



UNIVERSITY OF NAIROBI

FACULTY OF SCIENCE AND TECHNOLOGY

DEPARTMENT OF BIOLOGY

**IMPLICATIONS OF DIETARY VARIATION ON ABUNDANCE AND OCCUPANCY
RELATIONSHIPS IN A PREDOMINANTLY MUROID SMALL MAMMAL
COMMUNITY IN MPALA CONSERVANCY, KENYA**

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Thesis submitted to the Department of Biology in partial fulfilment of the requirements for the
award of degree of Master of Science in Biology of Conservation

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DECLARATION

I declare that this is my original work and has not been presented in any other University for a degree award.

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DEDICATION

I dedicate this thesis to my late dad Amos who passed on a few months before the start of my graduate school. Dad taught me to value hard work, dream, and live my dream. Dad's memories and a desire to make him proud have been my greatest cheerer. A very special feeling of gratitude to my loving mum Priscilla whose love for me knows no bounds, and my siblings Ted, Oscar, Mildred, Jack, and Winnie for their invaluable support.

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ABSTRACT

Positive interspecific relationship between abundance and occupancy (AOR) is among the most common patterns in ecology. This has been attributed to niche differences among species such that resource generalists are expected to be abundant and widespread compared to resource specialists (the Resource Breadth Hypothesis). Studies that have tested this hypothesis have failed in ascribing mechanisms because of using datasets across broad spatial scale. However, this hypothesis is better tested at a local scale for individuals to be tracked through time based on prevailing resources. This study sought to establish AOR and the driving mechanisms for the AOR in a predominantly muroid small mammal community in Mpala Conservancy. The Resource Breadth Hypothesis and the underlying mechanisms as predicted by the Niche Variation Hypothesis were tested. The study predicted that dietary generalists will be the most abundant and widespread species, and ones exhibiting the greatest among individual dietary variation (a prediction of the Niche Variation Hypothesis) as compared to dietary specialists. Abundance and occupancy were estimated from mark-recapture data by fitting N-mixture and single season occupancy models. The degree of dietary generalism and among individual dietary variation was estimated from sequenced plant DNA of fecal samples based on Shannon-Weaver diversity and proportional-similarity indexes. Occupancy increased with increase in abundance ($r = .87$), and both the Resource Breadth and Niche Variation Hypotheses were supported after fitting simple linear regressions across species. Overall regression for the test of these hypotheses were both statistically significant (ANOVA: $F_{1,3} = 27.44$, $p = 0.01$, regression: $R^2 = 0.87$ and $F_{1,3} = 17.30$, $p = 0.03$, $R^2 = 0.80$ respectively). Results indicate that the Niche Variation Hypothesis provides the mechanism by which the Resource Breadth Hypothesis explains the positive interspecific AOR, suggesting the need to account for individual differences when examining the drivers of abundance and distribution of species.

1.0 CHAPTER ONE: INTRODUCTION

1.1 Background

Across different groups of animals worldwide, ecological communities are dominated by one or a few species that tend to be both locally broadly distributed and common throughout their distributions, with many more that are locally narrowly distributed and only occurring in a few places (Gaston *et al.* 2000). This macroecological pattern—known as the abundance-occupancy relationship (AOR)—is among the most general in ecology. Because AORs have been reported across a diversity of taxa, geographic locales, and sampling regimes [e.g., plants: (Buckley & Freckleton 2010), insects: (Cowley *et al.* 2001); frogs: (Murray *et al.* 1998), birds: (Gaston & Blackburn 1996), and mammals: (**Fig 1.1 A**, (Boro 2017))], this macroecological pattern begs for a mechanistic explanation. On the contrary, negative correlations are extremely rare and where they occur they have been attributed to measurements of abundance in sites that are significantly different of the larger area sampled (Gaston *et al.* 2000).

The prevalence of positive abundance-occupancy relationships across broad spatial scales has led ecologists to hypothesize that individuals of abundant, widespread species might exhibit greater fitness (i.e., increased survival, increased reproduction, or both) compared to rare, restricted species (Gaston *et al.* 2000; Buckley & Freckleton 2010). But this pattern has been attributed alternatively, and most prevalently, to (1) differences among species in their abilities to move through the landscape, such that immigration from the surrounding region should significantly boost the commonness of widespread species, and should prevent local extinction of rare, restricted species (Hanski 1982); and (2) differences in resource-use flexibility among species, such that those that are able to use a broad array of resources should occur at more sites, and be relatively common where they occur (Brown 1984). A test in support of these two

explanations would mean differences in immigration and extinctions rates and ecological generalism at the species level might be the mechanism that leads to positive interspecific AORs.

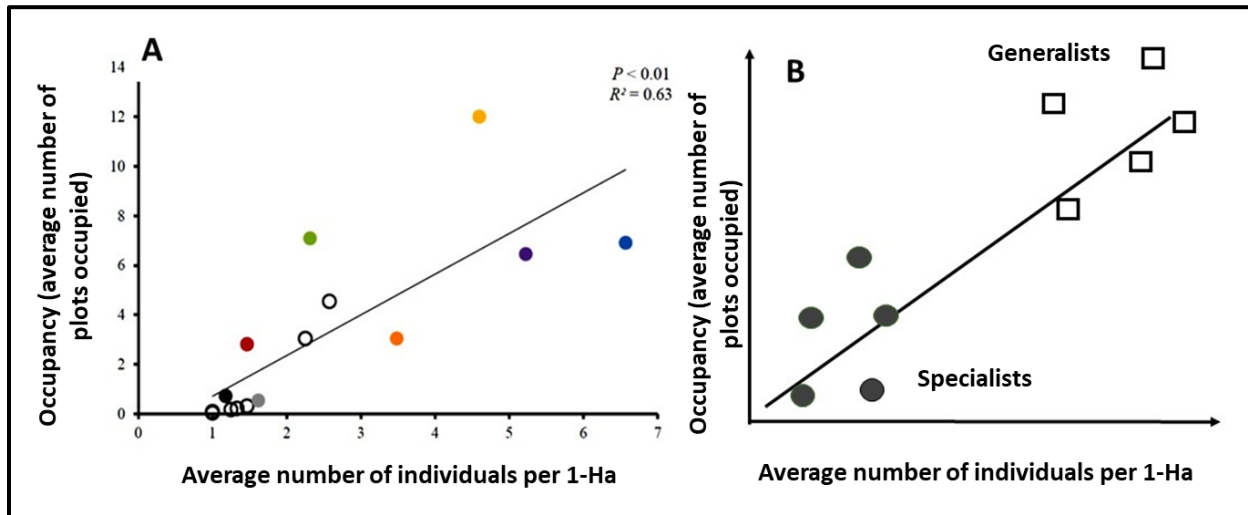


Figure 1.1: A positive abundance occupancy relationship in the small mammals of Mpala Conservancy from a previous study of 2009-2016 (Boro 2017).

Additionally, Van Valen (1965) suggests that a population is comprised of specialist individuals who use a narrow subset of resource available to the entire population (**Fig. 1.2**). As total niche width (TNW) expands from the rose coloured curve to the teal coloured curve, within individual diversity (WID) should contract, and the differences among individual diversity (AID) should expand (**Fig. 1.2**) (Araújo *et al.* 2011; Jesmer *et al.* 2020). Therefore, Van Valen would expect that populations with the largest TNW should exhibit the widest AID and if the Brown's Niche Breadth Hypothesis holds true, then widespread, abundant species should exhibit greater variation among individual diets compared to restricted, rare species.

Comparing to the Van Valen Hypothesis is the Optimal Foraging Theory that would predict individuals within populations should use a similar, broad set of resources and as total niche width (TNW) expands, individual niche width should expand as well thus contracting the differences among individuals (**Fig. 1.2**) (MacArthur & Pianka 1966; Jesmer *et al.* 2020). Therefore, the

Optimal Foraging Theory would expect that populations with the largest TNW should exhibit the narrowest AID and if the Brown's Niche Breadth Hypothesis holds true, then widespread, abundant species should exhibit lesser variation among individual diets compared to restricted, rare species.

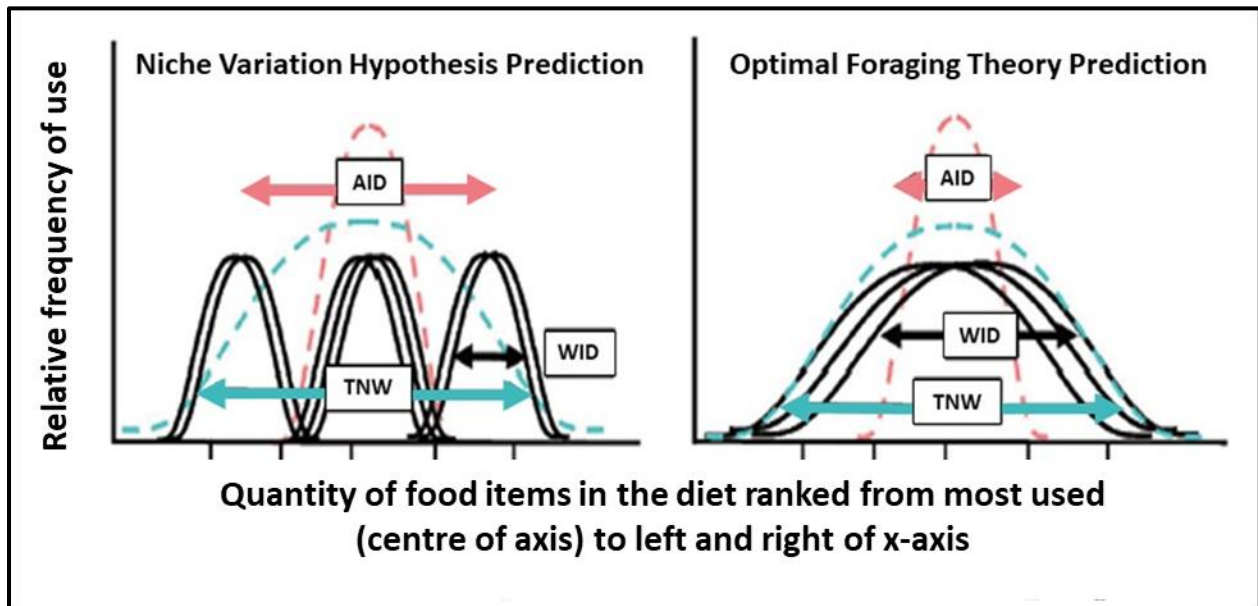


Figure 2.2: A modified illustration from Jesmer *et al.* (2020) on the predictions of the Niche Variation Hypothesis and the Optimal Foraging Theory on how individuals alter diet selection.

