturbed forest in Mount Kilimanjaro, Tanzania. The association of *M. minutoides* with herbaceous vegetation in this study is agreement with the report of Monadjem *et al.* (2015) who stated that *M. minutoides* has a widespread distribution in Africa and prefers grasslands habitats.

We also recorded other species in relatively low numbers: *P. fallax*, *L. rosalia* and *G. surdaster* were captured in farmland though the last was also captured in disturbed forest. The occurrence of *G. cf. raptor* and *H. arcimontensis* in only intact forest in this study might have been favoured by the greater canopy cover in this habitat compared to disturbed areas as they prefers areas of high canopy cover and connectivity to avoid predators (Lamani, 2014). *Graphiurus cf. raptor* was reported only in undisturbed forests in a Kenyan tropical forest (Mortelliti and Boitani, 2006) and protected forests in North Pare Mountains (Lema and Magige, 2018). As our sampling methodology was not targeted at arboreal rodents, this might account for the relatively low numbers of *G. cf. raptor*, *H. arcimontensis* and *Xerus* sp and failure to trap them in disturbed forest as

arboreal rodents are not easy to trap on ground (Madikiza *et al.*, 2016). *Crocidura hirta* was recorded in all habitats; similarly Kaleme *et al.* (2007) reported some *Crocidura* species in both undisturbed and disturbed habitats in western part of the Albertine Rift, eastern Democratic Republic of Congo.

In conclusion, we showed from our study the declining small mammal forest specialists (*B. hindei* and *L. kilonzo*) in disturbed forests and subsequent establishment of non-forest rodent species (*M. natalensis* and *M. triton*) in these habitats. Also, habitat disturbance led to modification of diversity and evenness of small mammal species in the Ukaguru Mountains with greater diversity and evenness observed in undisturbed forests compared to disturbed forest. These findings are of concern in conservation of this landscape and necessitates urgent conservation actions in this EAM block to limit the effects of anthropogenic activities in the landscape.

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Authors' contributions: OJA designed the study. OJA collected the data. OJA, PH and FBSM carried out vegetation characterization. OJA conducted statistical analysis. LSM, AWM and RHM supervised the work. All authors contributed to writing and have given final approval for publication.

Conflict of interest statement: The authors declare that they have no conflict of interest.

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Appendices

Appendix 2.1: Mitochondrial cytochrome b (cytb) gene sequences of the sampled small mammal species

>TZJA034-CVU967_19189674_C10.ab1 *Graphiurus cf. raptor*

ATCCGCAAATCCCACCCACTAATAAAAAATCCTTAATCACTCCTTTATTGATCTTCCAGCCCCAT
CCAACATTTTCAGCCTGATGAACTTCGGGTCCCTACTAGGTGCTTGCCTAGGTATTCAAATCCT
TACAGGACTATTCTAGCTATACACTACACAGCAGATACAGCTACAGCATTTTCATCTGTCACA
CACATCTGCCGAGACGTCAACTACGGCT-----

>TZJA001-CVU967_19189674_F8.ab1 *Hylomyscus arcimontensis*

TCCGAAAAACACACCCATTATTTAAAATTATTAATAACTCCTTCATTGATCTTCCTGCTCCATC
AAACATCTCATCATGATGAAATTTTGGCTCACTCTTAGGAATCTGCCTAATAATTCAAATCATT
ACAGGATTATTCTTAGCAATACACTATACATCAGATACAATAACAGCATTTTCATCAGTCACA
CATATCTGCCGAGACGTTAACTATGGCTGGCTAATCCGATATATACACGCAAACGGAGCATCA
ATATTTTTTTATTTGCCTATTTCTCCACGTAGGACGAGGTATATACTATGGATCCTACACTTTTTAT
AGAAACATGAAATATCGGAGTAGTCCTTCTCCTTGCAGTAATAGCTACAGCATTTATAGGCTA
CGTTCTTCCATGAGGTCAAATATCATTCTGAGGAGCAACAGTAATTACCAACCTACTTTCAGCA
ATCCCATACATTGGGACTACCTTAGTAGAATGAATCTGAGGTGGATTCTCAGTTGATAAATCC
ACCCTAACACGCTTTTTTCGCATTTTCATTTTATTCTCCCATTCATCATTACAGCCCTAGTAATTGT
TCACCTTCTATTCTTACACGAAACAGGCTCTAATAACCCAACCGGCCTAAACTCCGACTCAGA
CAAGATCCCATTCCACCCTTACTACACAATTAAAGACATCTTGGGAGTAATCTTAATAATTTTA
TTCCTAATAACCTTAGTACTGTTCTTCCCCGACCTCCTCAGTGACCCTGACAATTACACACCAG
CTAACCCACTAAACACCCCACCCCATATTAAACCAGAATGATACTTCTTATTTGCATACGCTAT
CCTTCGATCTATCCCTAATAAACTAGGAGGGGTCTAGCCCTATTATTATCTATTCTAGTACTA
ACACTACTACCATTCTCCACACTTCCA-----

>TZJA031-CVU967_19189674_B10.ab1 *Crocidura hirta*

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>TZJA043-CVU967_19189674_H10.ab1 *Lophuromys kilonzo*

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>TZJA029-CVU967_19189674_H9.ab1 *Beamys hindei*

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>TZJA010-CVU967_19189674_B9.ab1 *Grammomys surdaster*

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>TZJA067-CVU967_19189674_G11.ab1 *Praomys delectorum*

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>TZJA048-CVU967_19189674_B11.ab1 *Mus triton*

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>TZJA036-CVU967_19189674_D10.ab1 *Pelomys fallax*

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>TZJA013-CVU967_19189674_D9.ab1 *Lemniscomys rosalia*

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>dTZA40-CVU966_19189667_G11.ab1 *Mus minutoides*

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>TZJA039-CVU967_19189674_F10.ab1 *Mus minutoides*

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Appendix 2.2: Estimate of the minimum number alive (MNA) for *Praomys delectorum*
in the Ukaguru Mountains, Tanzania (H2 & L2 – intact forest; D1 & D2 –
disturbed forest)

Month	H2	L2	D1	D2
June2018	10	4	-	-
July2018	11	7	7	6
Aug2018	9	7	14	8
Sept2018	9	6	19	9
Oct2018	9	1	16	13
Nov2018	12	2	22	13
Dec2018	24	2	25	38
Jan2019	30	1	37	38
Feb2019	25	1	26	30
March2019	24	0	26	17
April2019	23	0	28	25
May2019	23	1	23	26
June2019	23	2	23	24
July2019	20	1	18	15
Aug2019	18	0	20	14
Sept2019	21	0	17	19
Oct2019	18	1	16	16
Nov2019	15	0	17	30
Dec2019	19	0	20	26
Jan2020	29	2	20	24
Feb2020	24	2	13	22

Appendix 2.3: Correlations of species with habitat parameters in the Ukaguru Mountains, Tanzania

	DSH	Litter	CanCov	GroCo	Herbs	Shrubs	Trees	BH	CH	GS	GR	LK	MN	MM	MT	PD
	v															
DSH	-															
Litter	0.00	-														
CanCov	0.72	0.57	-													
GroCov	0.50	0.77*	0.96**	-												
Herbs	-0.58	-0.70	-0.96**	-0.97**	-											
Shrubs	0.55	0.75*	0.96**	0.99**	-0.99**	-										
Trees	0.26	0.95**	0.73*	0.86*	-0.79*	0.84*	-									
BH	0.86*	0.51	0.91**	0.82*	-0.86*	0.85*	0.70	-								
CH	0.81*	-0.02	0.40	0.19	-0.31	0.27	0.14	0.68	-							
GS	-0.49	-0.44	-0.75*	-0.73*	0.62	-0.67	-0.57	-0.63	-0.27	-						
GR	1.00**	0.00	0.72	0.50	-0.59	0.55	0.26	0.86*	0.81*	-0.47	-					
LK	0.91**	-0.03	0.70	0.51	-0.53	0.52	0.26	0.77*	0.52	-0.46	0.91**	-				
MN	-0.50	-0.76*	-0.96**	-1.00**	0.98**	-0.99**	-0.86*	-0.82*	-0.19	0.71	-0.50	-0.51	-			
MM	-0.47	-0.70	-0.87*	-0.91**	0.82*	-0.86*	-0.81*	-0.75*	-0.22	0.94**	-0.46	-0.46	0.90**	-		
MT	-0.50	-0.60	-0.86*	-0.86*	0.93**	-0.91**	-0.68	-0.75*	-0.18	0.33	-0.52	-0.52	0.88*	0.58	-	
PD	0.02	0.89**	0.61	0.76*	-0.75*	0.77*	0.80*	0.47	0.05	-0.50	0.02	-0.13	-0.76*	-0.70	-0.61	-

Litter – Litter depth; GroCov – ground cover; CanCov – canopy cover; DistHum – Distance to human settlement; PD – *Praomys delectorum*; BH – *Beamys hindei*; LK – *Lophuromys kilonzo*; GR – *Graphiurus cf. raptor*; CH – *Crocidura hirta*; MN – *Mastomys natalensis*; MT – *Mus triton*; MM – *Mus minutoides*; GS – *Grammomys surdaster*.

** Significant at the 0.01 level; *Significant at the 0.05 level (one-tail test). The most abundant species in bold

CHAPTER THREE

EFFECTS OF FOREST DISTURBANCE ON THE SEX RATIO, POPULATION DYNAMICS AND REPRODUCTION OF *PRAOMYS DELECTORUM* IN THE UKAGURU MOUNTAINS, TANZANIA

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**EFFECTS OF FOREST DISTURBANCE ON THE SEX RATIO, POPULATION
DYNAMICS AND REPRODUCTION OF *PRAOMYS DELECTORUM* IN THE
UKAGURU MOUNTAINS, TANZANIA**

Abstract

Tropical small rodents in disturbed habitats face lower predation pressures and greater food resources which may impact positively on their population and demographic parameters. Though information on the population dynamics and reproduction of endemic *Praomys delectorum* abound, the impact of anthropogenic disturbances on these parameters is still not known. This study investigated the impact of anthropogenic disturbances on the breeding pattern, population structure and sex ratios of *P. delectorum*. Capture-mark-recapture technique was used to trap rodents from June, 2018 to February, 2020 in the Ukaguru Mountains, Tanzania, where four 70 m x 70 m grids were set, two in intact sites and two in disturbed sites). Significant males were trapped only in intact forest ($\chi^2 = 10.71$, $df = 1$, $p = 0.001$) compared to disturbed forests. The population density of *P. delectorum* varied temporally with peaks attained in the wet season in both habitats. Population structure showed few juveniles in most months and sub-adults accounted for the population increases in the wet seasons in all habitats. The proportion of reproductively active individuals varied temporally in both disturbed and intact forests while habitat disturbance showed no effect on the breeding activity of this species. Overall, these results suggest that rainfall and habitat disturbances as factors responsible for the varying sex ratios and population structure of *P. delectorum* in the landscape. Therefore anthropogenic disturbances should be discouraged in the Ukaguru Mountains.

Keywords: Rodents, habitat disturbance, rainfall, reproduction, population.

3.1 Introduction

Rodents show considerable fluctuations in population size at different times of the year and such dynamics are the result of underlying demographic parameters (Oli and Dobson, 1999). Environmental influences on population dynamics operate through their effects on the demographic parameters (Dobson and Oli, 2001); hence, linking population fluctuations with the underlying demographic parameters is crucial for a clearer understanding of population dynamics (Lima *et al.*, 2001a; Lima *et al.*, 2001b; Lima *et al.*, 2003; Benthem *et al.*, 2017). The environmental factors influencing demographic parameters include habitat quality (cover and food), predation pressure, temperature, humidity and rainfall (Batzli, 1986; Getz *et al.*, 2006; Lin and Batzli, 2001). However, in tropical rodents, rainfall is the most fundamental factor regulating demographic processes and population dynamics as primary productivity (food availability) is dependent on rains (Delany, 1972; Neal, 1981; Bronson, 1985; Bronson and Perrigo, 1987; Leirs *et al.*, 1989; Neal and Alibhai, 1991; Leirs *et al.*, 1994; Lima *et al.*, 2001b; Makundi *et al.*, 2006; Massawe *et al.*, 2007, 2012; Mason-Romo *et al.*, 2018). Due to the greater water availability and improved food quality and quantity that come with the rains, demographic parameters and ultimately population dynamics of rodents have been linked with rainfall pattern (Batzli, 1986; Christian, 1979; Degen *et al.*, 2004; Field, 1975; Jackson and van Aarde, 2004; Sicard *et al.*, 1993; Taylor and Green, 1976). Also, it is believed that a non-estrogenic chemical, 6-methoxy-2-benzoxazolinone (6-MBOA), found in sprouting vegetation (Berger *et al.*, 1981, 1977) is able to stimulate breeding in tropical rodents (Alibhai, 1986; Linn, 1991) though evidence for this is not widespread.

The montane forests in East Africa include those of the Eastern Arc Mountains (EAM) stretching across Tanzania to Kenya, recognized as a global biodiversity hotspot comprising vast array of endemic plants, invertebrates and vertebrates. The EAM blocks

are Taita (Kenya), North Pare, South Pare, West Usambara, East Usambara, Nguu, Nguru, Uluguru, Ukaguru, Rubeho, Malundwe, Udzungwa and Mahenge (all in Tanzania) (Burgess *et al.*, 1998; Burgess *et al.*, 2007; Rovero *et al.*, 2014). The Ukaguru Mountain is of particular interests because in comparison to other EAM blocks, little or no information exists on the ecology of the rodents found in the landscape (Gwegime *et al.*, 2014; Rovero *et al.*, 2014). Also, the Ukaguru Mountains provide habitat to many endemic and rare plant species, at least three strictly endemic amphibian species and 15 Eastern Arc endemic vertebrate species (Gwegime *et al.*, 2014; Rovero *et al.*, 2014). This EAM block is surrounded by villages whose population is expanding and encroaching activities threaten the biodiversity. Anthropogenic disturbances reported within the forests include tree cutting, wood collection, illegal hunting, grazing, clearance of forest for agriculture and pine plantation (Gwegime *et al.*, 2014). These anthropogenic activities may alter the spatial distribution of species, structure of their population and demographic parameters.

The delectable soft-furred mouse, *Praomys delectorum*, is endemic to moist montane forests in the East Africa (Bryja *et al.*, 2014; Cassola, 2016; Happold, 2013; Monadjem *et al.*, 2015) and threatened by deforestation and clearance of lands for agriculture and settlements which may impact on its distribution, demographic parameters and population structure (Makundi *et al.*, 2006; Cassola, 2016). This endemic mouse is nocturnal and terrestrial, forages on the ground in leaf litter and feeds on seeds, fruits and insects and its burrows at the roots of large forest trees and under fallen wood (Happold, 2013; Monadjem *et al.*, 2015). *P. delectorum* feeding habits have been reported to change in response to anthropogenic disturbances which positively impact on its density (Gitonga *et al.*, 2015). Populations of *P. delectorum* on Zomba Plateau, Malawi, were reported to breed during the late dry season and wet season, with population size low at the end of the

dry season and peaking at the end of wet season and individuals surviving at most for six months (Happold and Happold, 1989). Similarly, in the Magamba Forest Reserve, Usambara Mountains, Tanzania, reproductive activity occurred from the latter part of the wet season to early dry season with density greater in the wet season due to increased quality and quantity of food following the rains despite the stable environment of forest reserve. While the population structure in Usambara Mountains, Tanzania, showed a predominance of juveniles in the wet season and accounted for the high number of sexually inactive individuals (Makundi *et al.*, 2006), in the Zomba Plateau populations, Malawi, juveniles formed all of the population in the early dry season (Happold and Happold, 1989). This is an indication that the population structure of this species may vary with different habitats.

Anthropogenic forest disturbances may have impact on sex ratios, breeding patterns and population dynamics of rodents (Makundi *et al.*, 2006) as these man-made disturbances may modify the environmental factors that these rodents depend on. Previous studies have demonstrated that tropical rodents in disturbed habitats are exposed to lower predation pressures (Lambert *et al.*, 2003) and greater food resources (Ochoa, 2000) and interaction of both may impact positively on their population size and demographic processes (Lambert *et al.*, 2006). For example, populations of *Praomys jacksoni* in cultivated lands showed an extended breeding season than those in forest. The extended breeding season of populations in the cultivated area was attributed to the continuous supply of food from the growing crops (Happold, 1974; Rahm, 1970). The sex ratios of rodent species trapped can vary with habitats and seasons due to the differences in activities between sexes, changing behavior patterns or differing sex mortalities (Delany, 1972; Mlyashimbi *et al.*, 2020; Smith and Avenant, 2004) which could be modified by anthropogenic disturbances in their habitats. Likewise, as the age structure of a population

changes temporally depending on the breeding seasonality and survival rate (Delany, 1972; Happold and Happold, 1989), any effect of anthropogenic disturbances on the breeding seasonality and survival rate will definitely result in change in the population structure.

Though information on the population dynamics and reproduction of *P. delectorum* abound, the impact of anthropogenic disturbances on these parameters is still not known. Previously, in Taita Hills, Gitonga *et al.* (2016) reported that habitat alteration did not alter the litter size of *P. delectorum* although their study was characterized by a small sample size, lacked seasonal comparison and utilised placental scars and foetuses as litter size indicators which does allow comparison with other studies. Therefore, the aim of this present study was to investigate the impact of anthropogenic activities on the breeding seasonality, population structure (and dynamics) and sex ratios of *P. delectorum*. A comparison was made of the reproductive activity, sex ratio and population structure between intact and disturbed forests. It was expected that reproductive season will be longer, higher population size and the proportions of each sex will not defer from unity in disturbed forests where tree cutting and wood collection, cattle grazing, illegal hunting take place. Also, with greater food resources and reduced predation risks in disturbed forest, we expected to find a clear predominance of adult over a greater period in the populations in this habitat while the population structure in intact forests should not show clear pattern of dominance of any age category.

