Population Ecology of *Rhabdomys dilectus dilectus* in the Western Soutpansberg Mountains

Master of Environmental Sciences, University of Venda

Faculty of Science, Engineering and Agriculture
Department of Geography and Environmental Sciences
Candidate: Vümboni Harry Msimango
Student Number: 15014997

Supervisor:

- **Prof EM Stam**

Co-Supervisors:

- **Prof P.J Taylor**
- **Prof G Ganem.**

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Declaration

I, **Vümboni Harry Msimango**, of ID No **961114 5215 088**, Student No **15014997** declare that this dissertation is my own unaided work. It is being submitted for the degree of Master of Environmental Sciences in the University of Venda, Thohoyandou. It has not been. submitted before for any degree or examination in any other university.

Vümboni Harry Msimango

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Abstract

This thesis explores the population ecology of the four-striped grass mouse (*Rhabdomys dilectus dilectus*) at the Lajuma Research Centre, within the Luvhondo Nature Reserve in the Western Soutpansberg Mountains, South Africa. Conducted from July 2020 to November 2021, the study examined the species' population dynamics, habitat preferences, and reproductive patterns across three distinct ecological sites: Wetland, Wilderness Camp, and Patches. Specifically, it aimed to assess how environmental variables, such as rainfall and habitat characteristics, influence the distribution, abundance, and reproductive success of *R.d. dilectus* in these diverse habitats.

R.d. dilectus is known to inhabit mesic environments, favoring continuous vegetation cover while avoiding bare soil. However, findings from this study suggest that its habitat range may be slightly broader than previously documented. Extensive bi-monthly trapping sessions using PVC live traps baited with peanut butter, oats, sunflower seeds, and salt were conducted to capture individuals, which were then identified, measured, marked, and released. Habitat characteristics, including vegetation cover and composition, were assessed alongside local weather conditions. Statistical analyses, including non-parametric and parametric tests, Jaccard Similarity Index for vegetation comparison, and rarefaction curves for species diversity, were used to evaluate trapping success, the influence of environmental factors, and the composition of the small mammal community.

Results indicate that *R.d. dilectus* was the most abundant species across all study sites, with the highest population density observed in the Wetland due to its mesic conditions. Rainfall significantly influenced trapping success, with a delayed response linked to increased vegetation growth and resource availability, particularly in the Wetland. The Wilderness Camp exhibited greater species diversity, while the Patches had higher diversity indices despite lower overall species richness. Microhabitat conditions, such as grass cover and predation risk, played a crucial role in shaping the spatial distribution of *R.d. dilectus* and other small mammal species. Reproductive activity varied across sites, with continuous breeding observed in the Wetland, whereas the Wilderness Camp and Patches exhibited more sporadic reproductive patterns.

This research provides valuable insights into the ecological flexibility and habitat preferences of *R.d. dilectus*, expanding current knowledge of its population dynamics in heterogeneous environments. The findings highlight the role of environmental factors in shaping small mammal communities and offer important implications for the conservation management of rodent populations in fluctuating ecosystems.

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Keywords: *Rhabdomys dilectus dilectus, population ecology, genetic diversity, climate change, Luvhondo Nature Reserve, mesic environments, trapping methodology, demographic variability, reproductive behaviors, biodiversity dynamics.*

1. Introduction

1.1. Biological Model

The African rodent genus *Rhabdomys* (striped mice) is widely distributed in southern and eastern Africa. It is adapted to various conditions, from arid, semi-arid to mesic habitats, grasslands to savannas. Based on mtDNA phylogenetic analysis, the genus comprises at least four species belonging to distinct molecular clades occurring in different environmental conditions (du Toit et al., 2012). *R. bechuanae*, *R. intermedius* and *R. pumilio* occur in arid to semi-arid environments in southern Africa, whilst R. dilectus dilectus (hereafter, *R.d. dilectus*) and R. dilectus chakae (hereafter R.d. chakae) occur in semi-arid to mesic habitats including grasslands in southern and eastern Africa (Ganem et al., 2020). *Rhabdomys* is also a key and often the most abundant member of Afromontane grassland communities (Schradin & Pillay, 2004).