The study took advantage of the positive interspecific AOR in the small mammal community of Mpala Conservancy to test the Resource Breadth Hypothesis and the underlying mechanisms as predicted by the Niche Variation Hypothesis and the Optimal Foraging Theory (Boro 2017). This predominantly muroid small mammal community occupies a more similar dietary guild (Bergstrom 2013; Boro 2017), and the species are localized as envisioned by the Resource Breadth Hypothesis. Moreover, the abundance of this small mammals are strongly driven by food availability (Goheen *et al.* 2013) and thus, food as a resource was the most important niche metric for the test of the Resource Breadth Hypothesis.

1.2 Statement of the problem

Most studies that have tried to test the Resource Breadth Hypothesis have been fraught with difficulty in ascribing mechanism. This is because such studies compiled abundance and occupancy relationships using datasets that were collected across broad spatial scales and from wide ranging species i.e., birds. However, the Resource Breadth Hypothesis is better tested at a local scale to allow for individuals to be tracked through time as they are confronted with shifting resource availability in their localized home ranges. Moreover, the Niche Variation Hypothesis and the Optimal Foraging Theory both predict that as resources become limiting, the dietary niche width of the population expands. However, they provide contrasting predictions on the response of individuals diet to food limitation. This study will provide a better understanding of these fundamental ecological theories/ and hypotheses.

1.3 Justification

Globally, small mammals make up more than 50% of all wild mammalian biodiversity (Happold 2001), over 70% of African mammals (Happold 2001), and over 60% of the 390 species of mammals in Kenya (Musila *et al.* 2019). However, the lack of data on small mammals has persisted despite some species having not been sighted for a long time, and at least 33% of the ~463 species of African rodents being classified as data deficient on IUCN (Musila *et al.* 2019). This study contributes to the understanding of diets and the drivers of abundance and occupancy of small mammals in the east African savannas. Additionally, the diversity in small mammals and generally their fast-living life histories provides unique opportunities for testing classical ecological theories and hypotheses. These theories and hypotheses have shaped the world's general approaches to conservation and management of wildlife. Specifically, positive interspecific AOR has practical implications in determining the risk of extinction, risk of invasions, and identifying priority areas

for conservation or control of invaders (i.e., low local abundances increase the likelihood of stochastic extinctions, and local abundances and distribution extent may inform the status of a problem and the costs of eradication or control) (Gaston *et al.* 2000).

1.4 Research Objectives

The primary objective of the study was to analyze the implications of dietary variation on abundance and occupancy relationships in a muroid small mammal community in Mpala Conservancy. To achieve this objective the study quantified:

- i. The relationship between abundance and occupancy among the small mammals of Mpala Conservancy,
- ii. The relationship between abundance and dietary total niche width among the small mammals of Mpala Conservancy,
- iii. The relationship between dietary total niche width and among individual dietary variation among the small mammals of Mpala Conservancy.

1.5 Research hypotheses

- a) Occupancy increases with increase in abundance,
- b) Dietary total niche width increases with increase in abundance,
- c) Among individual dietary variation increases with increase in dietary total niche width.

2.0 CHAPTER TWO: LITERATURE REVIEW

2.1 The Superfamily Muroidea

Muroids are the most diversified of all mammals belonging to the order Rodentia, suborder Mymorpha and superfamily Muroidea. Muroids encompass the mice, rats, gerbils, and relatives all together forming a third of mammal species globally (Steppan *et al.* 2004). The superfamily Muroidea is subdivided into six families: Cricetidae (New World rats and mice, voles, hamsters, and relatives), Muridae (Old World mice and rats, gerbils, whistling rats, and relatives), Nesomyidae (African and Malagasy endemic rats and mice), Spalacidae (blind mole rats, African mole rats, zokors, and bamboo rats), Calomyscidae (mouse-like hamsters), and Platacanthomyidae (Malabar spiny dormouse and pygmy dormice) (Kingdon *et al.* 2013; Monadjem *et al.* 2015; Steppan & Schenk 2017). Out of the six families, African muroids belong to four families that can be further subdivided into 14 subfamilies: Muridae (5 subfamilies), Spalacidae (2 subfamilies), Nesomyidae (5 subfamilies), and Cricetidae (2 subfamilies) (Kingdon *et al.* 2013; Steppan & Schenk 2017).

Muroids are known to have a diversified omnivorous feeding habit that spans arthropods and different plants parts i.e., leaves, barks, shoots, and seeds (Nowak & Walker 1999; Kingdon 2004; Monadjem *et al.* 2015). In the east African savanna, where this study was done, muroids have been reported to feed on acacia seeds and seedlings (Goheen *et al.* 2010; Keesing & Young 2014), insects (Kingdon 2004), and leaves and grains of savanna grasses (Kinahan & Pillay 2008). Moreover, previous studies on muroids of this region show existence of diet generalism, seasonal diet switching, and specialization (Keesing 1998; Bergstrom 2013; Boro 2017). Bergstrom (2013) study of eight muroid species that form part of this study showed that all the species were omnivorous with only one species of the Subfamily Murinae, *Arvicanthis niloticus* being a

specialized grazer. One species of the Subfamily Gerbillinae, *Gerbiliscus robustus* preferentially fed on arthropods with a few plants, and three species (2 from Subfamily Murinae and 1 from Subfamily Cricetomyinae) were mixed feeders switching between grass and browse with seasons.

2.2 Dietary variation explanations and categorization

Van Valen (1965) introduced the concept of diet variation when he explained the two mechanisms by which population diet breadth occurs; (1) either the diet of individuals is an exact reflection of the entire population diet or (2) individuals of a population only but use a subset of the entire population diet. Ecologists have hence appreciated the existence of individual specialization cutting across vertebrates and invertebrates with more than 187 examples as of 2011 (Araújo *et al.* 2011). While Van Valen's niche variation hypothesis suggests that a population is composed of specialist individuals that specialize on some of the resources available to the entire population, optimal foraging theory predicts that individuals within a population use a similar set of resources and thus differences among individuals are minimal (Jesmer *et al.* 2020). Optimal foraging theory posits that individuals maximize their fitness by adopting foraging strategies that maximize energy intake at the lowest cost (MacArthur & Pianka 1966). Therefore, optimal foraging theory would predict that individuals will selectively forage on the most valuable resources to maximize energy intake and nutrition, and when preferred resources are limiting individuals will broaden their diets to include resources not previously preferred (i.e., a prediction of the optimal diet model).

Optimal foraging theory suggests that among individuals dietary variation arise because of differences in (1) rank preferences i.e., how individuals rank available food resources, (2) optimization criterion i.e., why individuals go for certain resources, and (3) social dominance i.e., hierarchy among individuals (Araújo *et al.* 2011). Preference ranks are based on the energetic value of a resource per handling time based on the ability to detect, capture, handle, and digest the

resource. Optimization criterion stem from differences in physiological requirements (i.e., breeding versus non-breeding individuals) (Tremblay *et al.* 2005), body size, predation risk aversion, and cognitive capacity (i.e., dietary specialization is expected to increase with high cognitive capacity: long-lived versus short-lived, adults versus juveniles (Codron *et al.* 2016)). Finally, the dominant or highly ranked individuals or species secure the best foraging areas excluding subordinates to less preferred resources and areas (Sol *et al.* 2005).

Niche differentiation may also occur because of competition among individuals or species for a preferred limited resource. The expansion may either lead to increased specialization in which case each individual or species expands their niches to a different unexplored alternative resource (Costa *et al.* 2008), or alternatively may lead to reduced specialization when most of the individuals or species expand their niches to similar alternative resources (Costa *et al.* 2008). Additionally, ecological opportunities (i.e., resource diversity and abundance, habitat heterogeneity, and environmental stability) may further lead to diet differentiation (Newsome *et al.* 2015). The east African pouched mice (*Saccostomus mearnsi*) in Mpala Conservancy specialized on grass seeds following an increase in seeds abundance in the rainy season (Keesing 1998), and the grey wolf (*Canis lupus*) in British Columbia became more specialized with increased habitat diversity (Darimont *et al.* 2009).

Lastly, resources can be released to other species or individuals through predation. This can lead to either increased specialization because of more opportunities or expanded niches that includes the released resources. Alternatively, the prey might change resource exploration strategies by either shifting to forage in the less risky sites (Creel *et al.* 2005), or shifting to the less preferred resources (Barnier *et al.* 2014). The shift releases resources to the risk versed individuals or species, but where all individuals or species are at risk, resource use may converge

in the less risky sites. Predators have both a direct and indirect effect on the prey, thus they shape the dynamics of a community in terms of trophic interactions, resource use, and fitness (Bastille-Rousseau & Wittemyer 2019).

Beyond the dietary generalist, switcher, and specialist classification, more insights in understanding resource selection has led to more different ways of classifying dietary strategies. Bolnick *et al.* (2003) subdivided individuals into three: pure generalists (totally overlapping diets), functional specialists (partially overlapping diets), and pure specialists (non-overlapping diets). Pagani-Núñez *et al.* (2016) further classified dietary strategies into four: obligate specialists, facultative specialists, facultative generalists, and obligate generalists. Morphologically and behaviorally, obligate specialists are adapted to exploiting a single resource and are usually very rare whereas obligate generalists utilize a broad variety of resources and will only exploit one resource when it is very abundant. Facultative specialists utilize one type of food but with a decline in the main food, they will utilize other niches opportunistically, whereas facultative generalists develop different new strategies to exploit alternative resources.