3.2 Material and Methods

3.2.1 Study area

This study was carried out in the Ukaguru EAM, located in Gairo District, Morogoro, Tanzania (36° 57'00'' – 38° 00' 00'' East and 06° 25' 00'' – 06° 57' 00'' South; Fig. 3.1).

The elevation of this landscape extends up to 2 250 m above sea level. The dry season is between June and September, with maximum temperature of 21°C recorded in January and minimum temperature of 17°C in July at lower altitudes (Lovett and Pócs, 1993). Generally, the vegetation type is montane and sub-montane forest. The montane forest is mainly characterised by the following tree species: *Polyscias fulva*, *Schefflera lukwangulensis*, *Garcinia volkensii*, *Ocotea usambarensis* and *Cussonia spicata*. Others are *Dombeya burgessiae*, *Clerodendrum* sp., *Macaranga capensis* and *Albizia gummifera*. The sub-montane forest is characterized by *Myrianthus holstii*, *Albizia gummifera*, *Allanblackia stuhlmannii* and *Bersama abyssinica*. High forest disturbances observed include tree cutting, clearance of forest for agriculture and grazing (Gwegime *et al.*, 2014). The human population surrounding the forest is at least 75 720 people (Gwegime *et al.*, 2014) and land outside the forest reserves is generally farmland. Crops commonly cultivated include: maize (*Zea mays*), beans (*Phaseolus lunatus*), Irish potatoes (*Solanum tuberosum*), common pea (*Pisum sativum*), pumpkin (*Cucurbita maxima*), banana (*Musa* spp), common pea (*Pisum sativum*) and cedar (*Cedrela odorata*).

3.2.2 Trapping

Capture-Mark-Recapture (CMR) technique was used to trap rodents between June, 2018 and February, 2020. Four 70 x 70m grids were set, two in intact sites (H2 and L2, 600 m apart) and two in disturbed sites (D1 and D2, 600 m apart) in the Masenge forests of Ukaguru Mountains, Tanzania (Fig. 3.1). Disturbed forest sites were in proximity (50 m) to human settlements and farmlands and characterized by cattle grazing, illegal hunting, tree cutting and wood collection while intact forest sites were devoid of human activities and were greater than 1 km from settlements. Each grid consisted of seven parallel lines, 10 m apart and seven trapping stations per line, also 10 m apart (a total of 49 trapping stations per grid). One Sherman LFA live trap (H.B Sherman Traps Inc., Tallahassee, FL)

was placed at each trapping station. Trapping of rodents was conducted for three consecutive nights every month. Traps were baited with peanut butter mixed with maize bran and inspected in the morning. The trapping station, sex and weight were recorded. The individuals were grouped into age classes base on weight and reproductive status: juveniles, sub-adults and adults (Carleton and Stanley, 2012; Gitonga *et al.*, 2016; Makundi *et al.*, 2006). The reproductive status of captured animals was recorded. In males, the breeding condition was determined by position of the testes, whether scrotal or abdominal. In females, the breeding condition was determined either by signs of pregnancy by palpation, lactation and/or perforate vagina (Makundi *et al.*, 2006). Toe clipping using number codes generated from CMR software *MARK* was employed in individual identification. Captured animals were identified to species levels using relevant keys (Happold, 2013; Monadjem *et al.*, 2015) and mitochondrial DNA from toe tissue was sequenced for species confirmation. Rainfall data were measured and recorded from the rain gauge installed in the plantation office about 7 km from the trapping grids. For logistic reasons, rainfall for October and November, 2018 could not be recorded; instead, the rainfall for October and November, 2019 were used.

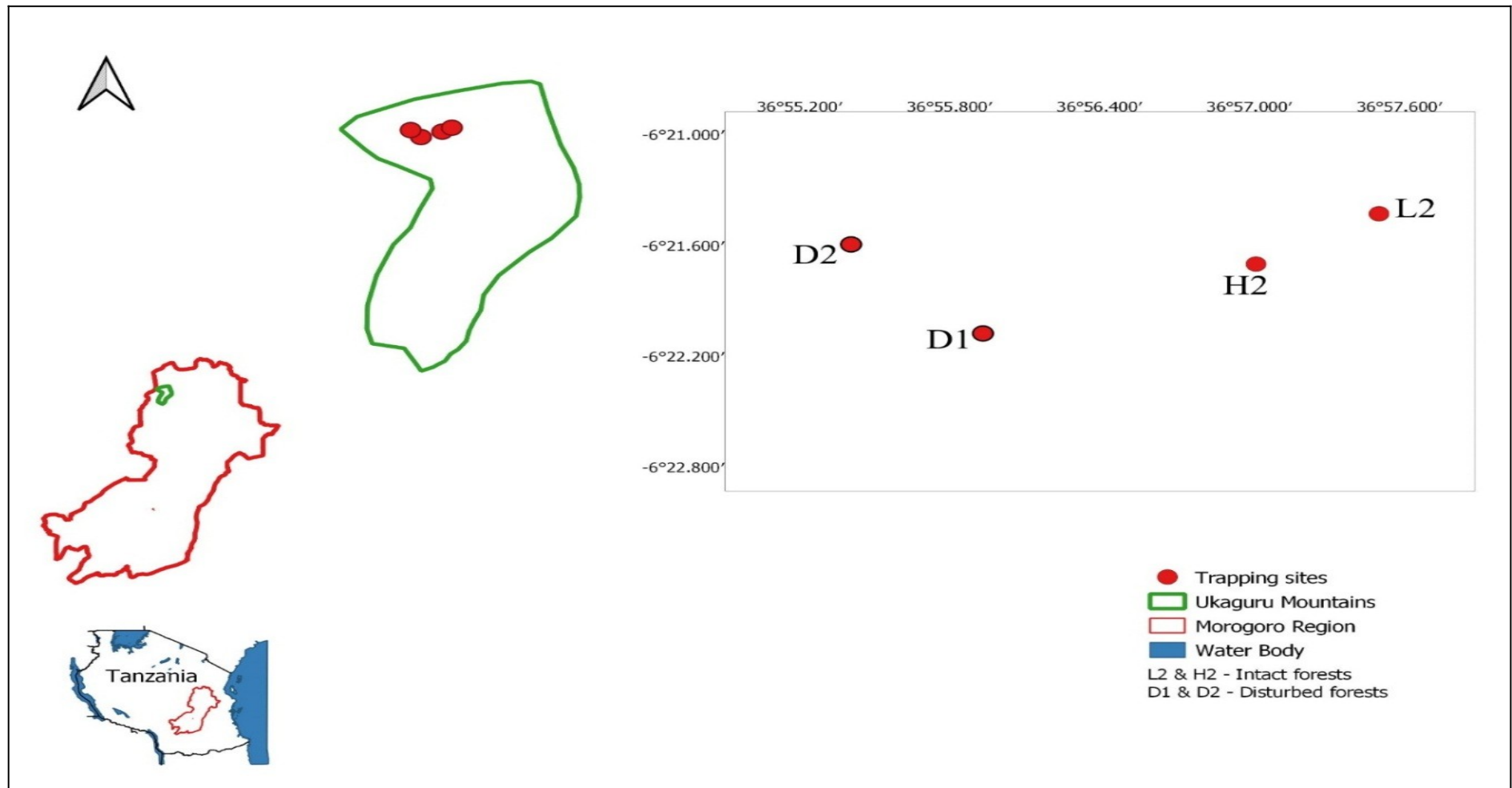


Figure 3.1: Study area and the coordinates of the trapping sites (map is not to scale).

3.2.3 Statistical analysis

The population density of *P. delectorum* was estimated using Minimal Number of animals Alive (MNA) as animals were not always recaptured for the three consecutive nights of trapping. This method uses the individuals capture histories where we noted the individual as alive for all the trap sessions between the first and last time of capture. In order to test for differences in abundance between two forest sites (disturbed and intact) and between seasons (dry and wet), we used a two-way analysis of variance (ANOVA) where seasons and habitats were considered as fixed factors and allowed to interact with each other. We excluded field L2 from the analysis since very few animals were captured during the whole study period (Fig. 3.2).

We represented the age categories as number/grid and compared them between the forest sites (both captures and recaptures were used). Proportions of reproductive active females and scrotal males were determined using percentage of the total individuals. This common method allowed us to compare the reproductive activities with other reports (Delany, 1972). Kruskal-Wallis and Mann-Whitney tests were used to analyze reproductive active females. Deviation from 1:1 ratio of male and female *P. delectorum* captured was tested using Chi square (χ^2) at 0.01 and 0.05 levels of significance.

3.2.4 Ethical considerations

This research was approved by the Sokoine University of Agriculture (SUA), Tanzania and Tanzania Forest Service Agency (TFS). Animal handling followed the guidelines of the American Society of Mammalogists (ASM) for the use of wild mammals in research and education (Sikes and Animal Care and Use Committee of the American Society of Mammalogists, 2016).

3.3 Results

3.3.1 Sex ratio

From the current study, it was observed that more males were caught in both intact and disturbed forests compared to females though only significant for intact forest ($\chi^2 = 10.71$, $df = 1$, $p = 0.001$; Table 3.1). Males predominated in both dry and wet seasons in all habitats though only significant during the wet season in intact forest ($\chi^2 = 12.09$, $df = 1$, $p < 0.001$; Table 3.1).

3.3.2 Population structure and dynamics

The population density of *P. delectorum* varied temporally with peaks attained in the wet seasons in both disturbed and intact forests (Fig. 3.2). Analysis of variance revealed that *P. delectorum* density was significantly higher during the wet season (mean $\pm$ SE: 22.62 ± 1.121) compared to the dry season (15.18 ± 1.225 ; $F_{1,55} = 17.44$, $P < 0.001$). There was no significant differences between the two forest types (D1: 20.35 ± 1.431 ; D2: 20.65 ± 2.064 ; H2: 18.86 ± 1.461 ; $F_{2,55} = 0.22$, $p = 0.81$) and the interaction was also not significant ($F_{2,55} = 0.94$, $p = 0.40$). In disturbed forest, high number of adults were found from April (late wet season) to September (the end of the dry season), while in intact forest, a greater number were found between October and January (wet seasons) (Fig. 3.3). In all habitats, juveniles were very few in most months while sub-adults accounted for the population increases in the wet seasons (Fig. 3.3).

3.3.3 Breeding pattern

We observed temporal variations in the proportions of reproductively active females and males in both intact and disturbed forests (Figure 3.4). Sexually active males were present throughout with peaks from June to November ($> 50\%$) in disturbed forest while July to December ($> 50\%$) in intact forests. A period of reduced proportion of sexually active

males from December to February was observed in disturbed forest while two periods of decreased scrotal male proportions, January to February and May to June were seen in intact forest (Figure 3.4). In intact forest the proportion of reproductively active females was higher between September and November, absent or decreased between December and March, though the first year witnessed greater number of active females in June and July and no active female was trapped in August while about 50% were active in April to June in the second year (Fig. 3.4). While in the disturbed forest, females showed greater reproductive activity from May to November with decline seen from December to March. Some months recorded no incidence of pregnant and lactating females in both forest types though there was no significant difference in reproductive activity across the months (months combined: $\chi^2 = 13.463$, $df = 11$, $p = 0.264$; first year: $\chi^2 = 13.541$, $df = 10$, $p = 0.195$; second year: $\chi^2 = 11.132$, $df = 8$, $p = 0.194$; Fig. 3.5). Combining the years, there was no significant difference in breeding activity between habitats ($\chi^2 = 3.390$, $df = 2$, $p = 0.184$; mean $\pm$ SE, H2: 3.41 ± 0.478 ; D1 = 3.63 ± 0.593 ; D2: 5.18 ± 0.801). Reproductive activity of females was lower in the first year (mean $\pm$ SE: 2.81 ± 0.380) compared to the second year (5.26 ± 0.554 ; Fig. 3.5). In the second year the reproductive activity did show significant difference between the forest types (first year: $\chi^2 = 1.393$, $df = 2$, $p = 0.498$; second year: $\chi^2 = 6.234$, $df = 2$, $p = 0.044$) where it was only significantly higher in D2 (disturbed forest; mean $\pm$ SE: 7.1 ± 1.099 compared to H2 (intact forest, 3.89 ± 0.564 ; Mann-Whitney $U = 14.50$, $p = 0.020$); there was no significant difference in reproductive activity either between H2 (3.89 ± 0.564) and D1 (4.78 ± 0.878 ; Mann-Whitney $U = 32.50$, $p = 0.473$) or D1 (4.78 ± 0.878) and D2 (7.11 ± 1.099 ; Mann-Whitney $U = 20.00$, $p = 0.068$).

Table 3.1: Sex ratio of *Praomys delectorum* in disturbed and intact forests of the Ukaguru Mountains, Tanzania.

	Habitat			H2		D1		D2	
	H2	D1	D2	Dry	Wet	Dry	Wet	Dry	Wet
Female	72	84	94	23	49	25	59	19	75
Male	117	111	120	27	90	33	78	25	95
χ^2	10.71**	3.74	3.16	0.32	12.09*	1.10	2.64	0.82	2.35
					*				
P-value	0.0011	0.053	0.075	0.5716	0.0005	0.2943	0.104	0.3652	0.125
		1	5				2		3

H2 – intact forest; D1, D2 – disturbed forests. Asterisks indicate that the male: female ratio significantly differs from 1:1 at ** $P < 0.01$, * $P < 0.05$.

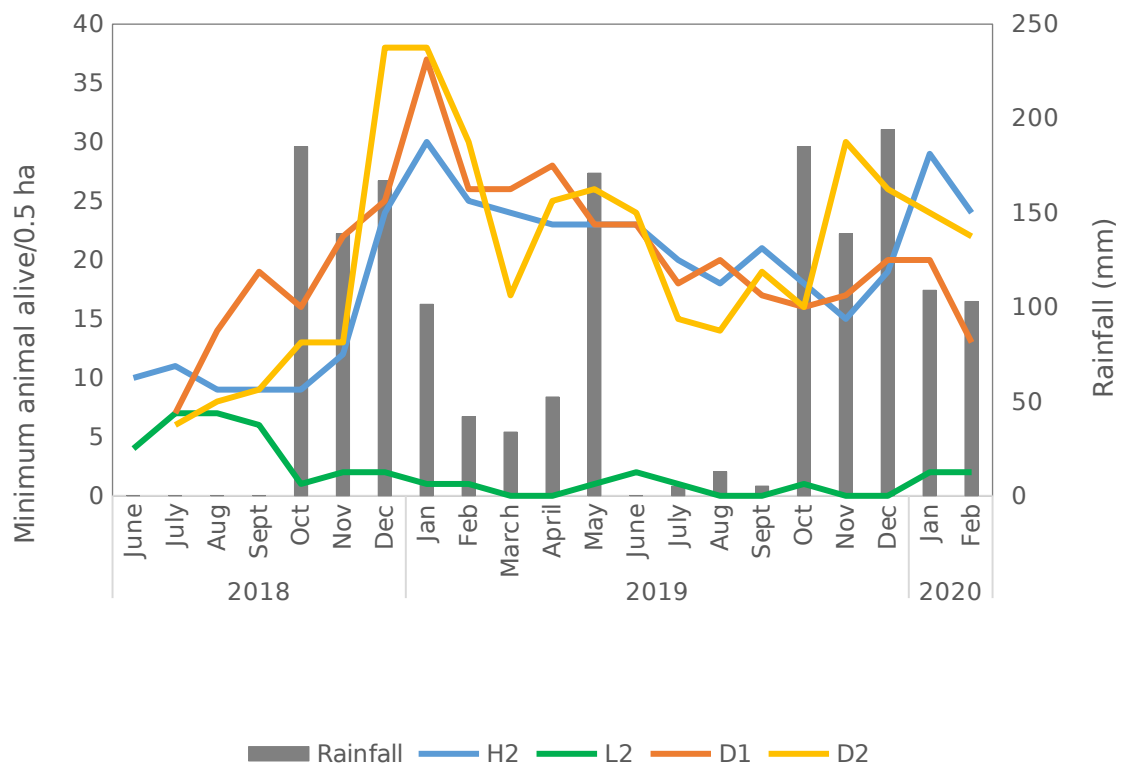


Figure 3.2: Population dynamics of *Praomys delectorum* in different habitats in the Ukaguru Mountains, Tanzania. (H2 – intact forest, L2 – intact forest; D1 – disturbed forest; D2 – disturbed forest)