An ancestral karyotype of 2n=48 has been identified in *R. pumilio*, *R. bechuanae and R. intermedius*. This same karyotype is present in *R.d. chakae*, while a derived karyotype having a fixed Robertsonian fusion mutation (2n=46) is found in *R.d. dilectus* from northern South Africa through to East Africa, except for populations from several Mountain ranges in eastern Africa which bear a recently derived karyotype of 2n=38 (Rambau *et al.,* 2003, Castiglia *et al.,* 2012). The distribution of different species and clades in southern Africa generally coincides with the boundaries of different biomes, with contact zones between species occurring at or near boundaries between biomes (du Toit *et al.*, 2012b; Meynard *et al.*, 2012; Taylor *et al.*, 2013, 2020)

R. bechuanae is distributed exclusively in the northwestern region of South Africa (Kotze, 2019). It occurs in the Northern Cape, the Northwest and the Free State provinces in South Africa. *R. intermedius* is endemic to South Africa, with a central/inland to a southerly distribution (Mackay, 2011; Ganem et al., 2020). The distribution of *R. pumilio* is from the coastal regions of the Western Cape to Southern Namibia (du Toit et al., 2012; Rymer et al., 2013; Ganem et al., 2020). A subspecies *R. pumilio* coastal B with a very limited distribution, was found in Fort Beaufort (du Toit *et al.,* 2012) and Grahamstown (Coetzer, Willem & Grobler, 2018) and the western limit of the coastal region of the Eastern Cape Province (Ganem et al., 2020). In all three of these locations, *R. pumilio* coastal B co-occurs with *R.d. chakae*, forming the southwestern limit of *R. pumilio's range*. *R. dilectus* has a mesic

distribution, i.e., it occurs in grasslands where the ratio of forbs to grass species can be 5-6:1 (Hallam, 2007). It is distributed across the Eastern parts of South Africa, Zimbabwe, Uganda, and Tanzania and is found in southern Angola (Castiglia et al., 2012; du Toit et al., 2012a; Ganem et al., 2020;Krásová et al., 2021).

Data suggest that the divergence between the lineages of *Rhabdomys dilectus dilectus* and *R. d. chakae* occurred relatively recently, during the Pleistocene epoch (approximately 1.66 to 2.2 million years ago), likely as a result of a vicariance event—specifically, the formation of physical barriers in the eastern savanna (Castiglia et al., 2012). Since the phylogeographic structure of the genus was clarified (Rambau et al., 2003; Du Toit et al., 2012; Castiglia et al., 2012), only a limited number of studies have focused on *R. d. dilectus*. These include works by Abu Baker and Brown (2010, 2014), which primarily addressed the species' ecology, alongside others that examined genetic and taxonomic aspects. Du Toit et al. (2012) incorporated 33 specimens of *R. dilectus*, originally collected by Rambau et al. (2003), in a broader phylogenetic analysis of *Rhabdomys*, providing a sufficient foundation for genetic studies.

Different species within the genus *Rhabdomys* occupy a wide range of habitats, from xeric to mesic environments, each with specific habitat preferences. *R.d. dilectus* is primarily found in mesic environments, favouring habitats with continuous cover while actively avoiding bare soil (Abu Baker & Brown, 2010; Dufour et al., 2015).

This study focuses on *R.d. dilectus* and was conducted at three sites within the Lajuma Research Centre, located in the Luvhondo Nature Reserve in the Soutpansberg Mountains of northern Limpopo Province, South Africa. The research aimed to monitor seasonal changes in the species' population demographics and assess the composition of the local small mammal community it inhabits. By doing so, it contributes to the limited understanding of *R.d. dilectus* population ecology (Abu Baker & Brown, 2010; Dufour et al., 2015).

Previous studies have explored various aspects of *R.d. dilectus* ecology. Abu Baker & Brown (2010) investigated its behavioural responses to perceived danger across different habitat conditions in the Luvhondo Nature Reserve. Dufour et al. (2015) examined its ecology in marginal semi-arid environments at the western edge of its distribution. This study builds on these works, expanding knowledge of the species' population dynamics in a mesic environment.