2.3 Abundance-occupancy relationships and diet variation

Evolutionary and community ecologists are currently interested in the direct and indirect implications of niche variation in shaping community dynamics. Such niche variations can be linked to fitness differences and evolutionary selection (Araújo *et al.* 2011; Newsome *et al.* 2015). Community niche variations among species and further among populations and individuals could help explain differences in commonness and rarity of species (i.e., positive abundance-occupancy relationships). Abundance-occupancy relationships studies attempt to explain the mechanisms leading to differences in abundance and occurrence of species. Positive interspecific AORs are one of the most common patterns in ecology. They occur across taxa, and it is the tendency of abundant

species to be widespread and the rare ones to be restricted in distribution (Gaston *et al.* 2000). The positive AORs are useful in applied ecology; such as in conservation of endangered species, harvesting of abundant species, managing of biological invasions, and inventorying biodiversity (Gaston *et al.* 2000; Buckley & Freckleton 2010). Ecologists have suggested several hypotheses to explain positive interspecific AOR: meta-population, vital rates, and resource use hypotheses.

The meta-population hypothesis postulates that immigration reduces the chances of a local population declining to extinction, thus differences in immigration and extinction rates result in positive AORs (Hanski & Gilpin 1991). The vital rates hypothesis suggests that species abundance and occupancy depend on birth and death rates throughout the occupied sites, such that a species will only persist and increase in abundance in a site it occupies only when birth rate is greater than death rate (Holt *et al.* 1997). Lastly, resource use hypothesis postulates that resource availability (abundance) and variety (niche breadth) explains differences in commonness and rarity of species (Gaston *et al.* 2000).

The resource use hypothesis stands out as an explanation of positive AOR because niche breadth is a representation of the abiotic and biotic needs and tolerances of a species, and is a diverse and central concept that spans aspects of ecology, evolution, and conservation (Carscadden *et al.* 2020). The resource availability and resource variety hypotheses under the resource use hypothesis posits that abundant, widespread species are generalists because they can use a variety of resources that are readily available. Contrastingly, the rare, restricted species are specialists because they utilize only a small subset of the available resources which are also scarce (Brown 1984). Both the resource use hypotheses and the optimal foraging theory would predict that dietary generalism should confer an advantage because individuals can thrive on a variety of resources.

Complementarily, the nutrient and detoxification constraints hypothesis posits that no one plant can adequately meet the nutritional needs of an individual, and that the mammalian detoxification system efficiently detoxifies secondary compounds from different plants than it does from a single plant species (Dearing *et al.* 2000; Nersesian *et al.* 2012). Thus, dietary generalists obtain maximum nutrition from foraging on a variety of plants with varying nutritional components, and at the same time enjoy efficient detoxification. Therefore, species that forage on high quality food (the optimal foraging theory), a variety of food resources (the resource use, and nutrients constraint and detoxification constraint hypotheses), and those differentiating among individuals (the niche variation hypothesis) are expected to burgeon in both abundance and occupancy.

This study builds on previous work from Boro (2017) that did not find support for the resource breadth hypothesis despite establishing a positive AOR in the small mammals of Mpala Conservancy. Boro (2017) and Bergstrom (2013) broadly classified the diet of these small mammals as browsers, grazers or mixed feeders based on C3 and C4 plants classification using stable isotopes. However, this study classifies diet at the lowest possible taxonomic unit appreciating the fact that species and individuals can specialize at higher resolution of species level other than the broader classification of grazer, browser, and mixed feeder.

3.0 CHAPTER THREE: STUDY AREA, MATERIALS AND METHODS

3.1 Study area location

Mpala Conservancy is a semi-arid savanna located north of the equator in central Kenya (latitude, $0^{\circ} 22' 24''\text{N}$ to $0^{\circ} 25' 08''\text{N}$; longitude, $36^{\circ} 51' 36''\text{E}$ to $36^{\circ} 52' 05''\text{E}$, **Fig. 3.1**). The conservancy covers 200 km^2 and supports both wildlife conservation and livestock production.

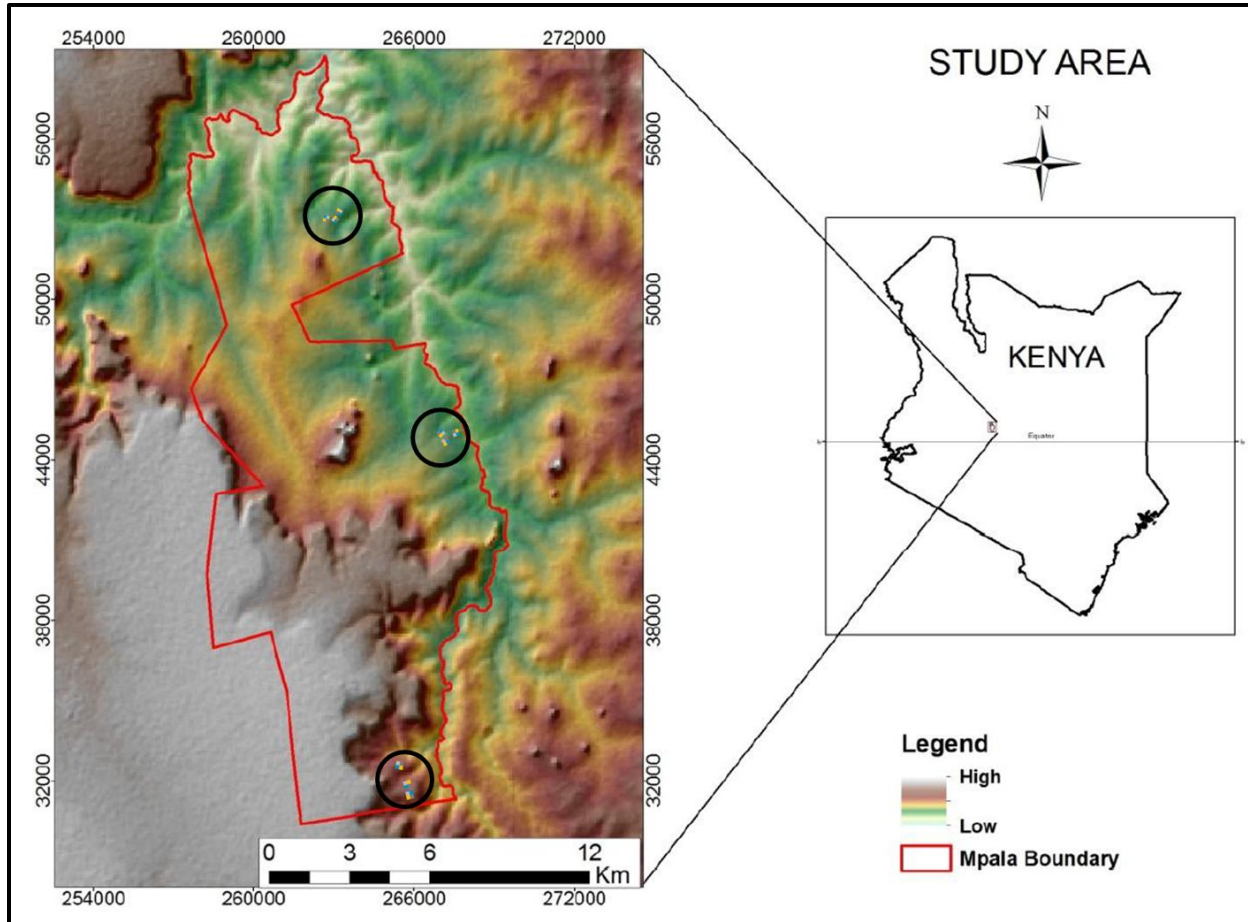


Figure 3.1: Terrain map of Mpala Conservancy and sites of UHURU experiment plots highlighted in black circles.

3.2 Soils and topography

Mpala Conservancy is on 1600-m elevation that is characterized by black cotton vertisol soil and infertile red sandy loam alfisol soils (Goheen *et al.* 2013).

3.3 Rainfall

Mpala Conservancy has a weak tri-modal annual rainfall pattern averaging ~600 mm per year. The rains peak in April-May, August-October, and a dry season from December to March (Goheen *et al.* 2013).

3.4 Flora and fauna

Mpala conservancy supports an understory of forbs and grasses, and an overstory of mostly Acacias: *Vachellia etbaica*, *Senegalia brevispica*, and *Senegalia mellifera* (Coverdale *et al.* 2016). Other species of woody plants include *Croton dichogamus*, *Grewia spp.*, and *Rhus vulgaris*. The understory mostly consists of *Digitaria milanjana*, *Cynodon dactylon*, *Pennisetum stramineum*, *Pennisetum mezianum*, *Enteropogon*, *Aristida spp.*, *Themeda triandra*, *Cyperus spp.*, *Chloris roxburghiana*, and *Eragrostis superba* (Augustine 2003).

The mammal community consists of African bush elephants (*Loxodonta africana*), Maasai giraffes (*Giraffa camelopardalis*), impalas (*Aepyceros melampus*), plains zebras (*Equus quagga*), Grevy's zebras (*Equus grevyi*), Guenther's dik-diks (*Madoqua guentheri*), cape hare (*Lepus capensis*), African lions (*Panthera leo*), leopards (*Panthera pardus*), spotted hyaena (*Crocuta crocuta*), cheetahs (*Acinonyx jubatus*), black backed jackal, aardwolf, white-tailed mongoose (*Ichneumia albicaudia*), common dwarf mongoose (*Helogale parvula*), common slender mongoose (*Herpestes sanguineus*), blotched genet (*Genetta maculata*), common genet (*Genetta genetta*), bat-eared fox (*Otocyon megalotis*), zorilla (*Ictonyx striatus*), and African wildcat (*Felis lybica*).

The targeted small mammal species for this study consisted of Hinde's bush rat (*Aethomys hindei*), Mearns's pouched mouse (*Saccostomus mearnsi*), fringe-tailed gerbil (*Gerbiliscus robustus*), Kellen's dormouse (*Graphiurus kelleni*), African grass rat (*Arvicanthus niloticus*), woodland

thicket rat (*Grammomys dolichurus*), Harrington's tateril (*Taterillus harringtoni*), and rufous elephant shrew (*Elephantulus rufescens*) (Alston *et al.* 2022).