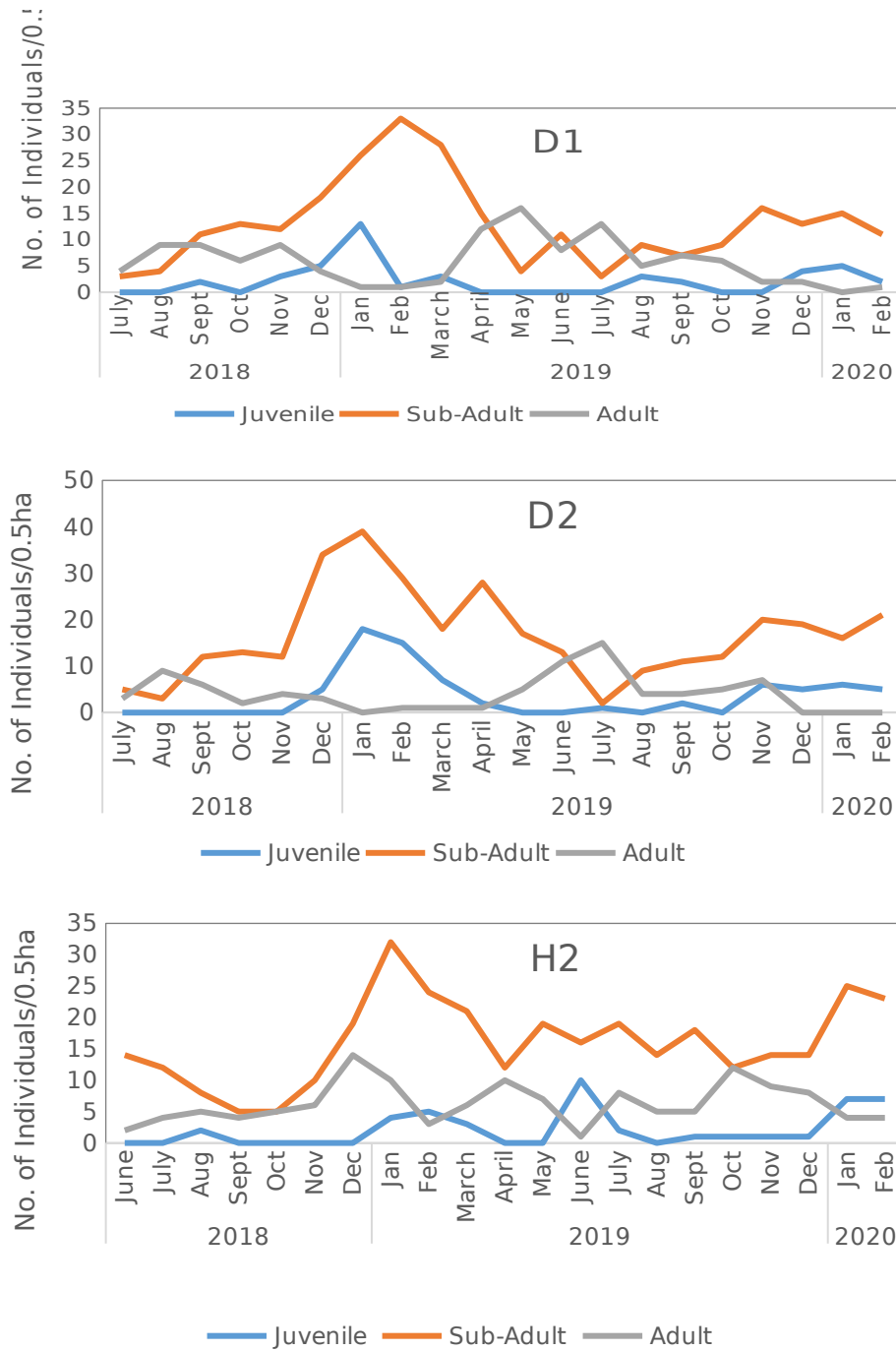


Figure 3.3: Monthly variation in the population structure of *Praomys delectorum* in Ukaguru Mountains, Tanzania (H2 – intact forest; D1 and D2 – disturbed forests; both captures and recaptures were used).

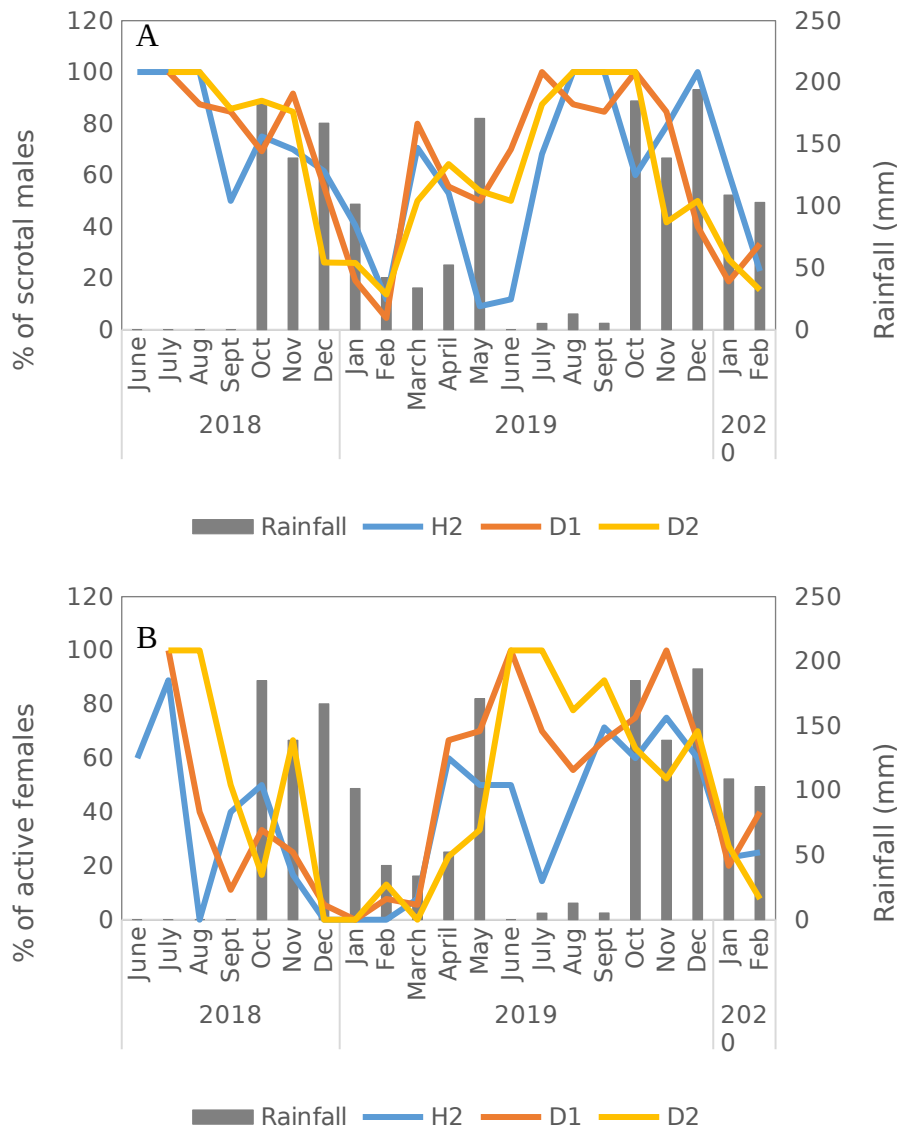


Figure 3.4: Monthly variation in the breeding conditions of *Praomys delectorum* in different habitats in the Ukaguru Mountains, Tanzania: (a) Male (b) Female (H2 – intact forest; D1 and D2 – disturbed forests; both captures and recaptures were used).

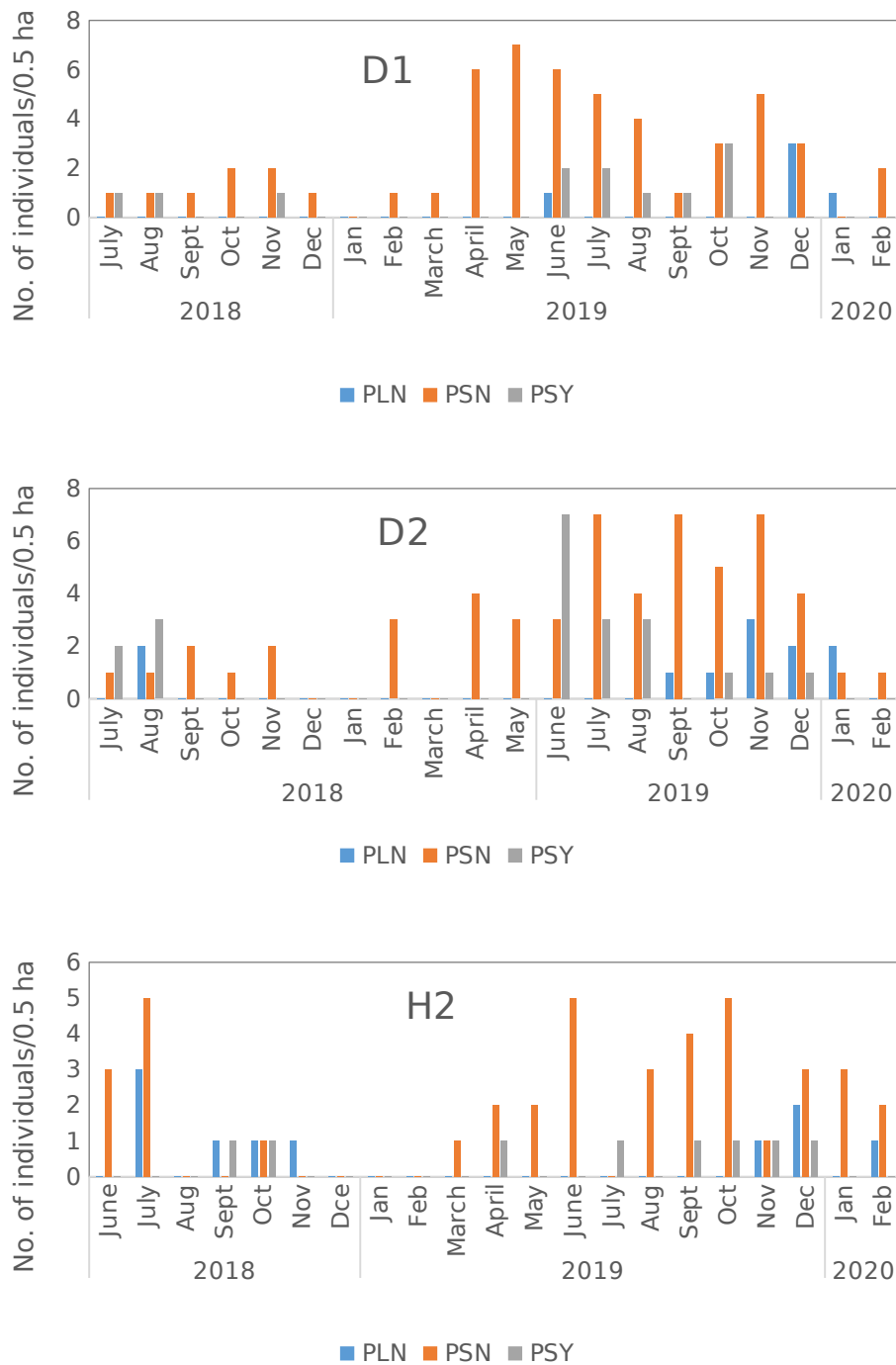


Figure 3.5: Variation in the reproductive activity of *Praomys delectorum* in the Ukaguru Mountains, Tanzania (PLN-lactating; PSY-pregnant; PSN-only perforated; H2 – intact forest; D1 and D2 – disturbed forests; both captures and recaptures were used)

3.4 Discussion

The results of the current study show that more males were caught in intact forest compared to disturbed forests with males significantly predominating only in the wet season in intact forest. The population density of *P. delectorum* varied temporally with peaks and greater densities attained in the wet seasons in both disturbed and intact forests though densities between the forest types was not significant. The population structure showed the predominance of sub-adults between January and March in all forest types. The proportion of reproductively active individuals varied temporally in both disturbed and intact forests while habitat disturbance showed no effect on the breeding activity of this species.

Significantly higher number of males were caught in intact forest compared to disturbed forests with significantly higher numbers of males only caught in the wet season. The proportion of males/females of rodent species trapped can vary with habitats and seasons due to the differences in activities between sexes, changing behavior patterns or differing sex mortalities (Delany, 1972; Mlyashimbi *et al.*, 2020; Smith and Avenant, 2004). A lower female survival in intact forests compared to disturbed forests might explain the highly male-biased sex ratios in intact forest (Ademola *et al.*, 2021). Also, predation pressure which may act stronger on females is greater in intact forest than disturbed (Lambert *et al.*, 2003, 2006; Ademola *et al.*, 2021). The reasons for the significant seasonal difference in the sex ratio, being greater for males in the wet season, is immediately not clear. It is likely that predation of females in this forest type was greater in the wet season. Alternatively, movement/dispersal of males in search of food or mates is greater during the wet seasons leading to greater probability of male being caught in this site. The abundance of *P. delectorum* varied seasonally, with significantly higher densities during the wet season compared to the dry season in both forest types. This may

suggest that *P. delectorum* exhibits a seasonal breeding pattern which starts at the beginning of the wet season (Happold, 2013). Indeed, rainfall has been shown to have a large effect on the timing of the breeding season in a wide variety of small mammals, since it affects the availability of food (Field, 1975; Leirs *et al.*, 1989; Taylor and Green, 1976) allowing the population to grow until food becomes more scarcely available at the beginning of the dry season leading to a decrease in the population size (Leirs *et al.* 1994). The reason for the low captures in field L2 is not clear. We suspect that the noise generated from tree felling in an adjacent pine plantation using chain saws and skidding may have shifted the home range of populations in this field. This experience was only peculiar to L2. Indeed exposure of rodents to noise leads to stress induction (Baldwin, 2007) and they may respond by fleeing farther away (Hawthorne *et al.*, 2011).

The population structure, dependent on the rate of recruitment and death, varies at different periods (Delany, 1972). In the present study, sub-adults occurred in January to March (mid wet season) in both forest types which are the products of the breeding activity in the preceding months (Makundi *et al.*, 2006). In intact forest, high number of adults occurred in the population between October and January (wet seasons) with sub-adults dominating throughout, while in disturbed forest, adults were prominent from April (late wet season) to September (the end of dry season). As population structure is determined by demographic parameters such as the length of the breeding season, survival and maturity rates (Happold and Happold, 1989), variations of the parameters between the forest types may account for the variations in the population structures between them. Our previous analysis showed that survival rate (though sex-biased) is higher in disturbed forest compared to intact forest while habitat disturbance showed no effect on maturation in both forest types (Ademola *et al.*, 2021). The low trapping of juveniles in all habitats could be due to their less sensitivity to traps and less activities as

this age category largely depend on their female parent for nourishment (Happold, 1979; Garshong and Attuquayefio, 2013). The population structure and dynamics of this species reflect its reproductive strategy to produce young when environmental factors are most favourable which is line with the general strategy of rodents (Delany, 1972; Taylor and Green, 1976).

In this study, we observed yearly variation in the reproductive activities of this rodent in both forest types, being reduced in the first year (June 2018 to May 2019) with some months showing no reproductive activity while the second year (July 2019 to February 2020) showed greater reproductive activities in both forest types. Yearly variation in the breeding activities of has been reported among/within rodent species. For example, populations of the deer mice, *Peromyscus* spp showed great variation in their breeding patterns both spatially and annually (Bronson, 1985). Similarly, the results of Makundi *et al.* (2006) demonstrated yearly variation in reproductive activity of *P. delectorum* in the Magamba Forest Reserve, north-east Tanzania. This variation may have arisen as a response of the animals to yearly differences in climatic factors or the animals developing greater trap awareness.

Our results show seasonality in the proportion of reproductively active male and female *P. delectorum* in both intact and disturbed forests. Pregnant and lactating females occurred prominently in July and September to November in intact forest while in disturbed forests as early as June way down to January. Our findings are similar to those of Happold and Happold (1989) and Stanley and Goodman (2011) who reported the occurrence of most pregnancies in the wet season though minimal breeding also happened in the early and late dry seasons in *P. delectorum* populations on Zomba Plateau, Malawi and the East and West Usambara mountains, Tanzania respectively. Similarly, Makundi

et al. (2006) reported high numbers of reproductively active female from latter part of the wet season to early dry season (April–July) with few males individuals scrotal at different times of the year showing with peaks the wet season in *P. delectorum* populations in Magamba Forest Reserve, the Western Usambara Mountains, Tanzania.

Breeding effort of many tropical rodents have been significantly correlated with rainfall as seasonal variation in primary productivity in the tropics is majorly controlled by rains (Delany, 1972; Field, 1975; Leirs *et al.*, 1989; Leirs *et al.*, 1994; Makundi *et al.*, 2006; Makundi *et al.*, 2007; Massawe *et al.*, 2007, 2012; Neal, 1981; Neal and Alibhai, 1991; Taylor and Green, 1976). Even in montane forests where most months of the year are characterized by rainfall, seasonal variation in quality and quantity of food resources and cover is expected which ultimately influences the demography and population dynamics of rodents (Delany, 1972; Makundi *et al.*, 2006). The addition of greater number of sub-adults in the middle of wet seasons (January to March) to the population results in the significantly higher densities during the wet season compared to the dry season in both forest types as the wet season is a period of optimal breeding for rodents (Field, 1975; Leirs *et al.*, 1989; Taylor and Green, 1976).