The effect of temporal and geographical scales on ecological determinants of biodiversity

Earth's biological systems have historically been influenced by their paleoclimates. Changes resulting from these historical climate occurrences have influenced speciation and ecosystem dynamics as they have altered the habitats and geographical ranges of species (Hewitt, 2011; du Toit *et al.,* 2012). Historically, long-term climate change from the Cenozoic to the mid-Pleistocene was found to be a critical driver of diversification (Couvreur *et al.,* 2021). During these periods, shifts in temperature, precipitation patterns, and the extent of glaciations led to the creation of new habitats and migration corridors, facilitating genetic divergence and the emergence of new species. However, understanding these processes requires not only examining long-term trends but also focusing on short-term adaptations, tolerance levels, and the scale and rate at which these processes operate. These factors are crucial for conservation efforts and modelling the extent to which present climate dynamics will affect biodiversity (Nogués-Bravo *et al.,* 2018).

Apart from temporal effects, geographical variation also shapes biodiversity. Dawson (2011) argues that while climate envelope models—models which describe relationships between species occurrences and bioclimate variables such as temperature and precipitation to define a species' climate niche (Wetland and Aquatic Research Centre, 2016; Meynard *et al.,* 2012)—are popular for describing the impact of climate change on biodiversity, they may have limitations. These models often do not account for non-climatic factors critical for a species' survival, such as habitat fragmentation, biotic interactions, and species-specific traits like exposure, tolerance, and adaptability. Moreover, spatially broad models may not necessarily predict the ecological responses of species at a local scale (Kuo & Sanford, 2009). For example, while a model might predict a species' range shift based on temperature increases, it might not account for local microhabitats that provide refuges from extreme conditions, leading to inaccuracies. While large-scale considerations are useful for understanding the broader context of climate change implications on biological communities, they may be limited in their assumption of homogeneity within species' ranges, potentially overlooking critical local adaptations and interactions.

Therefore, both temporal and geographical scales must be considered to develop a comprehensive understanding of climate change impacts on biodiversity. This includes recognizing the historical context of species' adaptations and the current, rapidly changing conditions that may require species to adapt at unprecedented rates. Integrating these perspectives can enhance predictive models and inform more effective conservation strategies that account for both broad-scale trends and local ecological complexities.

1.2. Climate Crisis and Biodiversity

The effects of recent climatic change on the spatial and temporal distribution of biota is well documented (Pecl *et al.,* 2017; Cameron & Scheel, 2001). Global Climate Change (GCC) models indicate imminent meteorological changes that will be observed in precipitation and temperatures over the next few decades (Cameron & Scheel, 2001; Schwartz, 2018; Nunez et al., 2019). According to Pecl *et al.* (2017), "Critically, the pervasive impacts of changes in species distribution transcend single systems or dimensions, with feedback and linkages among multiple interacting spatial and temporal scales and through entire ecosystems, inclusive of humans." The latter makes a case for why studying and understanding evolving ecosystems in the context of climate change is critical, as a wide array of environmental pressures drives ecological systems.

With growing concerns about climatological changes, understanding the adaptive capacities of various ecosystems, communities and organisms raises urgent and challenging questions in both fundamental and applied research (Pecl *et al.,* 2017). It is projected that global climate change may increase aridity in large parts of the world (Girvetz & Zganjar, 2014; Asadi Zarch et al., 2017). Such changes already impact many species, including grassland rodents such as *Otomys auratus* which has become locally extinct over most of the western Soutpansberg over the past century (Taylor *et al.,* 2016), making it urgent to evaluate the response capacity of small mammals to climate changes, in natural environmental conditions.

This study set out to understand the model species *R.d. dilectus* characteristics across different habitats and seasons to understand how its population ecology varies across habitats but also to have a model that could be useful to infer how sensitive such species may be to climate induced changes in their ecosystems.

1.3. Population Ecology

Populations are defined as groups of organisms of the same species populating a given geographical range, with some temporary or spatial isolation from other groups (Turchin, 2003; Pecl *et al.,* 2017; Ferris & Wilson, 1987; Krebs, 2013; Batzli, 2015). Population ecology is interested in exploring the size of plant and animal populations and the biotic and abiotic processes responsible for these sizes. It ultimately focuses on understanding the factors that influence the dynamics of a population (Rockwood, 2015).