3.5 Study design

This study was conducted within the Ungulate Herbivory Under Rainfall Uncertainty (UHURU) experimental plots. The experiment was established in 2008 and consists of nine blocks—three blocks in the north, three in the central, and three in the south of the Mpala Conservancy—each with four plots each measuring 100 x100 meters. Each plot has a permanently established sampling grid in the middle of the plot 20 meters from the edges. The sampling grid has a total of seven transects each measuring 60 meters long with seven trapping points that are spaced 10 meters from each other (**Fig. 3.2**). The transects run from south to north in reference to a south-north rainfall gradient on Mpala Conservancy. Since 2008, small mammal sampling has been done in two of the four plots in each block (golden and blue colored plots, **Fig. 3.2**). This study took advantage of this small mammal sampling to look at the abundance, occupancy, and diets of the different species.

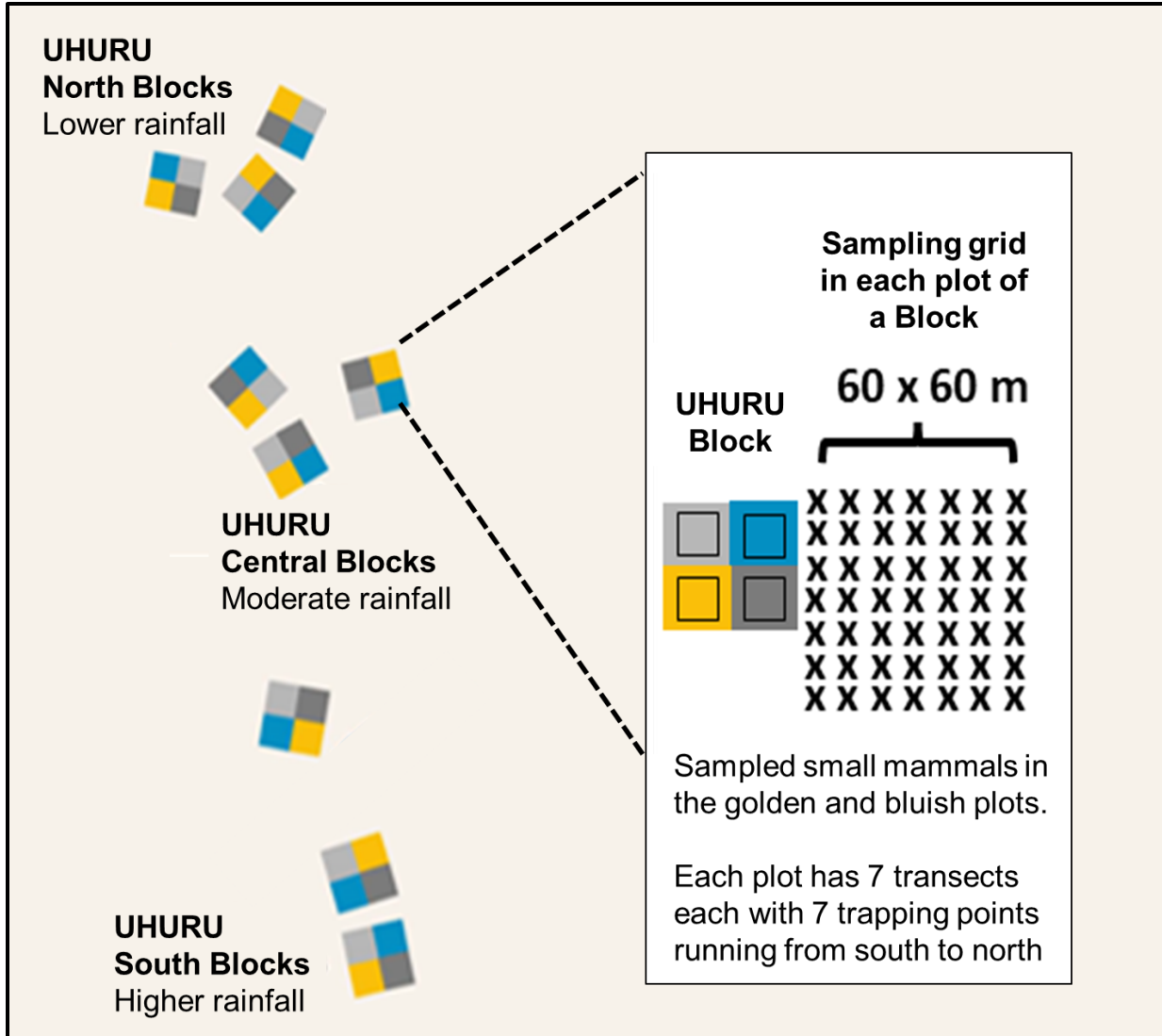


Figure 4.2: A schematic illustrating the study design and the sampling grid.

3.6 Small mammals trapping

Small mammals were sampled for nine sampling surveys by live trapping for four consecutive nights in each survey using Sherma live traps. There was a one-month period between each survey to allow for enough time for any changes to occur in a population. Sherman live traps were set and baited with a mixture of oats and peanut butter at 1700hr and checked early morning before sunrise. The whole nine sampling surveys had a trapping effort of 31752 (i.e., 49 traps per plot x 18 plots x 4 trapping nights per plot per sampling survey x 9 sampling surveys). Captured animals were

tagged with two unique numbered Monel fingerling ear tags on both ears to help with the identification and monitoring of specific individuals throughout the study period. The specific plot of capturing and subsequent recapturing of an animal was recorded alongside the sampling survey, the species identification, and individual identification numbers on the ear tags.

3.7 Fecal samples collection

Fresh fecal samples were collected directly from the animal into small clean plastic bags and immediately placed in ice packed cooler box. Most of the animals defecated immediately on handling and some only defecated with a light massage on the belly. Immediately after field, each fecal sample was crushed by hand in bag, transferred into vials filled with Lysis solution and Zymo Xpedition buffer to prevent the degradation of DNA content, thoroughly mixed by vibrating on a vortex for 30 seconds, and afterwards frozen at -20 degrees Celsius before DNA extraction and sequencing at Brown University, USA.

3.8 Plant chloroplast DNA extraction and DNA metabarcoding

Fecal samples were analyzed for plant chloroplast DNA following the protocol used in Kartzinel et al. (2015). Fecal DNA was extracted using the Zymo Xpedition Soil/Fecal DNA mini kit. Samples were processed in batches of 15 with an extraction blank for monitoring potential cross-contamination in the laboratory. The fecal DNA was amplified using the broad array plant taxa DNA meta-barcode marker: P6 loop of the chloroplast *trnL*(UAA) to facilitate plant identification (Coissac *et al.* 2007). The plant DNA meta-barcode sequences were then matched, checked for quality, and a plant type identification done by assigning taxonomic names based on a Mpala Conservancy specific plant DNA library comprising ~480 species. DNA sequences with nucleotide ambiguities were dropped, and identical sequences for each sample grouped and tallied within samples to allow for the quantification of relative read abundances (RRA). Relative read

abundances are proportions of unique plant type sequence reads in a sample divided by final sequence reads in that sample after quality control (Kartzinel *et al.* 2015). Meta-barcode sequences with 100% identity were assigned to a species and sequences matching multiple references were revised to the finest taxonomic level that encompassed all the DNA sequences. All the sequences were identified to family level, 72 % to genus level and 67% to species level.

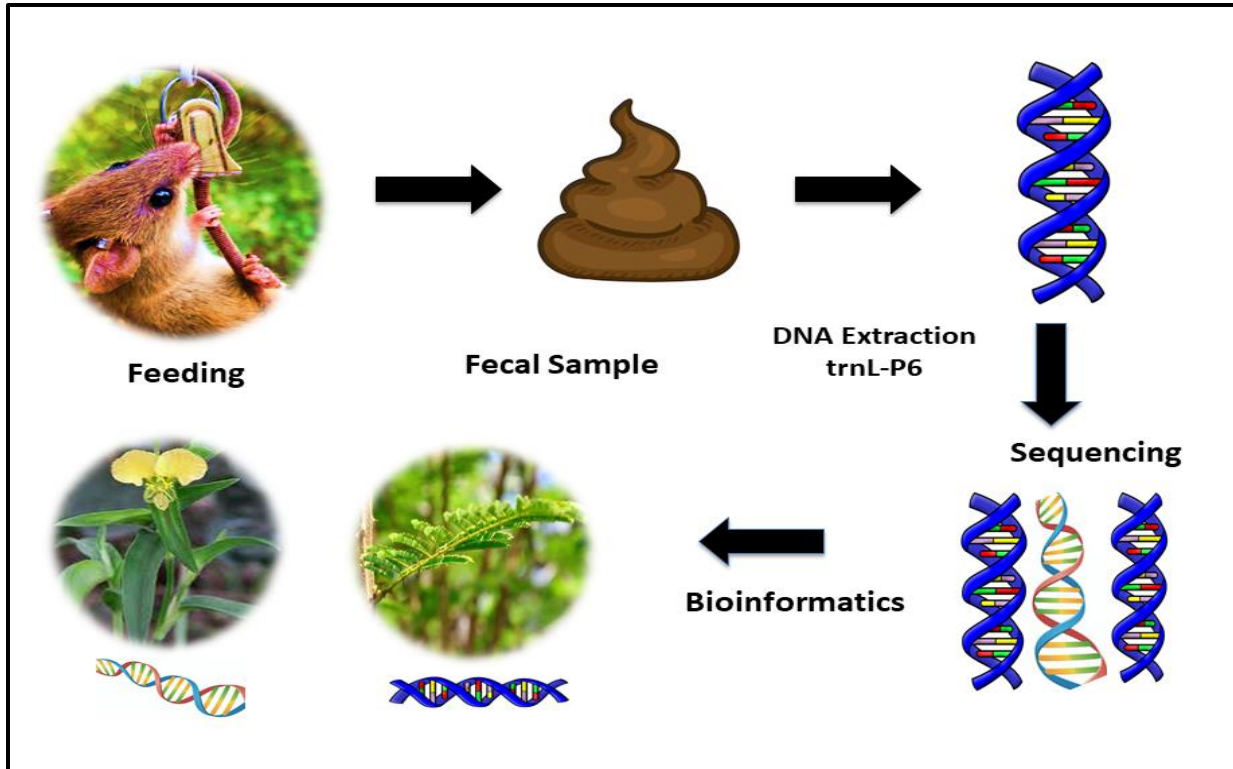


Figure 5.3: A summary of main steps involved in DNA extraction, analysis, and identification of plants consumed by a small mammal from a fecal sample.