Factors that may explain the seasonal reproductive response of rodents to rainfall have been put forward (Neal, 1981; Neal and Alibhai, 1991). This includes the concept that increased water availability following the rains triggers greater reproductive efforts by eliminating water stress (Christian, 1979; Degen *et al.*, 2004; Sicard *et al.*, 1993); this was demonstrated in the extended breeding season, greater number of pregnancies and higher proportions of lactating females in desert rodents (Christian, 1979). Also, improved nutritional quality and quantity of available food resources have been adjudged to initiate or elongate the breeding efforts in some rodents (Batzli, 1986; Field, 1975; Jackson and

van Aarde, 2004; Taylor and Green, 1976). Further, a non-estrogenic chemical, 6-methoxy-2-benzoxazolinone (6-MBOA) found in sprouting vegetation, has been reported to stimulate/initiate reproductive activity in some rodents in both temperate (Berger *et al.*, 1981, 1977; Dai *et al.*, 2016; Gower and Berger, 1990; Neal, 1981) and tropical regions (Alibhai, 1986; Linn, 1991). In a tropical rodent, *Tatera leucogaster*, the effects of 6-MBOA on its reproductive activity were inconclusive, owing to the small sample size employed and the likely confounding effect of limited/no access to water from the extreme dryness of prevalent in the study area; all of which would negatively masked the reproductive effects of 6-MBOA (Neal and Alibhai, 1991). As the occurrence of 6-MBOA in green vegetation varies with season, rodents use its appearance to signal availability of nutritional food resources and most favourable period for reproductive activities (Berger *et al.*, 1981).

In contrast to the reproductive stimulatory 6-MBOA, chemical inhibitors of breeding (cinnamic acids) that signal the qualitative decline of the food resource, have been identified in senescing vegetation; their occurrence is used as signals for the cessation of reproductive activities (Berger *et al.*, 1977). If greater availability of water were to be considered a major factor influencing the breeding seasonality of *P. delectorum*, we would expect to see greater reproductive effort in the middle of the wet season. Contrary wise, there was a decline of reproduction activities during this period which makes us exclude availability of water as a factor for the seasonal breeding of this forest dwelling species. Overall, it is likely that the synergistic action of several factors such as food, water and 6-MBOA/inhibitory chemical mediated through rainfall (Neal and Alibhai, 1991) would act together in regulating the reproductive activities of *P. delectorum* in Ukaguru Mountains.

Otherwise, some factors not yet known may be influencing the reproduction of this delectable soft-furred mouse. Further studies are required to shed light on the role of these factors in regulating reproduction in *P. delectorum*.

In summary, these results highlight that the population structure and dynamics of *P. delectorum* are largely influenced by length of the breeding season which is dependent on the rainfall. Also, the anthropogenic disturbances resulted in modification of the sex ratio and population structure but not the breeding activity. As the human population surrounding the Ukaguru Mountains and their encroaching activities increase, we discourage the continuous exploitation of the forests of this landscape even though the breeding and population dynamics of the delectable soft-fur mouse were not negatively affected; this is because unperturbed forests are irreplaceable in the conservation of biodiversity in general (Gibson *et al.*, 2011).

3.5 Acknowledgement

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CHAPTER FOUR

EFFECTS OF FOREST DISTURBANCE ON THE FITNESS OF AN ENDEMIC RODENT IN A BIODIVERSITY HOTSPOT

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EFFECTS OF FOREST DISTURBANCE ON THE FITNESS OF AN ENDEMIC RODENT IN A BIODIVERSITY HOTSPOT

Abstract

Praomys delectorum occurs abundantly in both disturbed and intact forests in the Ukaguru Mountains within the Eastern Arc Mountains (EAM), Morogoro, Tanzania. While previous studies have reported that anthropogenic disturbance such as grazing, wood cutting and harvesting has a positive effect on the population density of *P. delectorum*, the impact of habitat disturbance on its demographic traits is still unknown. We performed a capture-mark-recapture study in both disturbed and intact forest from June 2018 to February 2020 in order to investigate the effects of habitat disturbance on abundance as well as two demographic traits: survival and maturation of *P. delectorum* in the Ukaguru Mountains. We found no variation in abundance or maturation between intact and disturbed forests, but habitat type did affect survival. However, this effect was sex-dependent since female survival was higher in disturbed forests while male survival remained similar across the two forest types potentially due to differences in predation pressure or food availability between the two habitats. Continuous demographic monitoring of *P. delectorum* in EAM is necessary given that the increasing human population surrounding the landscape is leading to higher deforestation rates, and expansion of the pine plantation in the forest reserve.

Keywords: Survival and maturation rate, population density, *Praomys delectorum*, capture-mark-recapture, Eastern Arc Mountains, biodiversity hotspot

4.1 Introduction

Rodents, being the largest mammalian Order, are well represented in sub-Saharan Africa with 463 species adapted to heterogeneous environments and extant in all habitats and provide important ecosystem services (Monadjem *et al.*, 2015). Rodents, and other small mammals in general, provide food for predators (ophidian, avian and mammalian), regulate insect populations and modify the soil (structure, organic content and mineral cycling) which affects plant growth (Hayward and Phillipson, 1979). They consume and disperse seed (Hayward and Phillipson, 1979); for instance, in forest ecosystems, rodents are effective in seed dispersal by hoarding of seeds in caches which is a coping strategy for fluctuating seed supply (Corlett and Hughes, 2015). Nonetheless, most research on rodents in Africa has been focused on pest species, which are about 5 – 17 % of the African rodent species (Monadjem *et al.*, 2015; Mulungu, 2017; Swanepoel *et al.*, 2017) and data on non-pest species is rare. This research bias has potential consequences on the conservation of other, non-pest, rodent species in Africa (Swanepoel *et al.*, 2017).

The Eastern Arc Mountains (EAM) region, being one of the top 25 biodiversity “hotspots” worldwide with at least 800 endemic vascular plants, 136 endemic and 75 near-endemic vertebrates, is facing an alarming rate of anthropogenic disturbance (Burgess *et al.*, 1998, 2007; Myers *et al.*, 2000; Rovero *et al.*, 2014). One of these endemic vertebrates is the delectable soft-furred mouse, *Praomys delectorum* which occurs in moist montane forests of the EAM and the distributional range extends westward to north-central Tanzania, and southward to Malawi and northern Mozambique (Bryja *et al.*, 2014; Cassola, 2016; Happold, 2013; Monadjem *et al.*, 2015). However, this species is currently threatened by habitat loss due to deforestation and clearance of lands for agriculture throughout its distributional range (Cassola, 2016).

Praomys delectorum is a nocturnal, scansorial terrestrial rodent feeding on seeds, fruits and insects found in burrows associated with the roots of large forest trees and under fallen wood (Happold, 2013; Monadjem *et al.*, 2015). They are reported to be reproductively active during the late dry season and beginning of the wet season after which the population size increases with a peak at the end of the wet season and individuals surviving at most for six months (Happold, 2013). Information on the social and reproductive behaviour of *P. delectorum* is scarce, though other species of the same genus appears to be territorial (Monadjem *et al.*, 2015). *Praomys delectorum* is the dominant species in the Western Usambara Mountains in North-East Tanzania (Makundi *et al.*, 2006) and habitat disturbance has been found to affect their feeding habits, reproduction and parasitic infection rate in the Taita hills, Kenya (Gitonga *et al.*, 2015, 2016a, 2016b). Additionally, habitat disturbance has an effect on the population densities as well. Indeed, densities of *P. delectorum* has been reported to be higher in anthropogenically disturbed forest characterized by grazing, tree cutting and wood collection (Cassola, 2016; Gitonga *et al.*, 2015; Monadjem *et al.*, 2015). This may suggests that this species is able to use resources in anthropogenically disturbed habitats. However, none of these studies looked at the demographic characteristics, which is key in order to understand the viability of the populations in disturbed habitats.

Indeed, while studying the population sizes of *P. delectorum* in disturbed and undisturbed habitat will undoubtedly provide valuable information for the conservation of this species, it is not sufficient. This is due to the fact that density alone is not a good estimator of the viability of the population since it does not take the individuals' fitness into account (Van Horne, 1983). It is therefore important, in order to investigate the viability of the populations in disturbed habitats, to look at the demographic parameters that underlie these population dynamics (Oli and Dobson, 1999). Survival and maturation are two

important components affecting the fitness of animals and are therefore indispensable in order to get a better understanding of their population dynamics. Indeed, estimating survival and maturation and combining these with the population density will provide us with more information about the impact of anthropogenic forest disturbance on *P. delectorum* populations.

Within this study, we investigated the effects of anthropogenic forest disturbance on *P. delectorum* population density as well as survival and maturation in the Ukaguru Mountains within the EAM, Tanzania. We hypothesize that population densities will be greater in anthropogenically disturbed forests characterized by grazing, tree cutting and wood collection compared to undisturbed forests; because their feeding behaviour has been reported to change in response to anthropogenic disturbances which may have positive effects on reproductive efforts and ultimately on population density size (Gitonga *et al.*, 2015). Additionally, these changes in feeding behavior may also lead to a higher survival probability and maturation rate in disturbed areas compared to undisturbed forests as well. However, survival and maturation may vary between the wet and dry seasons, sexes and age classes, as has been found in other small mammals (Eccard *et al.*, 2002; Oli and Dobson, 1999; Previtali *et al.*, 2010). Most research on the effects of habitat disturbance on the population dynamics in African small mammals focused on the pestiferous *Mastomys natalensis* (Julliard *et al.*, 1999; Mayamba *et al.*, 2019; Sluydts *et al.*, 2007) and little information is available on *P. delectorum*. Our study will be the first to look at the effect of anthropogenic disturbance on both the population size and two demographic parameters of *P. delectorum* and is therefore important to fill this knowledge gap and will be useful to optimize the current conservation and management strategies of *P. delectorum* (Eberhardt, 1985; Paradis *et al.*, 1993; Oli and Dobson, 1999).

4.2 Material and Methods

4.2.1 Study area

This study was carried out in the Ukaguru Mountains within the EAM, located in the Gairo District, Morogoro, Tanzania (36° 57'00'' – 38° 00' 00'' East and 06° 25' 00'' – 06° 57' 00'' South; Fig. 4.1). The elevation of this landscape extends up to 2 250 meters above sea level. The estimated annual rainfall is 1 400 mm (Gwegime *et al.*, 2014). The dry season is between June and September, with maximum temperature of 21°C recorded in January and minimum temperature of 17°C in July at lower altitudes (Gwegime *et al.*, 2014).

The vegetation type in the Ukaguru Mountains is montane and sub-montane forest. The montane forest is mainly characterised by the following tree species: *Polyscias fulva*, *Schefflera lukwangulensis*, *Garcinia volkensii*, *Ocotea usambarensis* and *Cussonia spicata*. Others are *Dombeya burgessiae*, *Clerodendrum* sp., *Macaranga capensis* and *Albizia gummiifera*. The sub-montane forest is characterized by *Myrianthus holstii*, *Albizia gummiifera*, *Allanblackia stuhlmannii* and *Bersama abyssinica*. High forest disturbances observed include tree cutting, clearance of forest for agriculture and grazing (Gwegime *et al.*, 2014). The human population surrounding the forest is at least 75 720 people (EAMCEF, 2021) and land outside the forest reserves is generally farmland. Crops commonly cultivated include: pumpkin (*Cucurbita maxima*), banana (*Musa* spp), maize (*Zea mays*), Irish potatoes (*Solanum tuberosum*), common pea (*Pisum sativum*), beans (*Phaseolus lunatus*) and cedar (*Cedrela odorata*).

4.2.2 Trapping

Capture-Mark-Recapture (CMR) technique was used to trap rodents from June, 2018 to February, 2020. Two 70 x 70 m grids were set in intact sites (H2 and L2, 600 m apart)

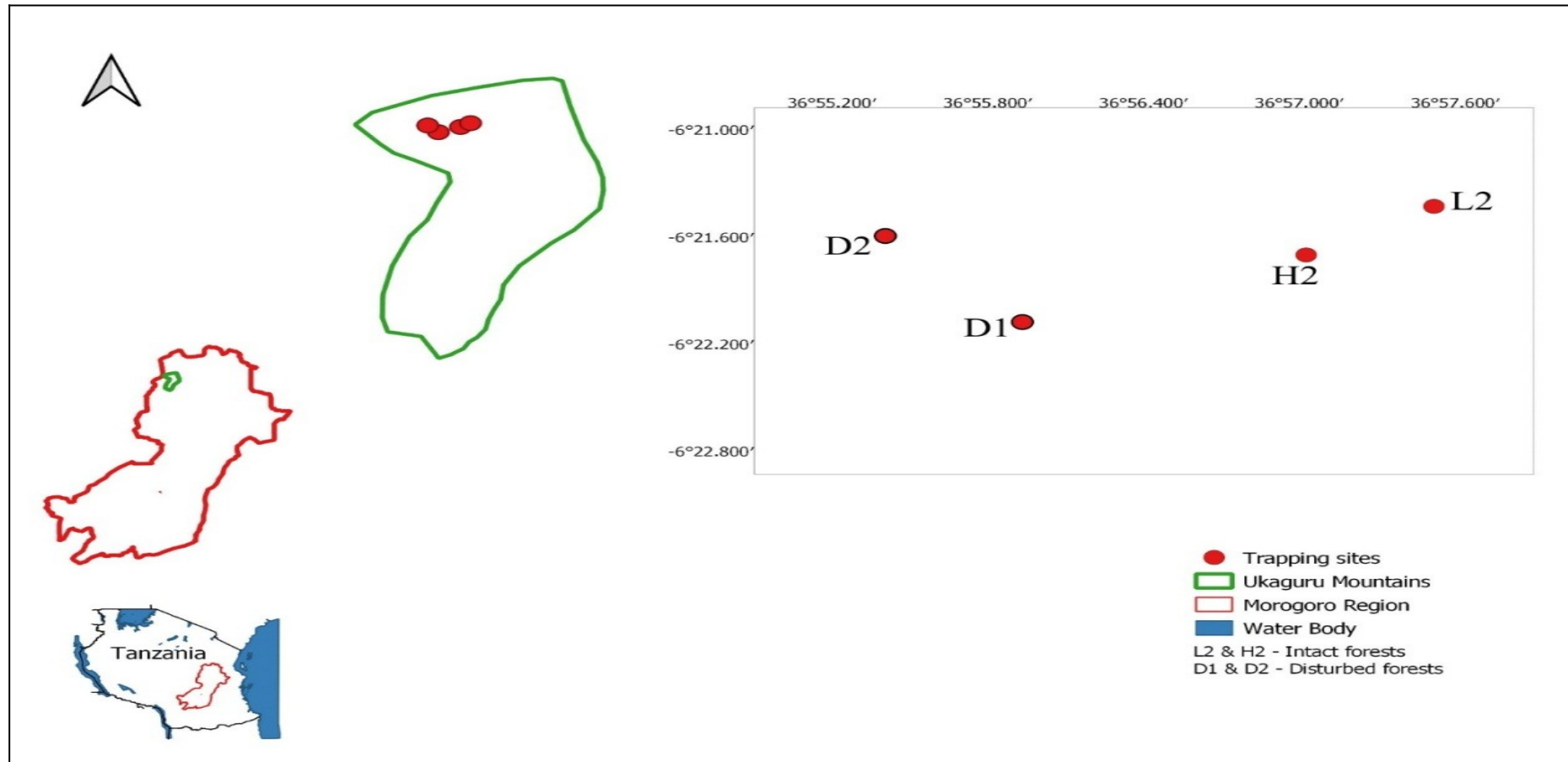


Figure 4.1: Study area and the coordinates of the trapping sites (map is not to scale).

and two grids were placed in disturbed sites (D1 and D2, 600 m apart; Fig. 4.1). The minimal distance (600 m) between the grids was sufficient to prevent migration between grids for small rodents. The two grids in the disturbed forest were in proximity (50 m) to human settlements and farmlands and were characterized by cattle grazing, illegal hunting, tree cutting and wood collection. The two grids in the intact forests were devoid of human activities and were greater than 3 km from disturbed forests. Each grid consisted of seven parallel lines, 10 m apart and seven trapping stations per line, also 10 m apart (a total of 49 trapping stations per grid). One Sherman LFA live trap (H.B Sherman Traps Inc., Tallahassee, FL) was placed at each trapping station. Trapping of rodents was conducted for three consecutive nights every month. Traps were baited with peanut butter mixed with maize bran and inspected in the morning. The trapping station, sex, weight and age were recorded. The reproductive status of captured animals was recorded and the individuals were divided into two age classes based on their reproductive status: juveniles (not reproductive active) and adults (reproductive active). In males, the breeding condition was determined by position of the testes, whether scrotal or abdominal. In females, the breeding condition was determined either by signs of pregnancy by palpation, lactation and/or perforate vagina (Makundi *et al*, 2006). Toe clipping using number codes generated from CMR software *MARK* was employed in individual identification (Borremans *et al.*, 2015). Captured animals were identified to species levels using relevant keys (Happold, 2013; Monadjem *et al.*, 2015) and confirmed by sequencing the mitochondrial cytochrome b gene.

4.2.3 Statistical analysis

For analysis, we decided to focus only on *P. delectorum* since this was the most dominant species in all four fields (Appendix 4.1).

4.2.3.1 Population density

The population density of *P. delectorum* was calculated for each trapping session using the M(h) jackknife estimator in the *DENSITY* software (Version 5.0; Efford *et al.* 2004). However, this method is only useable when animals are captured for three consecutive nights, which was not always the case (even though we trapped for three nights). We therefore decided to use the minimal number of animals alive (MNA) as an alternative measurement for density. This method uses the individuals capture histories where we noted the individual as alive for all the trap sessions between the first and last time of capture.

In order to test for differences in abundance between the two forest types (disturbed and intact) and between seasons (dry and wet), we used a generalized linear mixed model with the minimal number of animals alive, calculated for each trapping session, as the response variable and a negative binomial error distribution (since there was evidence for over-dispersion). We included season and forest type as fixed effects and allowed them to interact with each other. The field where the measurements were taken was included as a random effect. We excluded field L2 from the analysis since very few animals were captured during the whole study period (Fig. 4.2; Appendix 4.1). The statistical analysis was executed using the R software 3.5.0 (R Core Team, 2013) with the glmmTMB package (version 1.0.2.1; Brooks *et al.*, 2017). Differences in MNA between forest types and seasons were estimated using the effects package (version 4.1; Fox and Weisberg, 2019).