Population ecology aims to understand the factors that affect the distribution and abundance of a population, and the current study addresses aspects of the ecology of a population of *R.d. dilectus.*

Population processes result from interactions between extrinsic (e.g., food availability, temperature, competition, predation) and intrinsic (e.g., population density) environmental drivers. Previous studies found that for the semi desert species, *R. pumilio*, food availability was the main driver for variation in population sizes across spatio-temporal conditions (Maille et al., 2015; Hayes et al., 2017).

Whilst different populations pertain to the same species, their ecology, behaviour, physiology, and morphology may vary geographically (Andrewartha & Birch, 1986; Turchin, 2003). These attributes can be used to assess the similarities and differences between populations. This study assesses how local conditions influence population ecology and to a larger extent, determine if variation between populations follows variations in ecological conditions.

1.4. Aims

The general aim of this research is to describe the local ecology and population structure of *R.d. dilectus* at Lajuma Research Station in the Soutpansberg of Limpopo Province and assess the influence of several abiotic and biotic factors on seasonal and annual variations in the local small mammal communities, and the demography of *Rhabdomys* populations through correlative approaches.

1.4.1. *Research Objectives*

i. To characterise the small mammal community in three sites with different ecological characteristics and across seasons.

ii. To determine the population structure and demography of *R.d. dilectus* in the three sites across seasons and years.

iii. To determine how variation in abiotic (rainfall) and biotic (competition) factors across the three study areas may impact on *R.d. dilectus* population characteristics.

iv. To assess the influence of habitat characteristics and vegetation on the population characteristics of *R.d. dilectus.*

2. Literature Review

2.1. Climate, Habitat Transformation and Speciation of Rodents in Southern Africa

The Quaternary period significantly influenced the evolution and life history of southern African rodents, especially through climate oscillations and their effects on vegetation and topography, which facilitated allopatric divergence and speciation (Du Toit *et al.,* 2012; Rambau *et al.,* 2003; Lima *et al.,* 2002). These evolutionary processes have shaped current flora and fauna assemblages, extending beyond recent millennia and continuing to influence species and ecological dynamics at various scales (Du Toit *et al.,* 2012).

In Southern Africa, small mammals such as those in the four genera *Rhabdomys, Aethomys, Elephantulus*, and *MyOtomys* were notably affected by climate oscillations during the Plio-Pleistocene (Montgelard & Matthee, 2012). Topographical features like elevation, altitude, and river streams, in conjunction with climatic shifts, played a crucial role in gene flow and speciation, with high-elevation areas often serving as centres of endemism due to their conducive conditions for speciation (Steinbauer *et al.,* 2016).

During the Quaternary period, spanning approximately 2.6 to 2.9 million years ago to the present, climatic oscillations were identified as key drivers of rodent species divergence. Notably, three aridification periods potentially linked to the divergence of the *Rhabdomys* genus were observed (Meynard *et al.,* 2012; Montgelard & Matthee, 2012). Recent data indicates that current climate change is a major driver of species loss (Roman Palacios & Wiens, 2020). The aridification periods around 3.4 million years ago led to adaptations, diversification, and migrations of taxa due to habitat expansion or regression caused by increased aridity (Svenning *et al.,* 2015).

Montgelard & Mathee (2012) sought to correlate the divergence of genetic lineages with major paleoclimatic events to determine the role of climate in rodent diversification/speciation in Southern Africa. The latter study analysed sequences from nine rodent genera , i.e., *Aethomys, Otomys, MyOtomys, Rhabdomys, Mastomys, Saccostomus, Cryptomys*, and *Xeru*, focusing on mitochondrial cytochrome divergence over the last 5 million years. Phylogenetic and molecular dating analyses revealed that 29 out of 35 identified clades diversified during the Plio-Pleistocene, with the remaining clades linked to the upper Miocene period. These findings highlight the last 5 million years as significant in the evolutionary history of African rodents (Montgelard & Matthee, 2012).