3.9 Plant DNA reference library for Mpala Conservancy

To help with the identification of plant sequences from fecal samples, a plant DNA library consisting of plant species that occur throughout Mpala Conservancy and the adjacent Ol Jogi Conservancy was created. The reference library was created by collecting and identifying fresh plant materials at the Botany Department at National Museums of Kenya and the Smithsonian

Institution. The DNA from the plants voucher specimens was then extracted and sequenced for Chloroplast trnL(UAA) which is the gene region with the smaller DNA metabarcode gene regions that were used in fecal DNA analysis. A reference plant DNA library was then constructed with the plant DNA database from Mpala Conservancy and the global European Molecular Biology Laboratories (EMBL) database (release 118). The reference database produced 197 unique trnL-P6 sequences with 77% of the 1136 plant specimens being single or morpho species.

3.10 Data analysis and hypotheses testing

The small mammal trapping mark-recapture data was summarized to the number of unique individuals per species per sampled plot per sampling survey and sampling night. The summarized data was then used to estimate the abundance and occupancy of each species by fitting robust N-mixture and single season occupancy models respectively using the “unmarked” package in open-source R (Team 2016). The models assumed population closure within a sampling survey, and population openness between sampling surveys (MacKenzie *et al.* 2002; Royle 2004). The positive interspecific correlation between abundance and occupancy was evaluated by first testing for linearity by visualizing the data using a scatter plot, testing for normality of variables with the Shapiro-Wilk normality test, and finally testing for correlation.

A total of 756 fecal samples across sampling surveys were analyzed (*A. hindei* 247, *G. robustus* 220, *S. meansi* 273, *E. rufescens* 10, and *T. harringtoni* 6). Samples collected from the same individual over a 24hr period were assumed to be a representation of the same foraging decision (Araújo *et al.* 2011; Jesmer *et al.* 2020). Samples collected from the same individual but in different sampling surveys and those from the same sampling survey but from different trapping nights were treated as different because they represented different foraging decisions. To estimate Total Niche Width for each species, the RRA of plant species that were consumed by individuals

were converted into proportions and averaged for each species to have proportion of plants consumed by each species of small mammal. Total Niche Widths (TNW) was then calculated for each species based on Shannon-Weaver diversity index with a 1000 bootstraps for standard errors and confidence intervals using the R package “iNEXT” for rarefaction and extrapolation of species diversity (Hsieh *et al.* 2016). Sample based rarefaction and extrapolations allowed for standardized comparisons between species with different sample sizes by rarefying larger samples to smaller sample sizes and extrapolating smaller sample sizes to larger samples sizes. To assess how TNW varied as a function of abundance, the statistical significance of the relationship was tested under the null hypothesis (H₀) that the coefficients are equal to zero and an alternative hypothesis (H_a) that the coefficients are not equal to zero by fitting a simple linear regression across the species.

The degree of dietary Among Individual Variation was estimated from proportions of consumed plant species for each individual per species based on Schoener (1968) proportional-similarity index (PS_i) in R package “RInsp” (Zaccarelli *et al.* 2013). The estimates of PS_i were then estimated for each species. The proportional-similarity index is the measure of individual estimates of pairwise specialization as compared to the entire population. The index ranges from 0 (complete overlap of individual with the entire population diet) to 1 (zero overlap). Among Individual Dietary Variation (V) was then measured as $V = 1 - PS$, where PS is the mean PS_i such that $V = 0$ means individuals use exactly the same resources and V close to 1 indicates a greater Among Individual Dietary Variation (Pansu *et al.* 2019). To test whether diet generalism at a species level or population level occurs via increased among individual diet variation, the relationship between V and TNW mostly known as the niche-variation hypothesis (Van Valen 1965) was measured by fitting a simple linear regression across the species.

4.0 CHAPTER FOUR: RESULTS

The hypotheses of this study were tested on five species of small mammals from which fecal samples were collected. The species belonged to two mammalian orders (four species in order Rodentia and one species in order Macroscelidea (*Elephantulus rufescens*), and two families (four species of family Muridae: *Aethomys hindei*, *Gerbiliscus robustus*, *Saccostomus mearnsi*, and *Taterillus harringtoni*, and one species of family Macroscelididae: *E. rufescens*). The sample size of the analyzed fecal samples for chloroplast DNA varied greatly between species (247, 10, 220, 273 and six samples for *A. hindei*, *E. rufescens*, *G. robustus*, and *T. harringtoni* respectively).

The scatter plot of the relationship between abundance and occupancy was linear and the two p-values of abundance and occupancy were greater than the significance level 0.05 ($p = 0.6935$ and 0.6936 respectively) implying the distribution of the data were not significantly different from the normal distribution. The parametric correlation test between abundance and occupancy was positively correlated but not significant (Pearson correlation: $r = 0.87$, $p = 0.054$). *G. robustus* was the most abundant and widespread species whereas *T. harringtoni* was the rarest and most restricted species, with *A. hindei*, *S. meansi* and *E. rufescens* falling in the middle (**Fig. 4.1**). Despite *E. rufescens* being the second least abundant species in this community, it had a close similarity in occupancy to *A. hindei* and *S. meansi*.

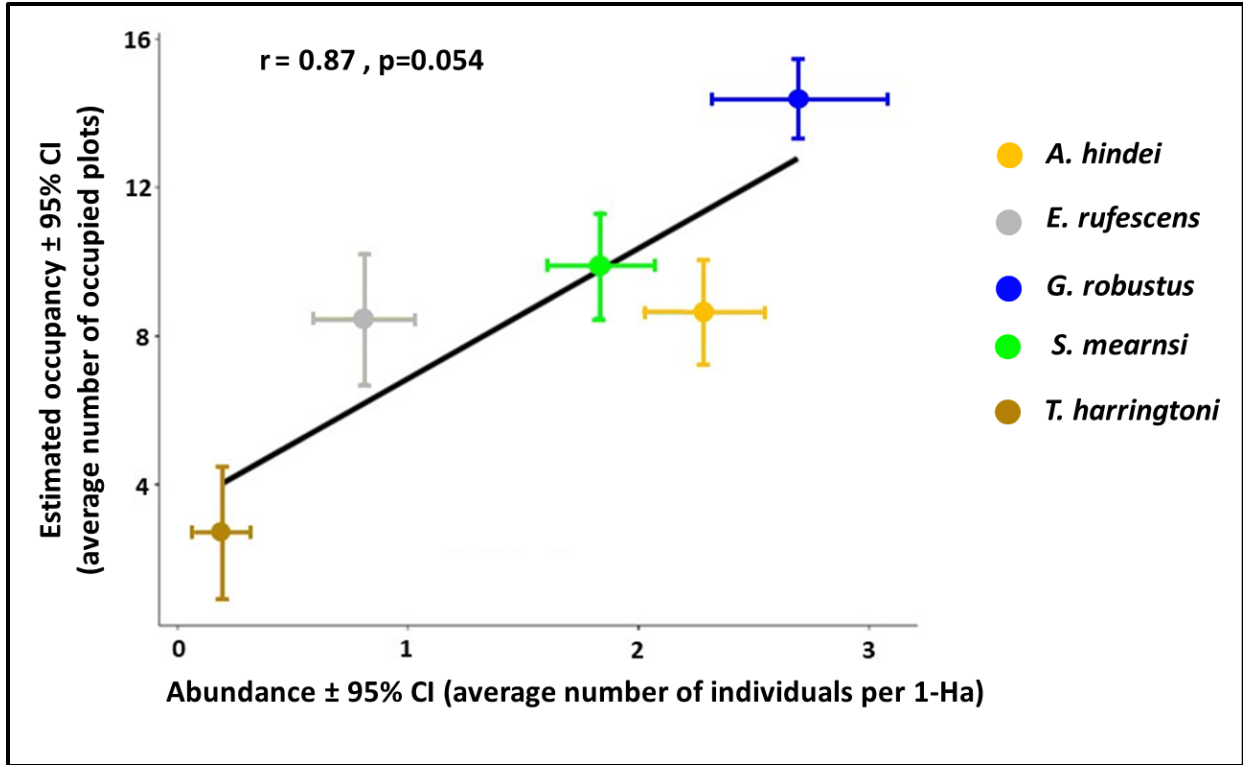


Figure 6:1: A positive correlation between abundance and occupancy.

A total of 146 plant species belonging to 103 genera and 48 families were identified across all the fecal samples. The family Fabaceae was the most preferred family in the diets of all the species accounting for $\geq 50\%$ of RRA followed by Family Malvaceae accounting for $\geq 10\%$ of RRA (6.4% - 19.6%). Malvaceae was more dominant in the diet of *E. rufescens* (19.6% RRA) but was $< 10\%$ for the remaining species. Poaceae accounted for $> 12\%$ RRA in the diets of the rarest species (*E. rufescens* and *T. harringtoni*) and was only $\sim 5.3\%$ in the remaining species. Genus *Vachellia* and *Senegalia* accounted for $> 40\%$ of RRA of all the species making them the most preferred food source. *Oxygonum sinuatum* (Family Polygonaceae) and *Tragus berteronianus* (Family Poaceae) accounted for 13.6% and 7.8% RRA for *T. harringtoni* diet but was $< 3.4\%$ and $< 0.5\%$ respectively for the other species (**Table 4.1**).

Table 1.1: Summary of the percent proportions of utilized plant species by small mammals of Mpala Conservancy.