4.2.3.2 Goodness of fit

A goodness-of-fit (GOF) test was carried out with the U-CARE software (Pradel *et al.*, 2003; Choquet *et al.*, 2009) prior to the survival analysis to evaluate potential

confounding factors such as an excess of transient animals and trap-dependence. The test did not show any deviation against the assumption on transience (see results), which are individuals that were captured only once during the whole trapping period. Additionally, the GOF test revealed no effect of trap dependence (see results), which suggests that the recapture probability of the individuals did not depend on the previous experience.

4.2.3.3 Survival and maturation analysis

Survival and recapture probabilities were estimated using multivariate multistate Cormack-Jolly-Seber model in E-SURGE V2.1.4 (Choquet *et al.*, 2009). This allowed us to estimate the effect of age (adult or juvenile), sex (male or female) and forest type (disturbed or intact forest) on both survival (ϕ) and maturation (Ψ) probabilities. We included three events (captured as adult/juvenile or not captured at all) and three states (captured as an adult or juvenile or not captured at all). Trapping was done using Pollock's closed robust design, where the population is assumed to be closed (i.e. no entry or exit of individuals into the population) within each trap session and open between trap sessions. Survival was therefore defined as the probability to survive from one month to the next and fixed to 1 within a trapping session, while the recapture probability was estimated within each session.

Survival and maturation probabilities were modelled in subsequent steps which reduced the amount of models that we needed to run. We first modelled survival after which we modelled maturation (Mariën *et al.*, 2018; Mayamba *et al.*, 2019; Sluydts *et al.*, 2007). Models were ranked using the sample size corrected Akaike's Information Criterion (AICc; Burnham and Anderson 2004), where the model with the lowest AICc value was the best fit for the data and selected as starting point for the next modelling step. Models that differed less than 2.0 units were deemed equally good.

4.2.3.4 Survival

Before we started with actual model reduction, we needed to test whether there was seasonal variation in survival (Table 4.1: seasonal effects). We therefore created three models where we allowed survival to vary either (1) between the two seasons separately for each year (Season * year: dry season: June 2018 – September 2018, wet season: October 2018 – May 2019, dry season: June 2019 – September 2019, wet season: October 2019 – February 2020), (2) between the wet and dry season but compiling the two years together (Season: dry versus wet season) or (3) by creating a model without seasonality (Table 4.1). Within these three models, we allowed survival to vary between the two age classes (adults and juvenile) and between males and females separately for intact and disturbed forests, since we allowed sex and age to interact with forest type (Table 4.1). We then selected, out of these three model, the model with the lowest AICc as a starting point for further model reduction. This was done in two substeps, where we first removed all the interactions between forest type and age and sex one by one until the three covariates (sex, age and forest type) had an additive effect (Table 4.1: reduction interactions). We then chose, out of these models, the model with the lowest AICc value as a starting point for the second substep, where we stepwise remove each covariate one by one until all three of them were removed (Table 4.1: reduction fixed effects). The model with the lowest AICc value, after this final step, was considered to be best fitted model concerning the survival within this study.

4.2.3.5 Maturation

After survival, we modelled maturation which is defined as the monthly probability for juveniles to become adults, i.e. to become reproductive active since adults and juveniles were differentiated from each other based on signs of sexual activity. We started the model reduction from a full model where maturation rate was allowed to differ between

the two sexes within each forest type (Table 4.1). We then removed the interaction and all covariates one by one only the intercept model remained (Table 4.1). The model with the lowest AICc value was the best fit for the data. Since variation in survival and maturation probabilities are the main focus of this work, we decided to use the same recapture parameters in every model. Recapture probability was fully time dependent and was allowed to differ between the four different fields.

4.2.4 Ethical considerations

This research was approved by the Sokoine University of Agriculture, Tanzania (reference: SUA/DPRTC/PFC/D/2017/0010/11) and Tanzania Forest Service Agency (TFS). Animal handling followed the guidelines of the American Society of Mammalogists (ASM) for the use of wild mammals in research and education (Sikes and Animal Care and Use Committee of the American Society of Mammalogists, 2016).

4.3 Results

4.3.1 Population dynamics

Population densities of *P. delectorum* as derived using the M(h) estimator and MNA showed concordance. The population density of *P. delectorum* varied temporally with peaks attained in the wet seasons in both disturbed and intact forests (Fig. 4.2). The generalized linear mixed model revealed that *P. delectorum* abundance was significantly higher during the wet season compared to the dry season (estimate $\pm$ SE: 0.378 ± 0.116 , $Z = 3.257$, $p = 0.001$; Fig. 4.3). There was no significant differences between the two forest types (-0.056 ± 0.157 , $Z = -0.357$, $p = 0.721$) and the interaction was also not significant (-0.042 ± 0.191 , $Z = -0.222$, $p = 0.824$).

4.3.2 Goodness of fit

The GOF test revealed no deviation against the assumption of transience (Test 3G.SR: $\chi^2 = 106.590$, $df = 96$, $p = 0.216$), not against trap dependence (Test M.ITEC, $\chi^2=80.173$, $df = 67$, $p = 0.130$). This suggesting that there was no excess of animals that were trapped only once during the study period and that there was no trap effect, in which the individuals became trap happy or shy when there were trapped during the previous night.

4.3.3 Model selection

4.3.3.1 Survival

We first studied if there were differences in survival between the different seasons by comparing two models with a seasonal effect (with and without time-dependence) and one without a seasonal component. The model without a seasonal component had a significant lower AICc value compared to the other two models with a season component, which suggests that *P. delectorum* survival does not change between seasons (Table 4.1). The highest ranking model (with the lowest AICc value; Table 4.1) revealed differences in survival between the disturbed and intact forests, but this was sex-specific. Indeed, the model showed that female survival was higher in disturbed forests (estimate $\pm$ SE: 0.650 ± 0.026) compared to intact forests (0.524 ± 0.044), while male survival was slightly lower in disturbed (0.595 ± 0.026) compared to intact forest (0.643 ± 0.030 ; Fig. 4.4).

The second best model was 1.700 units larger compared to the first model and had age as an additional additive effect (Table 4.1), where juvenile survival was always higher compared to adults for both females (disturbed forest: juveniles = 0.658 ± 0.030 , adults = 0.640 ± 0.032 ; intact forest: juveniles = 0.534 ± 0.047 , adults = 0.514 ± 0.047) as males (disturbed forest: juveniles = 0.608 ± 0.035 , adults = 0.589 ± 0.028 ; intact forest: juveniles 0.656 ± 0.038 , adults = 0.638 ± 0.032) in both forest types.

However, these differences in survival between adults and juveniles was small, and we decided to continue with the model with the lowest AICc value.

4.3.3.2 Maturation

The model with the lowest AICc value contained sex (Table 4.1) where males matured faster (0.090 ± 0.015) compared to females (0.060 ± 0.011). However, the second best model had only an intercept (0.073 ± 0.009) and was only 0.61 AICc units larger compared to the first model (Table 1), which suggests that these differences in maturation rate between males and females is not strongly supported.

4.3.3.3 Recapture probability

Each model ran with the same recapture parameters. The models showed that the recapture probability varied over time and that the recapture probability differed between the four fields (Appendix 4.2).

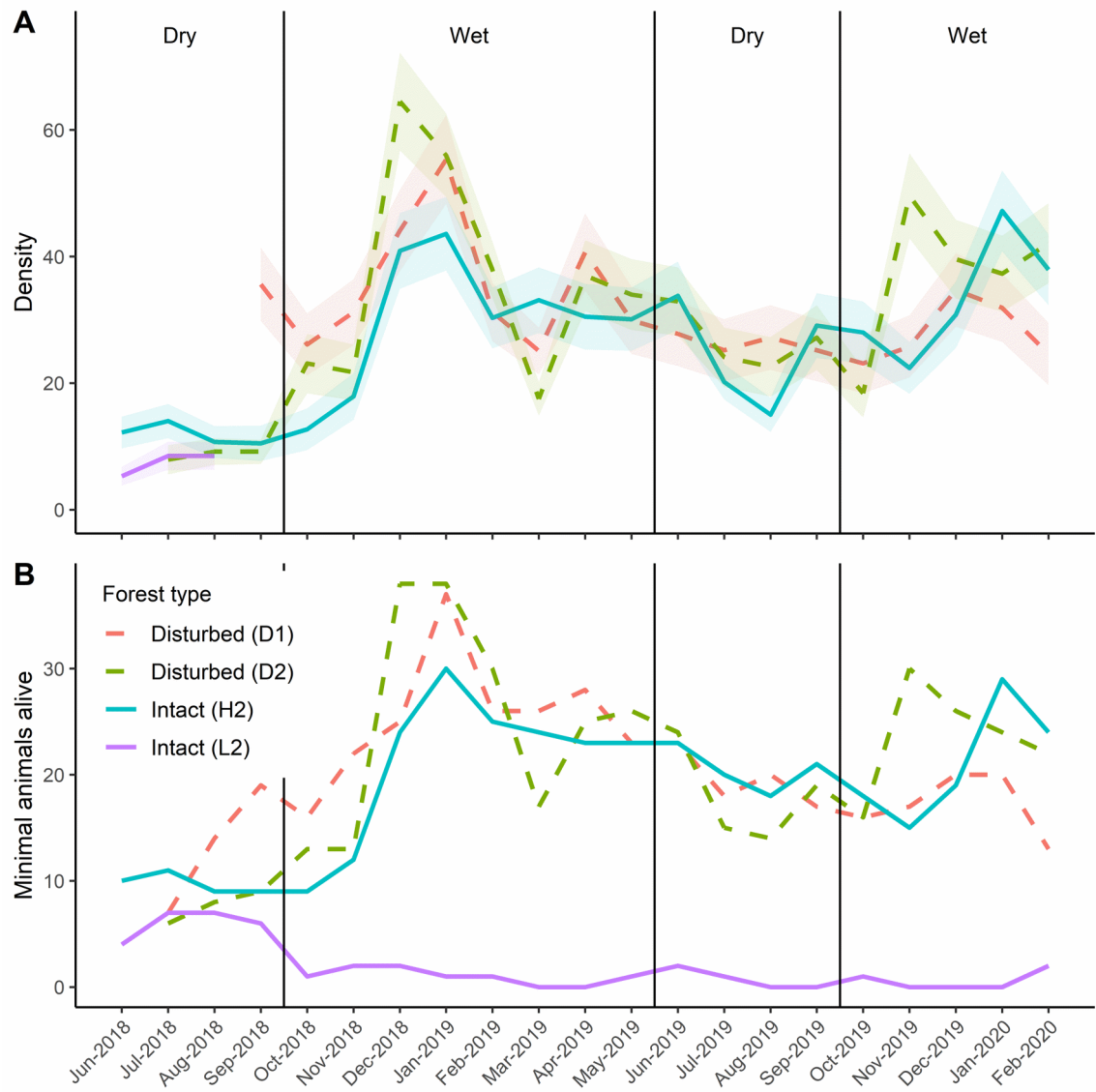


Figure 4.2: Population size of *Praomys delectorum* in both disturbed forests (dashed lines; field D1: red and D2: green) and intact forests (solid lines; field H2: blue and L2: purple) calculated using the two methods: (A) the M(h) jackknife estimator (B) the minimal number of animals alive.

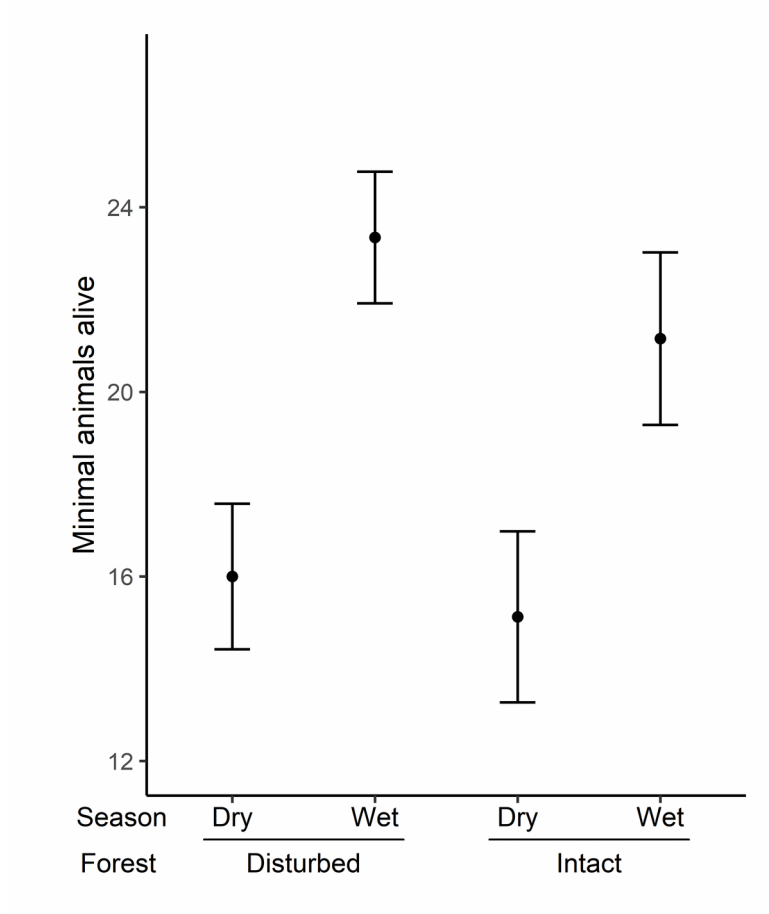


Figure 4.3: Predicted mean of the minimal number of animals alive for *Praomys delectorum* derived from the generalized linear mixed model during the dry and wet season within both the disturbed and intact forests with their standard errors.

Table 4.1: Modelling of survival and maturation. Highlighted models (bold) were selected in each step and used a starting point in subsequent steps. Models are ranked on the AICc from low to high.

Model	Survival	Maturation	Np	Deviance	AICc	Δ AICc
1) Survival						
<i>Seasonal effects</i>						
	F * (A + S)	i	32	5706.51	5770.51	0.00
	Season * [F * (A + S)]	i	38	5701.09	5777.09	6.58
	Season * year * [F * (A + S)]	i	50	5691.01	5791.01	20.50
<i>Reduction interactions</i>						
	F * S + A	i	31	5706.51	5768.51	0.00
	F * (A + S)	i	32	5706.51	5770.51	2.00
	F + S + A	i	30	5714.02	5774.02	5.50
	F * A + S	i	31	5713.69	5775.69	7.18
<i>Reduction: fixed effects</i>						
	F * S	i	30	5706.81	5766.81	0.00
	F * S + A	i	31	5706.51	5768.51	1.70
	i	i	27	5714.76	5768.76	1.95
	A	i	28	5714.36	5770.36	3.55
	F	i	28	5714.41	5770.41	3.59
	S	i	28	5714.76	5770.76	3.95
	F + A	i	29	5714.05	5772.05	5.24
	S + A	i	29	5714.35	5772.35	5.53
	F + S	i	29	5714.40	5772.40	5.59
2) Maturation						
	F * S	S	31	5704.20	5766.20	0.00
	F * S	i	30	5706.81	5766.81	0.61
	F * S	F	31	5705.27	5767.27	1.07
	F * S	F + S	32	5703.40	5767.40	1.20
	F * S	F * S	33	5701.44	5767.44	1.25

Note: for each model, the number of parameters (Np), deviance and AICc are given. Δ AICc is the difference in AICc between the respective model and the top ranked one. Each model was run with the same recapture probabilities. Abbreviations: S, sex (male or female); A, age (adult or juvenile); F, forest type (disturbed and intact forest); i, intercept; season (wet and dry season); season * year (dry season: June 2018 – September 2018, wet season: October 2018 – May 2019, dry season: June 2019 – September 2019, wet season: October 2019 – February 2020).