However, evidence for a correlation between lineage diversification and peak aridification in the Quaternary period was limited. Montgelard & Matthee (2012) suggested a continuous evolutionary process influenced by climatic oscillations over the last 5 million years, leading to cyclic shifts in vegetation structures and ranges, which appear to be more significant than peak aridification periods.

2.2. Habitat Patches and Spatial Heterogeneity

Habitat patches contribute to spatial heterogeneity, resulting in an uneven distribution o individuals and species across a given area. Abu Baker & Brown (2010) illustrated this by showing variations in species counts across different research stations and distances from patch edges within the former Luvhondo Nature Reserve (now Lajuma Research Centre).. Using live traps and giving up densities (GUD), a metric that measures the remaining food when a forager quits a patch, they illustrated how edge effects and habitat fragmentation impact populations (Verdolin, 2006). Higher predation risk is associated with increased GUD in areas with dense vegetation cover (Wheeler & Hik, 2014). The edge effect, which describes changes in population or community structures at habitat boundaries, leads to increased biodiversity at habitat edges (Didham *et al.,* 1998).

In this study, bushveld is characterized by patches of dense trees interspersed within open spaces, creating spatial heterogeneity that influences food availability, nest-site selection, and predation risk. Similar patterns have been observed in previous studies. Meynard et al. (2012) suggested that high abundances and low giving-up densities (GUD) occur in core habitats with dense vegetation, where food resources are plentiful, and predation risk is reduced. Conversely, lower abundances and higher GUDs indicate riskier habitats with fewer foraging opportunities. Their findings showed that trapping success increased with distance from wooded areas into grasslands, where GUDs were lower. Likewise, *R.d. dilectus* in this study perceived wooded patches as riskier and less opportunistic than more open habitats, with grasslands supporting higher trapping success and lower GUDs, indicating habitat preference (Meynard et al., 2012; Dufour et al., 2015).

The findings from this study align with those of Meynard et al. (2012) and Dufour et al. (2015) despite differences in geographic location. Meynard et al. (2012) conducted their research across the southern African subregion, including South Africa, Namibia, and Lesotho, while Dufour et al. (2015) focused on four nature reserves within the savanna and grassland biomes of central South Africa—three in the Free State Province and one near the North West Province boundary. Although this study was conducted in a montane environment, the results similarly highlight how habitat heterogeneity influences *R.d. dilectus* distribution and habitat selection. Across all sites, including those of Meynard et al. (2012) and Dufour et al. (2015), *R.d. dilectus* exhibited a preference for more open habitats with

lower GUDs and greater trapping success, reinforcing the broader ecological pattern of habitat use by this species.

2.3. Species Composition Across Different Altitudes

Mountains, being biodiversity hotspots, host diverse microhabitats influenced by distinct microclimates. Munyai & Foord (2012) investigated spatial variation and diversity along north-south altitudinal transects in the Soutpansberg, focusing on ant taxa's restriction to altitudinal zones and vegetation types. They also aimed to understand how biological communities might respond to climate change across altitudes. Mountains facilitate greater environmental control due to dispersal limitations, often leading to allopatric speciation.

Their study, conducted on the Soutpansberg, identified five vegetation types across different altitudes, using pitfall traps to sample ants. Ant richness and density were highest in warm, open habitats with bare ground and high temperatures, while medium to small-scale spatial variables accounted for significant variation in ant assemblages. Local environmental conditions, like rainfall and temperature, were more influential than regional processes (Munyai & Foord, 2012).

Northern slopes of the Soutpansberg mountains in Munyai and Foord (2012) had more specialist species, whereas southern slopes had more generalists. Temperature played a crucial role in structuring ant assemblages, suggesting that mountains might mask climate effects on these communities. Furthermore, Munyai and Foord (2012) predicted that an increase in CO_2 and rainfall threaten to alter thermal conditions, potentially affecting ant community structures. In addition, such predicted change also pose threats to rodent populations such as *R.d. dilectus* in grasslands due to changing vegetation cover through thicket expansion (Abu Baker & Brown, 2010).