Plant species	Plant Family	<i>G. robustus</i>	<i>A. hindei</i>	<i>S. mearnsi</i>	<i>E. rufescens</i>	<i>T. harringtoni</i>
<i>Blepharis maderaspatensis</i>	Acanthaceae	0.17	1.70	0.17	0.04	0.43
<i>Justicia</i>	Acanthaceae	1.12	2.21	2.77	0.34	0.19
<i>Ruellia</i>	Acanthaceae	0.54	1.39	0.36	0.47	0.09
<i>Psilotrichum elliotii</i>	Amaranthaceae	0.68	2.13	1.53	0.09	0.06
<i>Cynanchum</i>	Apocynaceae	0.98	4.59	2.64	2.55	0.58
<i>Chlorophytum</i>	Asparagaceae	2.01	0.46	1.14	0.13	0.16
Other <i>Commelina spp.</i>	Commelinaceae	1.77	0.45	0.42	0.23	0.65
<i>Commelina erecta</i>	Commelinaceae	2.04	0.51	0.71	0.64	0.38
Other <i>Ipomoea spp.</i>	Convolvulaceae	0.84	1.41	0.98	0.32	0.05
<i>Ipomoea obscura</i>	Convolvulaceae	0.28	1.75	0.71	0.92	0.83
<i>Crassula schimperi</i>	Crassulaceae	2.89	0.45	0.21	1.52	0.38
<i>Cyperus spp.</i>	Cyperaceae	1.27	0.55	0.11	0.10	1.45
<i>Croton dichogamous</i>	Euphorbiaceae	0.91	0.53	2.48	0.15	5.27
Other <i>Fabaceae spp.</i>	Fabaceae	0.89	0.72	2.40	0.26	0.16

<i>Indigofera spp.</i>	Fabaceae	1.24	1.52	1.05	4.07	5.26
<i>Senegalia brevispica</i>	Fabaceae	2.65	3.84	5.96	7.79	1.61
<i>Senegalia mellifera</i>	Fabaceae	18.38	15.41	15.31	20.24	7.26
<i>Vachellia spp.</i>	Fabaceae	26.82	40.20	48.01	25.39	40.25
<i>Ocimum filamentosum</i>	Lamiaceae	0.39	0.25	0.33	1.51	0.21
<i>Plectranthus spp.</i>	Lamiaceae	0.70	0.78	0.46	1.43	0.33
<i>Grewia kakothamnus</i>	Malvaceae	3.50	2.48	1.39	5.22	5.19
<i>Hibiscus spp. & Abutilon spp.</i>	Malvaceae	11.79	6.62	4.50	15.79	1.28
<i>Aristida spp.</i>	Poaceae	0.08	1.42	0.62	0.18	0.36
<i>Digitaria spp.</i>	Poaceae	1.71	0.17	0.42	4.00	0.48
<i>Pennisetum stramenium</i>	Poaceae	0.71	0.03	0.07	0.04	1.79
Other <i>Poaceae spp.</i>	Poaceae	8.47	0.72	0.87	3.93	1.11
<i>Tragus berteronianus</i>	Poaceae	0.41	0.02	0.01	0.00	7.78
<i>Oxygonum sinuatum</i>	Polygonaceae	3.43	0.14	0.29	0.69	13.57
<i>Solanum spp.</i>	Solanaceae	3.12	7.44	3.97	1.87	0.94
<i>Tribulus terrestris</i>	Zygophyllaceae	0.23	0.10	0.10	0.086	1.92

The dietary richness was greatest for the most abundant and widespread species (*G. robustus*) followed by second most abundant and widespread species (*A. hindei* and *S. meansi*) and was least for the rarest species (*E. rufescens* and *T. harringtoni*, **Fig. 4.2 A**). Rarefying of species with larger sample sizes to sample size of those with small sample size and extrapolating of species with low sample size to those with large sample size predicted greater dietary richness in the most abundant species (**Fig. 4.2 A**). The null hypothesis for the test of statistical significance of the relationship between TNW and abundance was rejected because the p-value for the intercept and predictor were both statistically significant. Total Dietary Niche Width and Among Individual Dietary Variation were greatest for the most abundant and widespread species (*G. robustus*, TNW = 3.28 ± 0.04) and the least for the rarest species (*T. harringtoni*, TNW = 2.70 ± 0.32). TNW was strongly and positively correlated with abundance ($F_{1,3} = 27.44$, $R^2 = 0.90$, $p = 0.014$; **Fig. 4.2 B**).

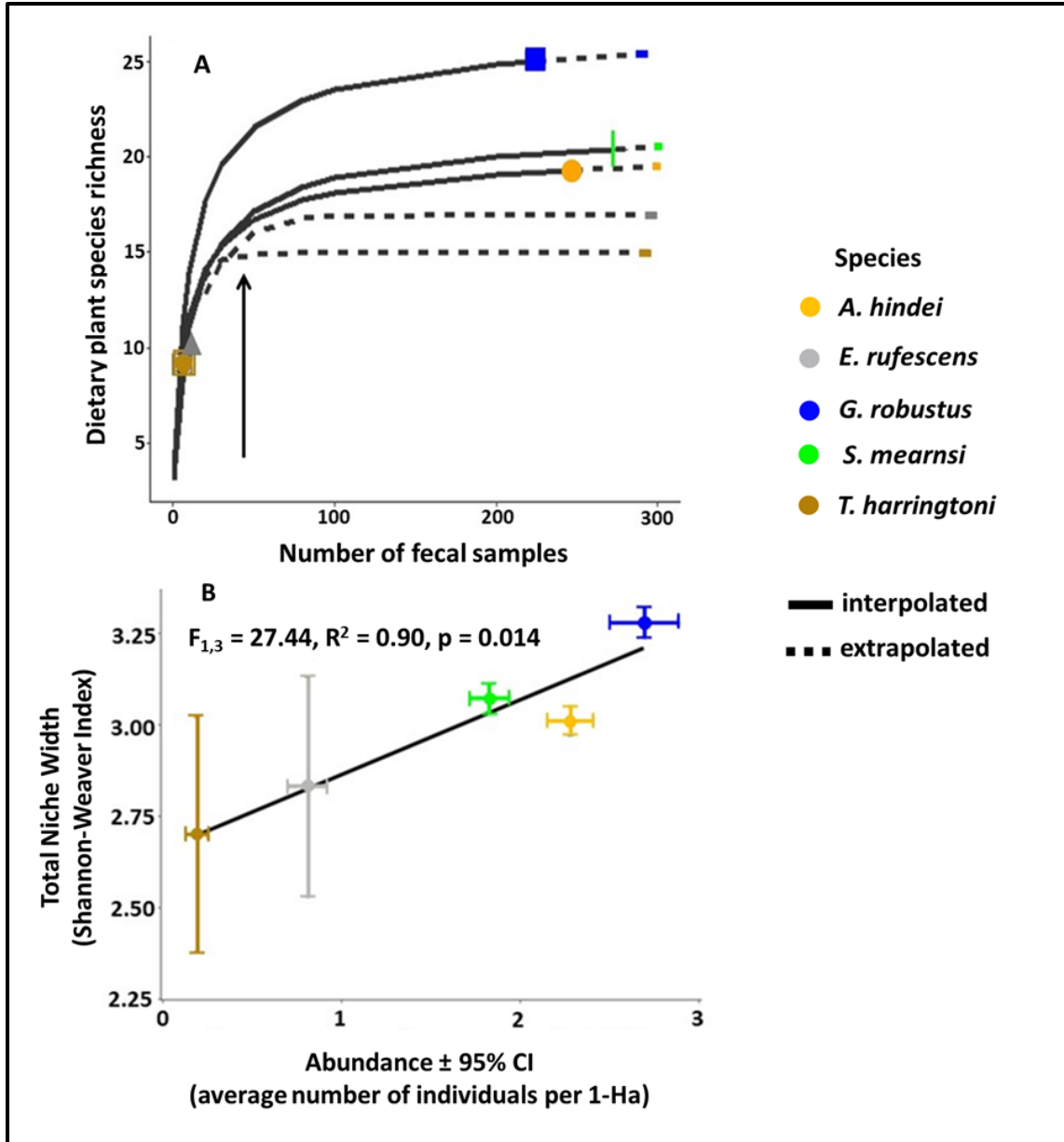


Figure 7.2: (A) A sample size based rarefaction (solid line segment) and extrapolation (dotted segment) sampling curve for species richness. (B) Statistically significant positive relationship between abundance and TNW.

The null hypothesis for the test of statistical significance of the relationship between among individual dietary variation and TNW was rejected because the p-value for the intercept and predictor were both statistically significant. The most abundant species with the highest TNW, *G.*

robustus, had the greatest among individual dietary variation (TNW = 3.28 ± 0.04 , V = 0.56 ± 0.02), whereas the rarest species with the lowest TNW, *T. harringtoni*, had the lowest among individual dietary variation (TNW = 2.70 ± 0.32 , V = 0.35 ± 0.10). Among individual variation was statistically significant and positively correlated to total niche width (ANOVA: $F_{1,3} = 17.30$, $p = 0.025$, regression: $R^2 = 0.85$, Fig. 4.3).

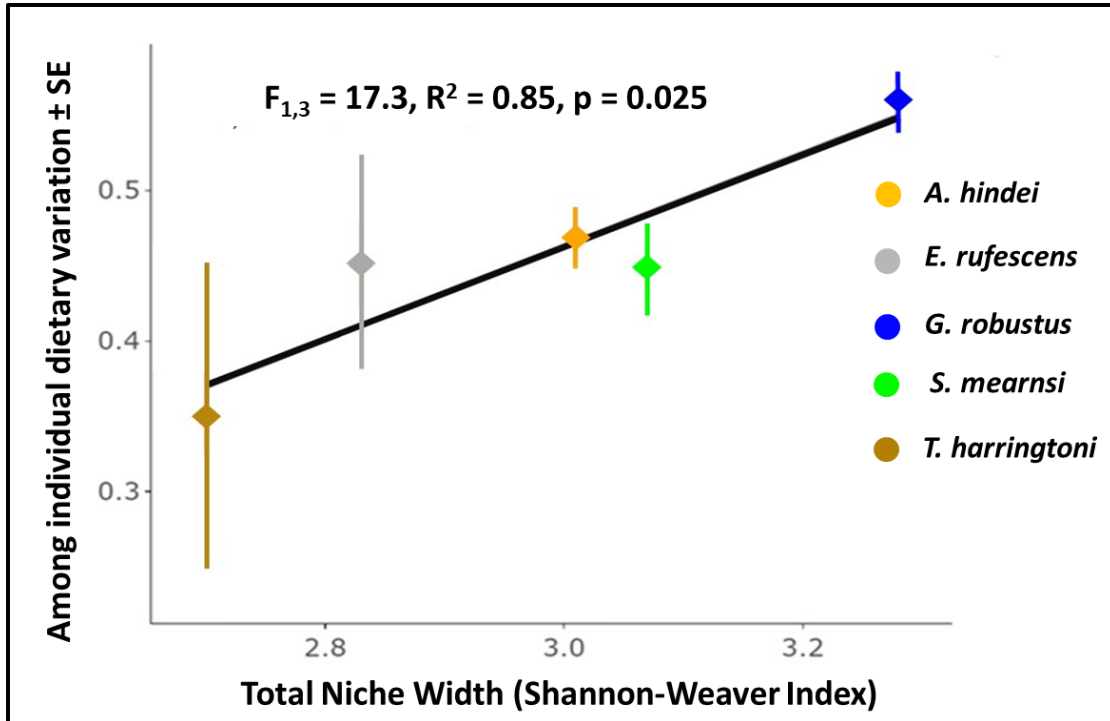


Figure 8.3: Statistically significant positive relationships between Total Niche Width and Among Individual Dietary Variation.