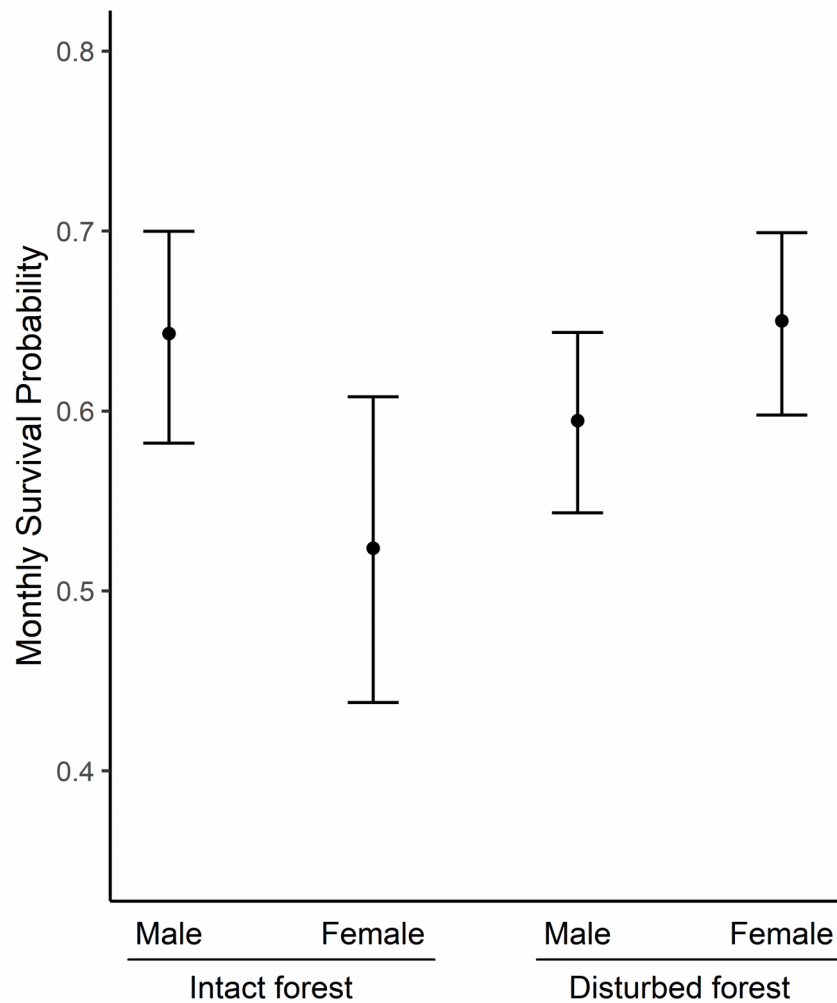


Figure 4.4: Monthly survival probability of male and female *Praomys delectorum* in disturbed and intact forests derived from the best fitted model. Females had an increased survival probability in disturbed forests compared to intact forests, while male had a similar survival probability in both forest types. Errors bars represent the 95% confidence interval

4.4 Discussion

Habitat disturbances due to anthropogenic activities have been found to affect survival and maturation of several vertebrate species (e.g. birds, rodents; Borges and Marini, 2010; Korfanta *et al.*, 2012; Cosset *et al.*, 2018), but this is the first study that looked at this effect on *P. delectorum*. We found that *P. delectorum* was the most dominant species in the Ukaguru Mountains in both disturbed and intact forests and that their density varied seasonally, being significantly greater during the wet season compared to the dry season. While forest disturbance had no effect on abundance or maturation, it did affect female survival, which was higher in disturbed forests compared to intact forests.

Praomys delectorum was the most dominant species in both disturbed and intact forests of the Ukaguru Mountains which is in line with other studies in montane forests in East Africa (Makundi *et al.*, 2006; Gitonga, 2007; Gitonga *et al.*, 2015, 2016a). However, the abundance of *P. delectorum* varied seasonally, with significantly higher densities during the wet season compared to the dry season which is similar to the findings of Makundi *et al.* (2006). This may suggest that *P. delectorum* exhibits a seasonal breeding pattern which starts at the beginning of the wet season (Happold, 2013). Indeed, rainfall has been shown to have a large effect on the timing of the breeding season in a wide variety of small mammals, since it affects the availability of food (Field, 1975; Leirs *et al.*, 1989; Taylor and Green, 1976) allowing the population to grow until food becomes more scarcely available at the beginning of the dry season leading to a decrease in the population size (Leirs *et al.*, 1994). The reason for the low captures in field L2 is not clear. We suspect that the noise generated from tree felling in an adjacent pine plantation using chain saws and skidding may have shifted the home range of populations in this field. This experience was only peculiar to L2. Indeed exposure of rodents to noise leads

to stress induction (Baldwin, 2007) and they may respond by fleeing farther away (Hawthorne *et al.*, 2011).

However, we found no differences in abundance between the disturbed and intact forests, which contradicts the general idea that members of the genus *Praomys* are more abundant in disturbed habitats than unperturbed habitats (Cassola, 2006; Monadjem *et al.*, 2015). Indeed, *P. delectorum* was reported to occur at higher densities in disturbed habitats compared to intact forests in Taita hills, Kenya (Gitonga *et al.*, 2015, 2016a). Potentially because these disturbed habitats are characterized by a lower predation risks (Lambert *et al.*, 2003) and a higher availability of food resources (Ochoa, 2000; Gitonga *et al.*, 2015, 2016a). It is currently unclear why our results deviate from this general assumption. A potential explanation is that using the minimal number of animals alive (MNA) as a proxy for density might have caused a bias in our data, since it does not take individual variation in capture probability into account (Pocock *et al.*, 2004). However, this explanation seems unlikely since the results from the MNA were similar to that from the M(h) jackknife estimator which takes variability in capture probabilities among individuals into account (Burnham and Overton, 1978). Alternatively, this may be the case of populations of the same species from different geographical regions responding differently to habitat disturbances (Frederiksen *et al.*, 2005).

Nevertheless, density alone is not sufficient to conclude on the viability of the populations in both disturbed and intact forests. Our models revealed a higher survival probability in disturbed forest, but only for females, while male survival remained similar between both forest types. This might result from differences in either predation pressure and/or resource availability between the two forest types which may act stronger on females than males. Small carnivores are probably the most important predators of *P. delectorum* and

selectively prey on females, since they are less mobile than males when pregnant or because of the scent and noises of their young reveal the location of their burrows (Happold, 2013; Korpimäki, 1985; Norrdahl and Korpimäki, 1998). However, the predation pressure on small mammals decreases in disturbed habitats since these predators are less abundant and diverse in anthropogenic disturbed habitats (Lambert *et al.*, 2003; Lambert *et al.*, 2006), potentially due to an increased mortality rate (Bonnet *et al.*, 1999), which may explain the higher survival rate of females in these habitats. However, more studies are required to show the impact of predators on this species in this landscape.

An alternative, non-mutually exclusive, explanation is variation in food availability between disturbed and intact forests. While food availability is vital for the survival of all rodents (Kennis *et al.*, 2012), females have been found to depend more heavily on food acquisition than males (Ostfeld, 1985). Survival of female Californian voles (*Microtus californicus*), for example, depended more heavily on the spatial and seasonal distribution on resources compared to males (Ostfeld, 1985). This may explain why female survival is higher in disturbed forests compared to intact forests, since food availability is considered to increase with habitat disturbance (Ochoa, 2000; Zhang *et al.*, 2009; Greenberg *et al.*, 2011). Indeed, forest disturbance has been found to alter plant communities (Hawthorne *et al.*, 2011) and to stimulate hoarding efforts by seed-caching rodents (Zhang *et al.*, 2009; Greenberg *et al.*, 2011).

While habitat disturbance affected survival, maturation remained similar between disturbed and intact forests. This may stem from the fact that food is continuously available in both habitat types. Both Leirs *et al.* (1997) and Sluydts *et al.* (2007) have shown that maturation rate in *M. natalensis* correlated positively with preceding

cumulative rainfall which triggered greater food availability. The finding of the current study is consistent with Mayamba *et al.* (2019) who reported that habitat did not affect maturation of *M. natalensis* in Uganda; the animals had continuous access to food resources and in no way was their normal growth and development impeded. Another best supported model showed maturation rate of females to be lower compared to males which may be due to response to pre- or post-natal stress or secretion of puberty-delaying pheromones in females (Oli and Dobson, 1999). However, longer trapping period is required to unravel which factors influence maturation rate in *P. delectorum*.

Population dynamics are driven by demographic parameters with some of these parameters acting on the population greatly than others (Oli and Dobson, 1999). In this study, whereas the population densities of *P. delectorum* varied seasonally, with significantly higher densities during the wet season compared to the dry season, survival and maturation rates were not seasonal in both forest types and therefore may not be the underlying demographic mechanisms responsible for such temporal changes in abundance. To account for the temporal variation in population density of *P. delectorum*, there is a need to investigate the effects of predation and other demographic parameters such as reproduction, recruitment and movement (dispersal). Populations of *P. delectorum* may be stable and viable in this landscape in spite of forest disturbances as indicated in the insignificant differences in population sizes between both forest types, and greater survival rate in disturbed forests. Also, this does not imply that forest disturbance should be left unchecked in this landscape as unperturbed forests are irreplaceable in the conservation of biodiversity (Gibson *et al.*, 2011). Though our findings suggest that forest disturbance affects the survival rate of *P. delectorum*, we recommend further long term studies in order to arrive at strong conclusions. The IUCN Least Concern conservation status of *P. delectorum* (Cassola, 2016) is uncertain given the

very frequent rates of anthropogenic disturbances in the EAM. Therefore, continuous demographic monitoring of *P. delectorum* in EAM is necessary given that human populations surrounding the landscape is increasing leading to deforestation, and expansion of the pine plantation in the forest reserve.

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Authors' contributions: OJA designed the study. OJA collected the data. OJA, BVB and HL conducted statistical analysis. LSM, AWM and RHM supervised the work. All authors contributed to writing and have given final approval for publication.

Data Accessibility Statement

We, the authors of this manuscript, have deposited the data used in the result section to public domain Dryad. <https://doi.org/10.5061/dryad.j6q573ncr>.

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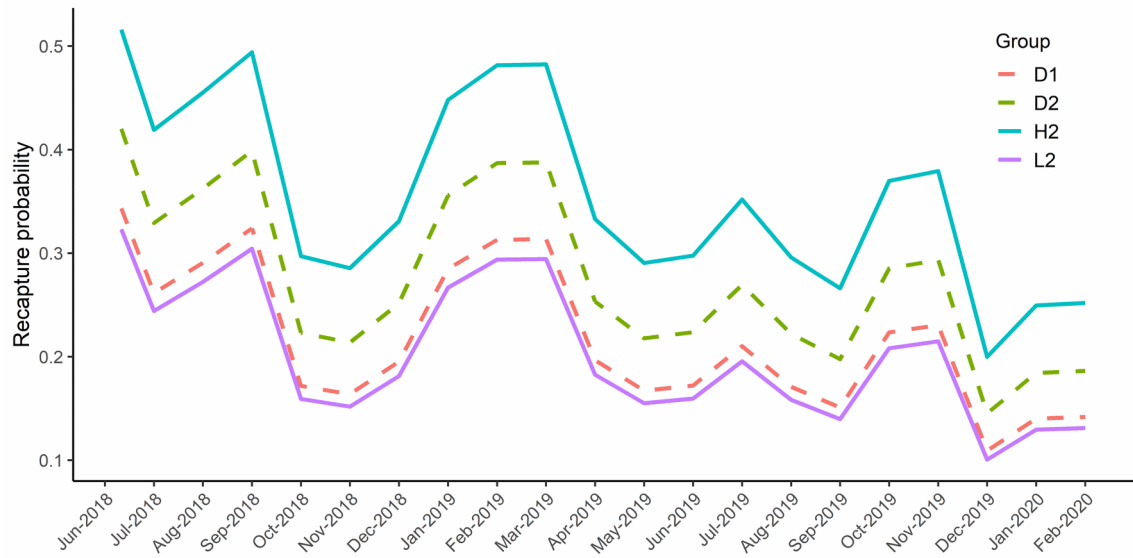
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Appendices

Appendix 4.1: Species composition of all captured small mammals in the disturbed (fields D1 and D2) and intact forest (fields H2 and L2). The total number of animals each species is given for each field.

Species	Disturbed forest		Intact forest	
	D1	D2	H2	L2
<i>Beamys hindei</i>	2	4	7	6
<i>Crocidura hirta</i>	0	2	8	4
<i>Grammomys surdaster</i>	0	1	0	0
<i>Graphiurus cf. raptor</i>	0	0	1	1
<i>Hylomyscus arcimontensis</i>	0	0	1	0
<i>Lemniscomys rosalia</i>	0	0	0	0
<i>Lophuromys kilonzoii</i>	1	1	8	17
<i>Mastomys natalensis</i>	0	1	0	0
<i>Mus minutoides</i>	0	0	0	0
<i>Mus triton</i>	10	18	1	0
<i>Pelomys fallax</i>	0	0	0	0
<i>Praomys delectorum</i>	195	214	190	25
<i>Xerus</i> sp.	1	0	0	0
Total	209	241	216	53

Appendix 4.2



Appendix 4.2: Recapture probabilities in both disturbed forests (dashed lines; field D1: red and D2: green) and intact forests (solid lines; field H2: blue and L2: purple) over the different sessions.

CHAPTER FIVE

DIETARY COMPOSITION AND NICHE OVERLAP OF RODENTS ACROSS DIFFERENT HABITATS IN THE UKAGURU MOUNTAINS, TANZANIA.

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DIETARY COMPOSITION AND NICHE OVERLAP OF RODENTS ACROSS DIFFERENT HABITATS IN THE UKAGURU MOUNTAINS, TANZANIA.

Abstract

This study aimed at investigating the dietary composition of rodents in the Ukaguru Mountains, Tanzania. Micro-histological analysis of the stomach contents of rodents collected from various habitats was carried out. In the diet of *Mastomys natalensis*, *Lemniscomys rosalia* and *Mus triton*, seed/grain showed greater importance (> 35, > 55 and 60% respectively) whereas for *Lophuromys kilonzo*i, plant materials were more important (> 55%) than other categories. Seed/grains were more important (> 20%) in the diet *Praomys delectorum*, while plant materials were more important (> 45%) in the diet of forest-dwelling *L. kilonzo*i. Food diversity for rodents in farmland was relatively low compared to forest dwelling rodents. Niche overlap between *L. kilonzo*i and *P. delectorum* was found to be relatively high. The seed food category recorded in *P. delectorum* (the dominant forest species) may be an indication that this species is vital in dispersal and regenerating the forest though the seeds as well could have been from herbaceous vegetation. Given the interspersed nature of the forests with farmlands and their proximity, this may favour the establishment of farm generalists in the forests.

Keywords: Rodents, diet, niche breadth, niche overlap, Eastern Arc Mountains.

5.1 Introduction

In response to limiting environmental resources, coexisting animals vary their times of activity, space use and/or foods eaten (Pianka, 1973); for example, in rodents, resource partitioning has been attributed to variation in diet, habitat and microhabitat preferences (Iwuala *et al.*, 1980; Pinotti *et al.*, 2011). Consequently, ecologists often pay attention to understanding the differential use of environmental resources by sympatric animal species (Schoener, 1974). Empirical evidence has shown that resource-niche partitioning is both vital to achieving greater biodiversity and adequate resource use in multispecies communities (Finke and Snyder, 2008). However, understanding the mechanisms promoting species biodiversity requires defining species coexistence (Sato *et al.*, 2018). Diet assessment can provide insights into mechanism of coexistence even among rodents (Sato *et al.*, 2018). Adequate information on the diet requirement of species is vital for gaining understanding of their natural history, potential competitive associations, impact of their foraging habits on community structure and breeding and management (Delany, 1971, 1972; Taylor and Green, 1976; Iwuala *et al.*, 1980; Litvaitis, 2000). By preying on seeds, tropical rodents are agents of seed dispersal significantly contributing to seedling recruitment in forest ecosystems (Brewer and Rejmánek, 1999). Thus, ecological studies on rodent diets are vital in forest management.

There is inadequate knowledge of the ecology of rodents in sub-Saharan Africa even for abundant taxa (Bryja *et al.*, 2019); this is particularly obvious when information is sought with regards to diet ecology in rodents. Most of the studies on diets of rodents in sub-Saharan Africa have focused on the pestiferous species that are of economic impact such as *Mastomys natalensis* (Mlyashimbi *et al.*, 2018; Mulungu *et al.*, 2011a, 2011b; Oguge, 1995) while information on diets of other species are scarce despite the role they play in ecosystems. Previously, the diet of the Natal multimammate mouse, *M. natalensis*, and

Gerbilliscus vicinus from fallow habitats in Central Tanzania has been reported (Mulungu *et al.*, 2011b). The authors showed that grain and vegetative materials were the most preferred food categories for these rodent species in different magnitude and making them coexist.

Studies on diet ecology of rodents dwelling in forest/forests interspersed with farms are sparse in East Africa. Anthropogenic disturbances such as tree felling have been shown to affect the diet of rodents. For example, in disturbed forest habitats, an alteration in feeding habits of *Praomys delectorum* has been reported (Gitonga *et al.*, 2015). Also, the rats *Leopoldamys sabanus* and *Maxomys rajah* significantly defecated more seeds in logged forests compared to those from unlogged (Wells *et al.*, 2009). *Lophuromys flavopunctatus* from Mount Elgon, Uganda at elevations up to 4200 m a.s.l. had a diet rich in invertebrates possibly due to the occurrence of the species in habitats and niches which may not support rodents (Clausnitzer *et al.*, 2003). *Lophuromys sikapusi* caught in disturbed vegetation was found to be majorly insectivorous though vegetable materials were present in their diets as well (Cole, 1975).

The Eastern Arc Mountains (EAM) are one of the top 25 biodiversity “hotspots” worldwide containing endemic animals and plants (Burgess *et al.*, 1998). Small mammal survey in June, 2018 in one of the EAM block, the Ukaguru Mountains, revealed *P. delectorum*, *Mastomys natalensis* and *Mus triton* as dominant species (Ademola, O. J., personal observation). Other species encountered include *Lophuromys kilonzoi* and *Lemniscomys rosalia*. Diets of these rodents have not been previously investigated in this landscape. The Ukaguru Mountains are under the threat of anthropogenic activities which impact on the diversity, ecology and the feeding/diets of the fauna species including rodents. The forest reserves are interspersed with farmlands (Gwegime *et al.*, 2014).

With the ability of rodents to vary their diets with habitats (Iwuala *et al.*, 1980), it is necessary to study their diet in the Ukaguru Mountains. Therefore, this study aimed at investigating the dietary composition and niche overlap of rodents in the Ukaguru Mountains, Tanzania. Within this study we addressed the following questions: a) Do the rodent species differ in diet item contribution across the habitats? b) Do rodent species within the same habitat show dietary niche overlap? The information generated from this study will be valuable in the conservation of forests of this landscape.