5.0 CHAPTER FIVE: DISCUSSION AND CONCLUSIONS

5.1 Discussion

Consistent with the expectation that occupancy increases with abundance or vice versa (Gaston *et al.* 2000), there was a strong positive correlation between abundance and occupancy in Mpala small mammal community even though the relationship was not statistically significant. Boro (2017), studying the same small mammal community on Mpala Conservancy but with 14 small mammal species found a statistically significant positive correlation between abundance and occupancy ($R^2 = 0.63$, $p < 0.01$). The statistically insignificant yet more strongly correlated positive relationship as compared to Boro (2017) could be attributed to the few datapoints (less diverse community) in construction of the AOR. This positive AOR seems to have persisted over time, and a recurring pattern would imply finding the underlying mechanisms that maintain the relationship.

Ecological niche is a diverse and central concept in ecology, evolution, and conservation (Carscadden *et al.* 2020). The niche represents the tolerances of a species, and the local distributions and abundance (i.e., realized niche) (Brown 1984). Different niche hypotheses (i.e., resource availability and resource variety (Brown 1984), nutrient constraint and detoxification constraint (Dearing *et al.* 2000; Nersesian *et al.* 2012), niche variation (Van Valen 1965; Jesmer *et al.* 2020), and optimal foraging theory (MacArthur & Pianka 1966; Jesmer *et al.* 2020)) share the prediction that resource generalism is advantageous for coping with environmental constraints. In accordance with the resource use hypothesis, specifically the niche breadth hypothesis, the abundance of small mammals increased with increase in TNW. A recent study by Brown *et al.* (2023) based on isotopic niches found that *G. robustus* the most abundant species, was more generalized and omnivorous compared to *T. harringtoni* a C4 specialist.

All the small mammals in this community preferred plants from the Genus *Vachellia* and Genus *Senegalia* which made up >40 % of the diet of each species. It is not clear if this preference was associated to the availability of these Genera in accordance with the resource availability hypothesis or whether the Genera are more nutritious. Pansu *et al.* (2019) did not find a correlation between resource utilization and availability in large mammalian herbivores of Gorongosa national park in Mozambique. Whether preference for the same food resource between the abundant, widespread, and rare, restricted species would further contribute to rarity of specialized species is not clear. When preferred resources are limited, species expand their niches to include the less preferred unexplored alternatives (Svanbäck & Bolnick 2005); in this case, generalists expand their niches to alternative resources unlike specialists. This may further exacerbate the rarity of the already rare species because of increased overlap.

Boro (2017) did not find support for the resource breadth hypothesis in this small mammal community despite the strong positive AOR. Diet breadth was estimated at a much coarser classification of C3 and C4 plants using stable isotopes i.e., browsers (C3 plants feeders), grazers (C4 plants feeders), and mixed feeders (C3 and C4 plants feeders). The study expected generalist (mixed feeders) to be abundant and widespread, and specialists (grazers and browsers) to be rare and restricted. The contrasting results could be as a result of the multiple dimensions in niche utilization. The taxonomical level at which the niche breadth is evaluated may yield differing conclusions. A species can be a specialist at higher taxonomical classification i.e., family level and the same species can be a generalist when the evaluation is done at a species level (Kartzinel & Pringle 2020).

Despite a similar prediction that total niche width expand as resources become limiting, the niche variation hypothesis (Van Valen 1965) and optimal foraging theory (MacArthur &

Pianka 1966) differ on how individuals select diet as food resources become limiting. The small mammals of Mpala Conservancy increased TNW with increase in abundance in accordance with the two hypotheses/ or theory. However, the most abundant and widespread species, which was also the one exhibiting the greatest TNW, increased TNW with increase in among individual dietary variation as predicted by the niche variation hypothesis. This finding points to a possibility of individuals differentiating resource use to mitigate intraspecific competition (Araújo *et al.* 2011; Pansu *et al.* 2019). However, this study did not compare the degree of TNW and among individual dietary variation under differing resource availability.

Pansu *et al.* (2019) found support for the niche variation hypothesis in narrow-muzzled species, but generally there was no clear evidence of greater individual variation in generalized species. Animals with narrow muzzles are expected to be more selective, which might be true for the small mammals of Mpala Conservancy. However, such a study will require collecting morphometrics data for comparisons among species and with diet. Manlick *et al.* (2021) also found support for the niche variation hypothesis using repeated stable isotope on individuals. Individuals increased foraging specialization to mitigate intraspecific and interspecific competition. However, this came at cost because the survival of specialized individuals declined while those of generalized individuals increased. The study concluded that flexible foraging strategies play a major role in the ability of species to deal with environmental changes.

5.2 Conclusion and recommendations

The Mpala Conservancy small mammal community is shaped by individual differences in resource use, such that individuals of abundant and widespread species increase and maintain their abundance and occupancy through individual differentiation in resource use. Mpala Conservancy being a semi-arid environment, experiences high variability in environmental variables such as

rainfall and food availability; species should employ strategies that overcomes these challenges. Abundant, widespread species seem to be differentiating resource use to alleviate competition. Keesing and Young (2014) and Kartzinel *et al.* (2014) showed that small mammals doubled in plots that excluded the large mammalian herbivores. This observation could point to a possibility of alleviation of competition following the exclusion of large mammals or simply improved cover. The effects of climate change, especially increased drought, are expected to stretch the individual differentiation even further, but this should be limited by available resources leading to declines even in the generalist small mammals. Moreover, continued specialization in individuals of these species may lead to differentiation within species to bring about sub-species or completely new species (Carscadden *et al.* 2020). Unfortunately, specialist species are expected to decline even further particularly if their preferred resources are affected (Kartzinel & Pringle 2020).

Future studies should attempt to assess resource use in species of conservation concern in a multidimensional approach. Species that specialize in all or most of the axis are at a greater risk of extinction in the event of environmental disturbances that affect their preference. Additionally, studies on niche breadth hypothesis should attempt to explain whether generalism in abundant, widespread species exacerbates extinction of rare, restricted species or promotes coexistence among specialist species by preventing one species from gaining fitness advantages over the other species. Lastly, direct measures of fitness (i.e., survival and reproduction) should be linked to resource use and abundance-occupancy relationships with the aim of taking a reductionist approach to explaining macroecological patterns.

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7.0 APPENDICES

Table 2.1: The taxonomical classification of the African muroids (Superfamily Muroidea) according to Kingdon *et al.* (2013).

<p>SUPERFAMILY</p> <p>MUROIDAE (mice, rats, gerbils, and relatives)</p>	<p>Family Cricetidae (Voles and Maned Rat)</p> <p>2 species in 2 genera and 2 subfamilies</p> <p>Subfamily Arvicolinae: <i>Genus Microtus</i> (Voles)</p> <p>Subfamily Lophiomyinae: <i>Genus Lophiomyis</i> (Maned Rat)</p>
	<p>Family Nesomyidae (Climbing mice, Fat mice, Swamp mouse, Rock mice, Pouched rats and mice, Large-eared mice, and White-tailed rat)</p> <p>34 species in 12 genera and 5 subfamilies</p> <p>Subfamily Cricetomyinae: <i>Genus Beamys</i> (Long-tailed Pouched Rat), <i>Genus Cricetomys</i> (Giant Pouched Rats), <i>Genus Saccostomus</i> (Pouched Mice)</p> <p>Subfamily Delanymyinae: <i>Genus Delanymys</i> (Delany's Swamp Mouse)</p> <p>Subfamily Dendromurinae: <i>Genus Dendromus</i> (African Climbing Mice), <i>Genus Dendroprionomys</i> (Velvet Climbing Mouse), <i>Genus Malacothrix</i> (Long-eared Mouse), <i>Genus Megadendromus</i> (Bale Mouse), <i>Genus Prionomys</i> (Bate's Climbing Mouse), <i>Genus Steatomys</i> (Fat Mice)</p> <p>Subfamily Mystromyinae: <i>Genus Mystromys</i> (African White-tailed Rat)</p> <p>Subfamily Petromyscinae: <i>Genus Petromyscus</i> (Pygmy Rock Mice)</p>

	<p>Family Spalacidae (Mole-rats and African root-rats)</p> <p>3 species in 2 genera</p> <p>Subfamily Spalacinae: <i>Genus Spalax</i> (Mole Rats)</p> <p>Subfamily Tachyoryctinae: <i>Genus Tachyoryctes</i> (Root-rats)</p>
	<p>Family Muridae (Old World rats and mice, vlei rats, gerbils and jirds)</p> <p>264 species in 50 genera and 5 subfamilies</p> <p>Subfamily Deomyinae: <i>Genus Acomys</i> (Spiny Mice), <i>Genus Deomys</i> (Rusty Link Rat), <i>Genus Lophuromys</i> (Brush-furred Rats), <i>Genus Uranomys</i> (Rudd's Brush-furred Mouse)</p> <p>Subfamily Gerbillinae: <i>Genus Ammodillus</i> (Ammodile), <i>Genus Desmodilliscus</i> (Brauer's Dwarf Gerbil), <i>Genus Desmodillus</i> (Cape Short-tailed Gerbil), <i>Genus Gerbilliscus</i> (Gerbils), <i>Genus Gerbillurus</i> (Hairy-footed Gerbils), <i>Genus Gerbillus</i> (Gerbils), <i>Genus Meriones</i> (Jirds), <i>Genus Microdillus</i> (Peel's Pymy Gerbil), <i>Genus Pachyuromys</i> (Fat-tailed Jird), <i>Genus Psammomys</i> (Sand Rats), <i>Genus Sekeetamys</i> (Bushy-tailed Jird), and <i>Genus Taterillus</i> (Taterils)</p> <p>Subfamily Leimacomyinae: <i>Genus Leimacomys</i> (Buttner's Forest Mouse)</p> <p>Subfamily Murinae: <i>Genus Aethomys</i> (Veld Rats), <i>Genus Apodemus</i> (Field Mice), <i>Genus Arvicanthis</i> (Grass Rats), <i>Genus Colomys</i> (African Water Rat), <i>Genus Dasymys</i> (Shaggy Rats), <i>Genus Dephomyys</i> (Defua Rat), <i>Genus Desmomys</i> (Scrub Rats), <i>Genus Grammomys</i> (Thicket Rats), <i>Genus Heimyscus</i> (African Smoky Mouse), <i>Genus Hybomys</i></p>

	<p>(Forest Mice), <i>Genus Hylomyscus</i> (Wood Mice), <i>Genus Lamottemys</i> (Mount Oku Rat), <i>Genus Lemniscomys</i> (Grass Mice), <i>Genus Malacomys</i> (Swamp Rats), <i>Genus Mastomys</i> (Multimammate Mice), <i>Genus Muriculus</i> (Ethiopian Striped Mouse), <i>Genus Mus</i> (Old World Mice and Pygmy Mice), <i>Genus Mylomys</i> (Mill Rats), <i>Genus Myomyscus</i> (Meadow Mice), <i>Genus Nesokia</i> (Bandicoot Rat), <i>Genus Nilopegamys</i> (Ethiopian Water Rat), <i>Genus Oenomys</i> (Rufous-nosed Rats), <i>Genus Pelomys</i> (Creek Rats), <i>Genus Praomys</i> (Soft-furred Mice), <i>Genus Rattus</i> (Rats), <i>Genus Rhabdomys</i> (Four-striped Grass Mouse), <i>Genus Stenocephalemys</i> (Ethiopian Rats), <i>Genus Stochomys</i> (Target Rat), <i>Genus Thallomys</i> (Acacia Rats), <i>Genus Thamnomys</i> (Thicket Rats), and <i>Genus Zelotomys</i> (Broad-headed Mice)</p> <p>Subfamily Otomyinae: <i>Genus Otomys</i> (Vlei Rats), <i>Genus Parotomys</i> (Whistling Rats)</p>
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Table 3.2: Counts of small mammals per species per sampled plot for each sampling survey (y1: y9).

Species	Plot	y1	y2	y3	y4	y5	y6	y7	y8	y9
AEHI	CENTRAL1CON	0	0	0	0	0	0	0	0	0
ELRU	CENTRAL1CON	1	3	3	1	1	1	2	1	0
GERO	CENTRAL1CON	2	3	6	3	2	16	1	5	1
SAME	CENTRAL1CON	0	0	0	0	0	1	0	1	0

TAHA	CENTRAL1CON	0	0	0	0	0	0	0	1	0
AEHI	CENTRAL2CON	0	0	0	0	0	0	0	0	0
ELRU	CENTRAL2CON	2	0	1	0	1	0	1	1	0
GERO	CENTRAL2CON	2	0	1	0	0	3	0	2	0
SAME	CENTRAL2CON	0	1	0	0	0	0	0	0	0
TAHA	CENTRAL2CON	0	0	0	0	0	10	1	0	1
AEHI	CENTRAL3CON	1	0	0	0	0	0	0	0	0
ELRU	CENTRAL3CON	0	0	0	0	0	0	0	2	0
GERO	CENTRAL3CON	2	6	10	2	2	13	1	3	3
SAME	CENTRAL3CON	0	0	0	0	0	0	0	0	0
TAHA	CENTRAL3CON	0	0	0	0	1	4	0	0	0
AEHI	CENTRAL1LMH	10	8	11	14	14	16	9	23	22
ELRU	CENTRAL1LMH	9	6	9	5	2	2	5	7	4
GERO	CENTRAL1LMH	7	7	8	0	4	8	6	2	9
SAME	CENTRAL1LMH	10	4	7	7	9	11	10	14	6
TAHA	CENTRAL1LMH	0	0	0	0	0	0	0	0	0
AEHI	CENTRAL2LMH	7	2	14	12	3	30	13	5	2
ELRU	CENTRAL2LMH	3	0	1	2	0	0	1	1	1
GERO	CENTRAL2LMH	2	0	0	0	0	15	4	11	4
SAME	CENTRAL2LMH	5	1	0	5	1	7	2	8	2
TAHA	CENTRAL2LMH	0	0	0	0	0	0	0	0	0
AEHI	CENTRAL3LMH	1	2	5	0	0	3	2	3	4
ELRU	CENTRAL3LMH	11	1	1	1	2	0	0	0	0

GERO	CENTRAL3LMH	8	6	10	3	2	19	5	3	3
SAME	CENTRAL3LMH	0	3	4	17	13	18	14	5	9
TAHA	CENTRAL3LMH	1	0	0	0	0	0	0	0	0
AEHI	NORTH1CON	0	0	0	0	0	0	0	0	0
ELRU	NORTH1CON	1	0	2	0	1	1	0	0	0
GERO	NORTH1CON	0	0	2	0	0	0	0	5	1
SAME	NORTH1CON	0	0	0	0	0	0	0	0	0
TAHA	NORTH1CON	0	0	0	0	1	3	1	1	0
AEHI	NORTH2CON	0	0	0	0	0	0	0	0	0
ELRU	NORTH2CON	0	0	0	0	0	0	0	0	0
GERO	NORTH2CON	0	0	0	3	1	4	1	5	1
SAME	NORTH2CON	0	0	0	0	0	0	0	0	0
TAHA	NORTH2CON	0	0	0	0	0	0	0	0	0
AEHI	NORTH3CON	0	0	0	0	0	0	0	0	0
ELRU	NORTH3CON	5	0	0	0	2	0	0	1	0
GERO	NORTH3CON	0	0	0	3	2	1	10	2	3
SAME	NORTH3CON	0	0	0	0	0	0	0	0	0
TAHA	NORTH3CON	0	0	1	1	0	0	1	0	1
AEHI	NORTH1LMH	3	1	12	22	19	22	19	20	9
ELRU	NORTH1LMH	1	1	2	1	2	0	1	3	0
GERO	NORTH1LMH	3	10	4	3	9	15	6	8	0
SAME	NORTH1LMH	0	0	1	0	0	3	11	6	3
TAHA	NORTH1LMH	0	0	0	0	0	0	0	0	0

AEHI	NORTH2LMH	0	0	1	0	0	4	9	9	2
ELRU	NORTH2LMH	0	0	0	0	2	0	0	0	0
GERO	NORTH2LMH	4	5	1	1	4	8	13	6	0
SAME	NORTH2LMH	0	0	0	9	3	20	16	6	12
TAHA	NORTH2LMH	0	0	0	0	0	0	0	0	0
AEHI	NORTH3LMH	0	0	1	0	5	5	3	7	13
ELRU	NORTH3LMH	0	0	0	0	2	0	0	0	2
GERO	NORTH3LMH	1	3	0	7	10	0	6	22	3
SAME	NORTH3LMH	0	0	1	1	7	3	7	3	11
TAHA	NORTH3LMH	0	0	0	0	0	0	0	0	0
AEHI	SOUTH1CON	0	0	0	0	0	1	0	0	0
ELRU	SOUTH1CON	0	0	0	0	0	1	1	0	0
GERO	SOUTH1CON	3	1	1	0	2	5	3	3	2
SAME	SOUTH1CON	0	0	1	1	0	1	5	4	0
TAHA	SOUTH1CON	0	0	0	0	0	0	0	0	0
AEHI	SOUTH2CON	0	0	1	4	0	0	5	1	0
ELRU	SOUTH2CON	0	0	0	0	0	0	1	2	0
GERO	SOUTH2CON	0	0	0	5	7	2	10	11	13
SAME	SOUTH2CON	0	2	0	6	3	2	1	3	5
TAHA	SOUTH2CON	0	0	0	0	0	0	0	0	0
AEHI	SOUTH3CON	0	0	0	0	0	0	0	0	0
ELRU	SOUTH3CON	0	0	0	0	3	0	2	0	0
GERO	SOUTH3CON	1	6	7	4	0	2	3	2	0

SAME	SOUTH3CON	2	4	0	0	0	0	4	1	2
TAHA	SOUTH3CON	0	0	0	0	0	0	0	0	0
AEHI	SOUTH1LMH	5	7	40	27	20	37	14	32	28
ELRU	SOUTH1LMH	0	0	2	1	0	0	0	0	0
GERO	SOUTH1LMH	0	6	1	3	9	21	16	17	11
SAME	SOUTH1LMH	13	9	23	27	29	51	50	26	15
TAHA	SOUTH1LMH	0	0	0	0	0	0	0	0	0
AEHI	SOUTH2LMH	8	15	34	46	40	38	20	29	28
ELRU	SOUTH2LMH	0	1	0	0	2	0	0	3	2
GERO	SOUTH2LMH	7	11	19	18	18	5	1	15	13
SAME	SOUTH2LMH	3	4	2	2	8	15	22	16	8
TAHA	SOUTH2LMH	0	0	0	0	0	0	0	0	0
AEHI	SOUTH3LMH	4	14	13	7	3	15	12	20	11
ELRU	SOUTH3LMH	0	5	0	0	7	2	1	0	0
GERO	SOUTH3LMH	7	4	9	2	3	10	1	18	10
SAME	SOUTH3LMH	0	2	4	4	3	17	0	2	4
TAHA	SOUTH3LMH	0	0	0	0	0	0	0	0	0