5.2 Materials and Methods

5.2.1 Study area

This study was carried out in the Ukaguru Mountains, located in Gairo District, Morogoro, Tanzania (36° 57'00'' - 38° 00' 00'' East and 06° 25' 00'' - 06° 57' 00'' South; Fig. 5.1). The elevation of this landscape extends up to 2 250 m above sea level. The estimated annual rainfall is 1 400 mm (Gwegime *et al.*, 2014). The dry season is between June and September, with maximum temperatures of 21°C recorded in January and minimum temperatures of 17°C in July at lower altitudes (Gwegime *et al.*, 2014).

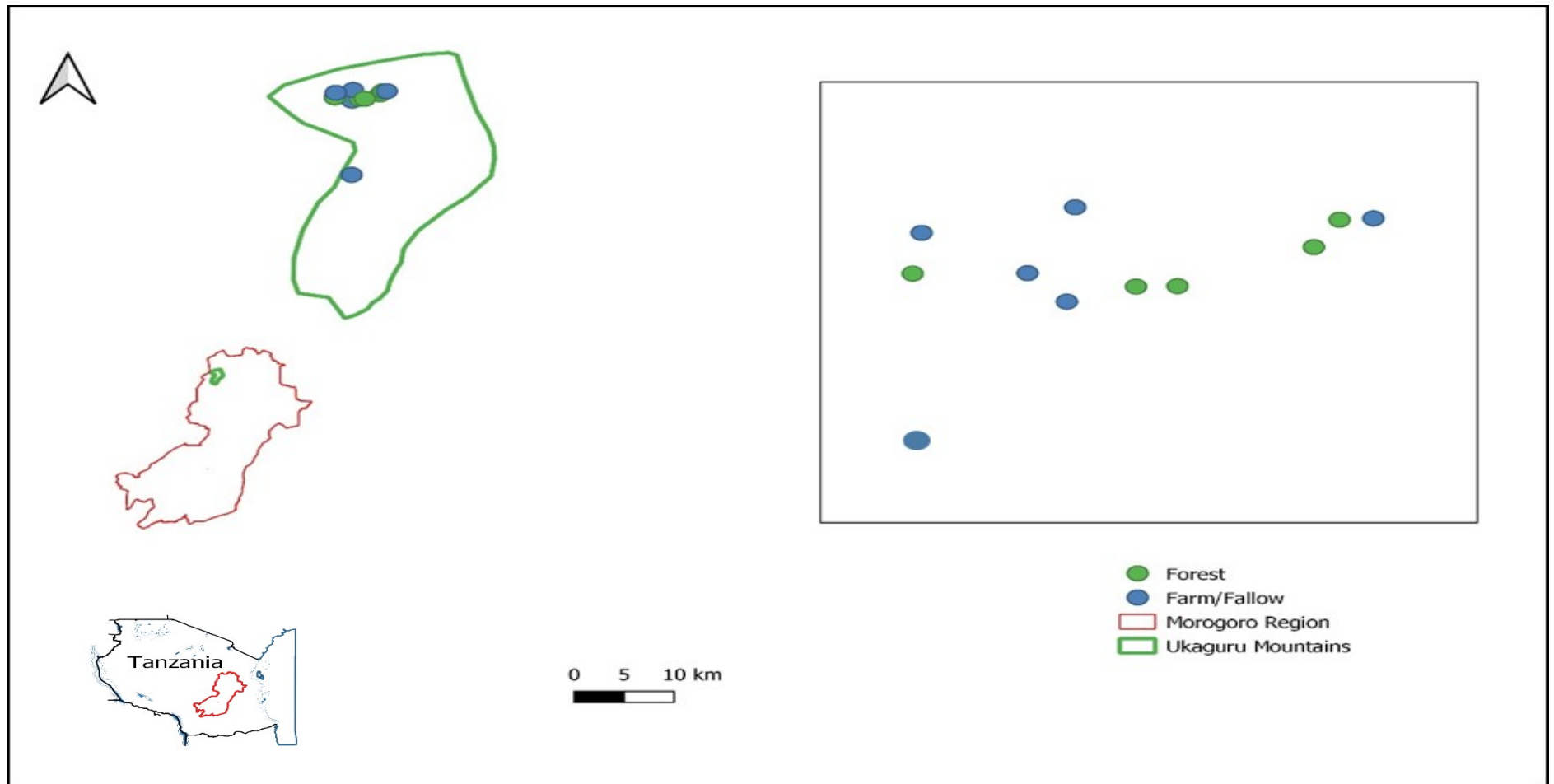


Figure 5.1: A sketch of the study area and trapping transects (not to scale)

Generally, the vegetation type is montane and sub-montane forest. The montane forest is mainly characterised by the following tree species: *Polyscias fulva*, *Schefflera lukwangulensis*, *Garcinia volkensii*, *Ocotea usambarensis* and *Cussonia spicata*. Others are *Dombeya burgessiae*, *Clerodendrum* sp., *Macaranga capensis* and *Albizia gummifera*. The sub-montane forest is characterized by *Myrianthus holstii*, *Albizia gummifera*, *Allanblackia stuhlmannii* and *Bersama abyssinica*. High forest disturbances observed include tree cutting, clearance of forest for agriculture and grazing (Gwegime *et al.*, 2014). The human population surrounding the forest is at least 75 720 people (Gwegime *et al.*, 2014) and land outside the forest reserves is generally farmland. Crops commonly cultivated include: pumpkin (*Cucurbita maxima*), banana (*Musa* spp), maize (*Zea mays*), Irish potatoes (*Solanum tuberosum*), common pea (*Pisum sativum*), beans (*Phaseolus lunatus*) and cedar (*Cedrela odorata*).

5.2.2 Trapping

Removal trapping technique was used in the survey for rodents from September, 2018 to September, 2019 and May, 2020. Sampling was carried out in the Mamiwa-Kisara North Forest Reserve and adjoining farm/fallow lands of Masenge village in the Ukaguru Mountains, Tanzania. Ten transect lines were set separately in forests and farm/fallow lands with fifty snap traps in each habitat spaced 10 m apart. Trapping of rodents was conducted for three consecutive nights per month at interval of about 4 weeks and traps were baited with peanut butter mixed with maize bran and inspected in the morning. Captured animals were identified to species levels using relevant keys (Happold, 2013; Kingdon, 1997; Monadjem *et al.*, 2015).

5.2.3 Micro-histological analysis of the stomach

Intact stomachs of individuals from the kill traps were removed and preserved in 70% alcohol for food category analysis. Subsequently, stomachs were cut open, spread out in Petri dish and sorted out using a stereomicroscope. Stomach contents were identified as seeds, fruits, plant materials (pods, roots, stems and leaves), invertebrates, animal hairs and unidentified matter (Smith *et al.*, 2002). Also, the presence of starch indicative of seeds/grains was determined by using a Lugol's iodine solution.

5.2.4 Diet analysis

Diet analysis followed the method of Smith *et al.* (2002). The following parameters were determined: Percentage contribution (PC) – proportion of each food item in the volume of the particular stomach's contents estimated to the nearest 10 %, with an additional category of 5 % where the item was present but contributed less than 10 % to stomach-content volume; percentage of stomach (PS) otherwise referred to as percentage occurrence – the number of stomachs a food category occurred out of the entire stomachs examined. Diet diversity was calculated, following Ebersole and Wilson (1980), as Levins' index (Levins, 1968) as

$$1/\sum P_i^2,$$

where, P (=PC/100) is the proportion of each diet category. Levins' index ranges from 1 to n (n = total number of food categories) and was used to calculate diversity indices of the rodents. Diversity was standardized to a scale of 0.0 to 1.0 by using Hurlbert's method (Krebs, 1989).

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

where, B_s is Levins's standardized niche breadth,

B is Levins's measure of niche breadth, and n is the number of possible resource states.

An importance value was also calculated for each diet item (Cooper and Skinner, 1978) using the formula:

$$IV = PC \times PS / 100$$

where, IV is the importance value

PC is the percentage contribution

PS is the percentage of stomach

Relative importance value of a particular item was taken as the importance value of that item expressed as a percentage of the sum of the importance values for all items ($100 \times IV / \sum IV$).

Niche overlap measure was computed using the following symmetric formula:

$$O_{jk} = \frac{\sum_i^n P_{ij} P_{ik}}{\sqrt{\sum_i^n P_{ij}^2 \sum_i^n P_{ik}^2}} \quad (\text{Pianka, 1973, 1974}),$$

where, O_{jk} = Pianka's measure of niche overlap between species j and k , P_{ij} and P_{ik} = are proportions of the i th resource used by the j th and k th species, respectively. Overlap values obtained from this equation vary from zero (no overlap) to one (total overlap).

Statistical analysis was carried on percentage of stomach (occurrence) in each site; however, for a species trapped in different habitats, this was analysed across sites. The statistical analysis was restricted to seed/grains, plant materials in both sites, (though invertebrates was included in forest) due to the zero/low occurrence of other food categories. Normality of the dataset was determined by carrying out Kolmogorov-Smirnov (K-S) test (see Appendices 5.1 and 5.2). Angular transformation was carried in

cases where the K-S test was significant ($p < 0.05$). One-way analysis of variance (ANOVA) was carried for species in farm/fallow while t-test was used for species from forest. In addition, Mann-Whitney test was used for seed category in the forest as the Levene's test for equality of variances was significant, $p < 0.05$. The analysis was carried out using IBM SPSS Statistics for Windows, Version 21.

5.2.5 Ethical considerations

The research clearance for this study was granted by the Sokoine University of Agriculture (SUA), Tanzania (reference: SUA/DPRTC/PFC/D/2017/0010/11) and Tanzania Forest Service Agency (TFS).

5.3 Results

Micro-histological analysis was carried out on stomach contents of 81 individuals of five rodent species: *P. delectorum* (22), *Mastomys natalensis* (18), *Mus triton* (15), *Lemniscomys rosalia* (8) and *Lophuromys kilonzoi* (9 each from forest and farm/fallow land).

5.3.1 Percentage of stomach (occurrence)

Seeds/grains and plant materials predominated ($> 70\%$ of the stomachs) in the diet of *M. natalensis*, *Lemniscomys rosalia* and *M. triton* while invertebrates occurred less frequently ($< 30\%$; Table 5.1). Plant materials predominated in the diet of *Lophuromys kilonzoi* while other food categories were present in $< 50\%$ of the stomachs (Table 5.1). For forest-dwelling rodents, seeds/grains and plant materials predominated ($> 70\%$ of the stomachs) in the diet of *P. delectorum* followed by invertebrates (ca. 60% of the stomachs), while plant materials and invertebrates were most prevalent in individuals of *Lophuromys kilonzoi* ($> 75\%$ of the stomachs; Table 5.1). Analysis of variance showed

that the percentage occurrence of seed/grains and plant materials in stomachs of rodents captured in farm/fallow land was significantly different (seed/grain: $F_{3,46} = 3.92$, $p = 0.01$; plant materials: $F_{3,46} = 4.19$, $p = 0.01$). The Least Significant Difference (LSD) post hoc test showed that the food categories were not significantly different between any of *Mus triton*, *Mastomys natalensis* and *Lemniscomys rosalia* ($p > 0.05$) while only *Lophuromys kilonzo*i consumed significantly higher amount of plant materials and significantly lower amount of seed/grains compared to other species in the same habitat ($p < 0.05$, Appendix 5.3). Significant differences were observed between *P. delectorum* and *Lophuromys kilonzo*i on seed and plant materials occurrence (seed/grain: Mann-Whitney $U = 47.50$, $p = 0.02$; plant materials: $t = -2.663$, $df = 29$, $p = 0.01$) while percentage occurrence of invertebrates was not significantly different between these two species ($t = 0.47$, $df = 29$, $p = 0.64$). *Lophuromys kilonzo*i across sites did not show any significant difference in any of the food categories (seed/grain: $t = -0.81$, $df = 16$, $p = 0.43$; plant materials: $t = -0.62$, $df = 16$, $p = 0.55$; invertebrate: $t = 0.70$, $df = 16$, $p = 0.49$).

5.3.2 Percentage contribution

From the farm/fallow land settings, seed/grain dominated the stomach contents of *Mastomys natalensis*, *Lemniscomys rosalia* and *Mus triton* followed by plant materials whereas this only contributed about 60% in the diet of *Lophuromys kilonzo*i (Table 5.2). In all species, invertebrates contributed less than 5% (Table 5.2). In *P. delectorum*, seed/grain dominated (about 25%) followed by plant materials while the latter dominated the stomach contents of forest-dwelling *Lophuromys kilonzo*i with fruits, hairs, invertebrates and seed/grain proportionally contributing less (Table 5.2).

5.3.3 Relative importance

In the diet of *Mastomys natalensis*, *Lemniscomys rosalia* and *Mus triton*, seed/grain showed greater importance (> 35, > 55 and 60% respectively) whereas for *Lophuromys kilonzoi* (farm), plant material was important (> 55%) (Table 5.3). Seed/grains were more important (> 20%) in the diet *P. delectorum*, while plant materials were more important (> 45%) in the diet of forest-dwelling *Lophuromys kilonzoi* (Table 5.3). Other food categories were present but had less than 10% RI values in all habitats.

5.3.4 Niche breadth and niche overlap

Food diversity for rodents in farm/fallow land was relatively low compared to forest dwelling rodents (Table 5.3). *Lemniscomys rosalia* showed the lowest food diversity while *Lophuromys kilonzoi* caught in farmland had relatively high food diversity (Table 5.3). Food diversity of forest dwelling *Lophuromys kilonzoi* was relatively higher than *P. delectorum* in the same habitat. Niche overlap was lowest between *Lemniscomys rosalia* and *Lophuromys kilonzoi* (0.39) and highest between *M. triton* and *Lemniscomys rosalia* (Table 5.4). Niche overlap between the forest dwelling species was relatively high (Table 5.4).

Table 5.1: Percentage of stomachs with different food types of rodents in the Ukaguru Mountains, Tanzania

	<i>Mastomys natalensis</i> Farm/fallow (n=18)	<i>Mus triton</i> Farm/fallow (n=15)	<i>Lemniscomys rosalia</i> Farm/fallow (n=8)	<i>Lophuromys kilonzoi</i> Farm/fallow (n=9)	<i>Lophuromys kilonzoi</i> Forest (n=9)	<i>Praomys delectorum</i> Forest (n=22)
Seed/Grain	77.78	86.67	87.50	33.33	22.22	72.73
Plant materials	88.89	73.33	75.00	100.00	100.00	72.73
Invertebrates	16.67	26.67	12.50	44.44	77.78	59.10
Hairs	0.00	6.67	0.00	0.00	44.44	18.19
Fruits	0.00	6.67	0.00	33.33	33.33	4.55
Others	100.00	86.67	100.00	88.89	100.00	100.00

n – number of individuals

Table 5.2: Percentage of food types in the diets of rodents in the Ukaguru Mountains, Tanzania

	<i>Mastomys natalensis</i> Farm/fallow (n=18)	<i>Mus triton</i> Farm/fallow (n=15)	<i>Lemniscomys rosalia</i> Farm/fallow (n=8)	<i>Lophuromys kilonzoi</i> Farmfallow (n=9)	<i>Lophuromys kilonzoi</i> Forest (n=9)	<i>Praomys delectorum</i> Forest (n=22)
Seed/Grain	43.33	53.67	60.63	15.56	6.11	25.91
Plant materials	22.78	19.33	14.38	43.89	37.22	19.32
Invertebrates	3.06	3.33	0.63	5.56	8.33	10.23
Hairs	0.00	0.67	0.00	0.00	8.89	1.82
Fruits	0.00	2.33	0.00	15.56	11.11	2.05
Others	30.83	20.67	24.38	19.44	28.33	40.68

n – number of individuals

Table 5.3: Relative importance of food types in the diets and niche breadth of rodents in the Ukaguru Mountains, Tanzania

	<i>Mastomys natalensis</i> Farm/fallow (n=18)	<i>Mus triton</i> Farm/fallow (n=15)	<i>Lemniscomys rosalia</i> Farm/fallow (n=8)	<i>Lophuromys kilonzoi</i> Farm/fallow (n=9)	<i>Lophuromys kilonzoi</i> Forest (n=9)	<i>Praomys delectorum</i> Forest (n=22)
Seed/Grain	39.52	58.37	60.09	7.01	1.68	23.54
Plant materials	23.74	17.79	12.21	59.30	45.93	17.55
Invertebrates	0.60	1.12	0.09	3.34	8.00	7.55
Hairs	0.00	0.06	0.00	0.00	4.87	0.41
Fruits	0.00	0.20	0.00	7.01	4.57	0.12
Others	36.15	22.48	27.61	23.35	34.96	50.83
Niche breadth	0.40	0.34	0.25	0.51	0.60	0.51

n – number of individuals

Table 5.4: Niche overlap for dietary partitioning between rodents in the Ukaguru Mountains, Tanzania

	<i>Mastomys natalensis</i> (Farm/fallow)	<i>Mus triton</i> (Farm/fallow)	<i>Lemniscomys rosalia</i> (Farm/fallow)	<i>Lophuromys kilonzoi</i> (Farm/fallow)	<i>Lophuromys kilonzoi</i> (Forest)	<i>Praomys delectorum</i> (Forest)
<i>Mastomys natalensis</i> (Farm/fallow)	-	0.97	0.96	0.74	X	X
<i>Mus triton</i> (Farm/fallow)	0.97	-	0.99	0.66	X	X
<i>Lemniscomys rosalia</i> (Farm/fallow)	0.96	0.99	-	0.39	X	X
<i>Lophuromys kilonzoi</i> (Farm/fallow)	0.74	0.66	0.39	-	X	X
<i>Lophuromys kilonzoi</i> (Forest)	X	X	X	X	-	0.81
<i>Praomys delectorum</i> (Forest)	X	X	X	X	0.81	-

Niche overlap: 0 (no overlap) to 1 (total overlap); X (no interaction between species from different habitats).

5.4 Discussion

These results show that *Mastomys natalensis*, *Lemniscomys rosalia*, *Mus triton* and *P. delectorum* majorly consumed seeds/grains and plant materials though they also consumed other food categories. Also, plant materials were most important in the diet of *Lophuromys kilonzo*i irrespective of habitat though those individuals caught in the forests showed greater food diversity. Rodents from farm/fallow land showed relatively low niche breadth compared to those caught in forests. While niche overlap between the forest-dwelling species was relatively high, it was lowest between *Lemniscomys rosalia* and *Lophuromys kilonzo*i, and highest between *M. triton* and *L. rosalia*.

In the current study, results from the stomach contents of all rodents investigated collaborate previous findings that the rodents are omnivores (Hanney, 1965; Iwuala *et al.*, 1980; Monadjem, 1997; Clausnitzer *et al.*, 2003; Odhiambo *et al.*, 2008; Mulungu *et al.*, 2011a; Happold, 2013; Gitonga *et al.*, 2015). The dominant contribution of seed/grains in the diet of rodent species caught in agricultural settings maybe an indication of their pest status and opportunistic tendency (Odhiambo *et al.*, 2008).

Furthermore, our results show the predominance of grain in the diet of *M. natalensis* with plant materials and invertebrates also occurring in the stomach. Similar results were obtained for *M. natalensis* where seeds were found to be the primary food item in grassland (Oguge, 1995) and fallow land habitats (Mulungu *et al.*, 2011a; Mulungu *et al.*, 2014). This species has been shown to feed on seeds and insects throughout the year and utilizing plant materials when seeds/grains become scarce (Taylor and Green, 1976; Mlyashimbi *et al.*, 2018). The significance of seeds/grain in the diet of *M. natalensis* over other diet categories was suggested to be due to its greater preference and search efforts for seeds (Rabiu and Rose, 1997). It has also been reported that

M. natalensis preferred most maize seeds depending on availability (Odhiambo *et al.*, 2008). Recently, Mulungu *et al.* (2014) and Mlyashimbi *et al.* (2018) confirmed the dominance of seeds and leaves/stems in the diet of *M. natalensis* in irrigated rice agro-ecosystems and semi-arid areas in Tanzania respectively. *Mastomys natalensis* has been reported to feed on the skin and muscle of other vertebrates such as frogs and rodents (Taylor and Green, 1976; Odhiambo *et al.*, 2008). Evidence of vertebrate occurring in diet of *M. natalensis* was lacking from this study.

Seed was the major component of the diet of *L. rosalia* with other plant materials and invertebrates occurring in small quantities. Elsewhere, in a grassland community *L. rosalia* fed on plant materials throughout the year with insects being eaten most during wet months (Field, 1975). It has also been reported that *Lemniscomys barbarous* from agricultural areas in Ethiopia feed majorly on leaves (Gadisa and Hundera, 2015). In the current study, *M. triton*, being an omnivore, consumed all food categories but seeds/grain formed the bulk of the diet. The current findings are similar to those reported by Ogue (1995) on the food categories of *M. triton* in Kenya.

This study found that most of the rodents consumed seed/grains and plant materials. Agricultural habitats provide green grasses and seeds which support the prolific breeding and growth of rodents (Mlyashimbi *et al.*, 2018). Therefore, it is not surprising that seeds/grains and plant materials formed the bulk of the diet of rodents caught in these areas. Seeds and plant materials have been shown to be vital for rodents to breed. For example, seed availability triggered breeding in *Mus musculus* (Bomford, 1987a, 1987b). *Arvicanthis* spp and *M. natalensis* were found to commence breeding when the main item of diet was often cereals with the former switching diet with the cessation of breeding (Taylor and Green, 1976). Recently, the proportion of vegetative materials in the diet of

M. natalensis was shown to be positively correlated with its breeding (Mlyashimbi *et al.*, 2018).

The relatively low niche breadth observed for species found in farm habitats in this study could be attributed to the major contribution of seed/grains to their diet (Mulungu *et al.*, 2011a) as agricultural habitats are less heterogeneous (Gadisa and Hundera, 2015) and unstable, characterized by cyclic periods of ploughing, planting and harvesting (Taylor and Green, 1976). This might as well explain why *M. natalensis* overlapped greatly with *M. triton* and *L. rosalia* in its food items. The relatively low overlap in food niche between *Lemniscomys rosalia* and *Lophuromys kilonzoï* may be due to the proportion of seed/grain and plant material consumed; plant materials were more important for *Lophuromys kilonzoï* while seeds were important for *Lemniscomys rosalia*.

The presence of hairs in the diet of some species from this study might have arisen from grooming (Shiels *et al.*, 2013) or occasional cannibalism of individuals from the same species. *Lophuromys flavopunctatus* was reported to feed on remains of other snap-trapped mammals (Clausnitzer *et al.*, 2003) and frogs or toads (Hanney, 1964). From this study, plant materials were more important in the diet of *L. kilonzoï* from both forest and farmland. Studies on the diet ecology of *L. kilonzoï* are scarce except for other members of the same genus. Clausnitzer *et al.* (2003) reported that invertebrates contributed most (63%) to the diet of *L. flavopunctatus* from Mount Elgon, Uganda. They accounted for a diet rich in invertebrates to be as a result of the occurrence of the species in habitats and niches which may not support rodents generally. In addition, *Lophuromys sikapusi* caught in disturbed vegetation was found to be majorly insectivorous though vegetable materials were present in their diets as well (Cole, 1975). In a similar study, 81% insect occurrence was reported in stomachs of *Lophuromys* spp from Malawi (Hanney, 1964). Invertebrates

are good sources of dietary protein to rodents which are necessary for maintenance of growth and reproduction in varying quantities (Field, 1975). This food category has been reported to be essential for the survival of *Lophuromys* spp as they failed to survive beyond one week in captivity unless fed with insects, worms or frogs (Hanney, 1964). The quality and quantity of food consumed by rodents may vary with availability and habitats (Field, 1975; Gitonga *et al.*, 2015). This was obvious in the food categories consumed by *L. kilonzo*i occurring in forest in contrast to those caught in farms.

Dietary information on *P. delectorum* is scarce while this species forages on the ground in leaf litter (Happold, 2013). *Praomys delectorum* samples collected in this study showed a dominance of seeds/grains in their diet with other plant materials, fruits and invertebrates occurring in small quantities. A predominance of vegetable materials with occurrence of insects was reported in *P. delectorum* from Malawi (Hanney, 1965). Similarly, studies in lowland forests in Ghana revealed that *Praomys tullbergi* and *Praomys stella* (members of the same genus) were mainly vegetarian with stomachs containing small quantities of insects (Cole, 1975).

Of the forest-dwelling rodents investigated in the Ukaguru Mountains, *P. delectorum* consumed relatively high proportion of seed compared to *L. kilonzo*i that depended majorly on plant materials in its diet. The bulk of seeds in the diet of *P. delectorum* (the dominant forest species) may be an indication that this species is vital in dispersal and regenerating the forest though the seeds as well could have been from herbaceous vegetation. Notwithstanding, small mammals have been shown to contribute to seed consumption in South East Asian forests and vital in seed dispersal (Wells *et al.*, 2009). In comparing *L. kilonzo*i caught from both forest and agricultural habitats, those from the forests showed greater food diversity as they fed on all food categories. Niche overlap

between *P. delectorum* and *L. kilonzo* was relatively high. While noting that both *P. delectorum* and *L. kilonzo* are both nocturnal and terrestrial, though the former sometimes climb trees, the relatively high overlap in utilization of food resources may not be indicative of competition but rather reflective of the heterogeneous nature of their habitat. The forest presents a heterogeneous environment with abundance and variety of foods for rodents. This scenario coupled with different foraging habits of *P. delectorum* and *L. kilonzo* permit coexistence of both.

Studies on diet ecology of rodents dwelling in forest/forests interspersed with farms are sparse in East Africa. The methodology employed in the stomach analysis has been successfully used to characterize food categories of rodents elsewhere (Mulungu *et al.*, 2011a, 2011b, 2014; Mlyashimbi *et al.*, 2018) though our sample size was small. Trapping efforts were geared towards capturing at least 10 individuals monthly for each of the five rodent species but was not possible. Generally in the tropics, obtaining ample sample size within fixed period is a major challenge in studying diet ecology of small mammals (Shadbolt, 2010). This study is not totally absolved from this difficulty which limited seasonal comparison of the diets of the rodents.

In conclusion, farm and forest dwelling rodents in the Ukaguru Mountains, Tanzania were found to be omnivores. Our results indicated that the relatively low niche breadth observed in rodents caught in farms could be attributed to the major contribution of seed/grains to their diet while forest dwelling rodents showed greater food diversity owing to the more heterogeneous and stable nature of forests compared to farms. The abundance of food resources in both habitats would have permitted coexistence of rodent species though they overlapped in utilization of food resources. Given the interspersion of the forests with farms and their proximity, this may favour the establishment of opportunistic

farm generalists in forests adjoining farms especially when foods become less abundant during the off farming seasons. However, our data did not permit analysis of seasonal variation of food categories; we therefore recommend further studies on effects of seasons on the diets of rodents of the Ukaguru Mountains, Tanzania.

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Data Availability Statement

Data sharing is not applicable to this article as the findings of the stomach contents analyzed are available within the article.

Conflict-of-interest: The authors declare that they have no conflict of interest.

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Appendix 5.2: Kolmogorov-Smirnov test for Normality for percentage food contributions of all species

		Farm/fallow Species		Forest Species	
		Seed/Grain	Plant materials	Seed/Grain	Plant materials
N		50	50	31	31
Normal Parameters	Mean	44.2000	24.2000	20.1613	24.5161
	Std. Deviation	33.04851	21.02865	24.64697	18.63486
Most Extreme Differences	Absolute	0.169	0.150	0.213	0.137
	Positive	0.169	0.150	0.213	0.137
	Negative	-0.144	-0.125	-0.207	-0.132
Kolmogorov-Smirnov Z		1.198	1.062	1.184	0.762
Asymp. Sig. (2-tailed)		0.113	0.209	0.121	0.607

N – number; Std. – standard; Asymp. Sig. – Asymptotic significance

APPENDICES**Appendix 5.1:** Kolmogorov-Smirnov test for *Lophuromys kilonzo*i across sites

		Seed/Grain	Plant materials	Invertebrates
N		18	18	18
Normal Parameters	Mean	10.8333	40.5556	6.9444
	Std. Deviation	21.57409	22.54987	8.24958
Most Extreme Differences	Absolute	0.414	0.144	0.204
	Positive	0.414	0.144	0.204
	Negative	-0.308	-0.088	-0.200
Kolmogorov-Smirnov Z		1.758	0.611	0.867
Asymp. Sig. (2-tailed)		0.004	0.849	0.440

N – number; Std. – standard; Asymp. Sig. – Asymptotic significance

Appendix 5.3: Least significant differences (LSD) post hoc results for the food percentage contributions

Dependent Variable			Mean Difference (I- J)	Std. Error	Sig.	95% Confid Lower Bound
Seed/Grain	MN	LM	-17.29167	12.93362	0.188	-43.3257
		MT	-10.33333	10.64118	0.337	-31.7529
		LK	27.77778*	12.42622	0.030	2.7651
	LM	MN	17.29167	12.93362	0.188	-8.7424
		MT	6.95833	13.32564	0.604	-19.8648
		LK	45.06944*	14.79016	0.004	15.2984
	MT	MN	10.33333	10.64118	0.337	-11.0863
		LM	-6.95833	13.32564	0.604	-33.7815
		LK	38.11111*	12.83375	0.005	12.2781
	LK	MN	-27.77778*	12.42622	0.030	-52.7905
		LM	-45.06944*	14.79016	0.004	-74.8405
		MT	-38.11111*	12.83375	0.005	-63.9441
Plant materials	MN	LM	8.40278	8.17232	0.309	-8.0472
		MT	3.44444	6.72380	0.611	-10.0899
		LK	-21.11111*	7.85171	0.010	-36.9158
	LM	MN	-8.40278	8.17232	0.309	-24.8528
		MT	-4.95833	8.42002	0.559	-21.9070
		LK	-29.51389*	9.34540	0.003	-48.3252
	MT	MN	-3.44444	6.72380	0.611	-16.9788
		LM	4.95833	8.42002	0.559	-11.9903
		LK	-24.55556*	8.10921	0.004	-40.8785
	LK	MN	21.11111*	7.85171	0.010	5.3064
		LM	29.51389*	9.34540	0.003	10.7026
		MT	24.55556*	8.10921	0.004	8.2326

CHAPTER SIX

6.0 GENERAL CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

This study has provided information on the small mammals of the Ukaguru Mountains within the Eastern Arc Mountains, Tanzania. It was shown that the small mammals of the landscape are under continuous danger of anthropogenic disturbances resulting in marked modification of their habitats. Also revealed from the study is the declining of small mammal forest specialists (*Beamys hindei* and *Lophuromys kilonzoi*) in disturbed forests and subsequent establishment of non-forest rodent species (*Mastomys natalensis* and *Mus triton*) in these habitats. Habitat disturbance led to modification of diversity and evenness of small mammal species in the Ukaguru Mountains with greater diversity and evenness observed in undisturbed forests compared to disturbed forest.

Due to a higher relative abundance recorded for *Praomys delectorum* compared to other species in the forests of the study site, this species is the dominant species in these habitats. This study also showed that the population density of *P. delectorum* varied seasonally, being significantly greater during the wet season compared to the dry season. Also, it was revealed that forest disturbance has no effect on its abundance or maturation but it did affect female survival, which was higher in disturbed forests compared to intact forests. The study further highlighted that the population structure and dynamics of *P. delectorum* are largely influenced by length of the breeding season which is dependent on the rainfall. Also, the anthropogenic disturbances resulted in modification of the population structure and sex ratio but showed no effect on the breeding activity of this species.

Therefore, populations of *P. delectorum* may be stable and viable in this landscape in spite of forest disturbances as indicated in the insignificant differences in population sizes between both forest types, and greater survival rate in disturbed forests.

Furthermore, this study confirms that rodents dwelling in farm/fallow lands and forests in the Ukaguru Mountains are omnivores. A relatively low niche breadth observed in rodents caught in farm/fallow lands can be attributed to the major contribution of seed/grains to their diet while forest dwelling rodents showed greater food diversity owing to the more heterogeneous and stable nature of forests compared to farm/fallow lands. The abundance of food resources in both habitats would have permitted coexistence of rodent species though they overlapped in utilization of food resources.

6.2 Recommendations

The findings of the present study are of concern in conservation of this landscape and necessitate urgent conservation actions in this Eastern Arc mountain block to limit the effects of anthropogenic activities in the landscape. The following recommendations are made:

- i. As the human population surrounding the Ukaguru Mountains and their encroaching activities increase, continuous exploitation of the forests of this landscape should be discouraged as this was shown to modify the habitats of the small mammals and reducing their diversity and evenness. This can be achieved by mounting effective patrols in the forest reserve and enlightening the human populations living adjacent to the forests on the need to conserve wildlife.
- ii. In this study, whereas the population densities of *P. delectorum* varied seasonally, with significantly higher densities during the wet season compared to the dry

season, survival and maturation rates were not seasonal in both forest types and therefore may not be the underlying demographic mechanisms responsible for such temporal changes in abundance. To account for the temporal variation in population density, there is a need to investigate the effects of other demographic parameters such as movement (dispersal).

- iii. Even though anthropogenic disturbances did not negatively affect the population dynamics, sex ratio, reproduction and survival of the delectable soft-fur mouse, this does not imply that forest disturbance should be left unchecked in this landscape as unperturbed forests are irreplaceable in the conservation of biodiversity in general. More so the anthropogenic disturbances may affect other forest specialists albeit less abundant (*B. hindei* and *L. kilonzoï*); therefore it is recommended to determine the effects of the anthropogenic disturbances on these species.
- iv. The IUCN Least Concern conservation status of *P. delectorum* is uncertain given the very frequent rates of anthropogenic disturbances in the EAM. Therefore, continuous demographic monitoring of *P. delectorum* in the EAM is highly recommended given that human populations surrounding the landscape is increasing leading to deforestation and expansion of the pine plantation in the forest reserve.
- v. Given the interspersed nature of the forests with farms and their proximity, this favours the establishment of opportunistic farm rodent generalists in forests adjoining farms especially when foods become less abundant during the off farming seasons. It is therefore recommended that the forest boundaries should be well

demarcated and farmlands should be situated far from the forest boundaries (at least 400 m).

- vi. The insufficient data for diet studies did not permit analysis of seasonal variation of food categories; further studies are necessary to look at the effects of seasons on the diets of rodents of the Ukaguru Mountains.
- vii. As the sampling survey was restricted to the use of only Sheman traps, this study might have underestimated the small mammal diversity in the Ukaguru Mountains. Therefore, it is recommended that future studies should employ different types of traps in the survey of small mammals in this study site. Similarly, the DNA barcoding was restricted to some representative samples and not for all captured individuals. It is recommended that that future studies should carry out molecular identification of all captured individuals especially for sympatric species (such as *Mus triton* and *Mus minutoides*).