2.4. The Distribution of Rodents in Afromontane Ecosystems

With climate change and anthropogenic influences at the centre of global biodiversity decline, it has become imperative to determine the extent to which climate change, if not mitigated, could drive organisms to extinction, thereby compromising ecosystem quality (Botes *et al.,* 2006). Taylor *et al.* (2015) aimed to utilize various scientific models to assess how climate change could contract habitats and potentially influence the geographical range and distribution of various flora and fauna. While climate change threatens biodiversity at different altitudinal ranges, there was very limited data on its influence on Afromontane taxa prior to Taylor et al., (2015)'s study.

Using ecological niche models (ENMs), various scenarios can predict how different ecological communities will be affected by climate change (Taylor *et al.,* 2016). A MaxEnt model was employed

with various BIOCLIM predictors, along with CSIRO MK3.0, to model future climate variables. The Jack-Knife test assessed the impact of each variable on ecosystems in isolation. This model determined that the distribution of *Otomys auratus* would contract southwards, limiting it to higher altitudes (Taylor *et al.,* 2016). MaxEnt is used to model species distribution using presence-only data, which consists of known presences and a separate sample of locations from the population (Ward *et al.,* 2009; Elith *et al.,* 2011).

ENMs base their outcomes on factors such as dispersal patterns, land cover, the extent of protected land, and the adaptability of flora and fauna to transformed landscapes. For instance, based on different dispersal patterns, *Otomys angoniensis* was projected to expand its range, overlapping with *Otomys auratus* (Taylor *et al.*, 2016) Land cover maps present evidence of rapid anthropogenic development threatening natural habitats and their species. Bioclimatic models predict that projected climatic conditions will transform grasslands into Savanna biomes in Mpumalanga, North-West, Gauteng, and Limpopo (Taylor *et al.*, 2016). Under medium risk scenarios, tropical savanna biome species are predicted to replace or outcompete grassland biome species (Taylor *et al.*, 2016). *Otomys angoniensis* and *Otomys auratus* are thus ideal indicator species for the dynamics that may occur in grasslands and savanna biomes. This may impact the population dynamics of *Rhabdomys dilectus* in the Afromontane landscape of the Lajuma Research Centre, which hosts *Otomys*, *Rhabdomys*, *Mus minutoides*, *Dendromus mystacalis,* and some *Aethomys*species (Abu Baker & Brown, 2010).

Data spanning over 90 years confirms the historical shifts likely to affect animal and plant communities as ecosystems transform (Taylor et al., 2016). These transformations are indicated by transitions from open grasslands to dense woodlands, likely exacerbated by bush encroachment and other factors. Fauna on mountains is expected to experience the effects of climate change more intensely if dispersal opportunities are limited. The study and models utilized indicate that the effects of climate change will initially and more severely impact tropical, lower elevation mountains (Taylor *et al.*, 2016).

2.5. Spatial and Reproductive Differentiation of Small Terrestrial Mammals in the Western Soutpansberg Mountain

Small mammal distribution is affected by environmental variables and potential habitat transformations, whether natural or human induced. Rodents, which account for the largest portion of mammals globally, exhibit a ubiquitous distribution due to their high adaptability to evolving environmental conditions and relatively short reproductive cycles (Takele *et al.,* 2011; Chekol *et al.,* 2012).

Biotic and abiotic processes play significant roles in structuring small mammal communities, particularly rodent communities. With habitat transformation and climate change at the forefront of conservation concerns, exploring community composition, identifying habitat preferences, and monitoring population dynamics are crucial for understanding the changes induced by climate change (Pecl *et al.,* 2017; Dufour *et al.,* 2019). For instance, variables such as rainfall significantly influence the reproductive output of small mammals (Nemakhavhani 2015; Taylor *et al.* 2016).

Ecological processes are expected to influence the structure of ecological communities more significantly than competition, particularly concerning species composition of similarly sized mammals. These processes impact fluctuating populations, reproductive rates, and life expectancy (Nemakhavhani, 2015). Vegetation cover also influences species composition and population structures, with species such as *Rhabdomys dilectus* closely associated with habitats featuring good grass cover, while *Otomys* species prefer savanna, subtropical, and tropical grasslands.

Reproductive success in small mammals depends on factors such as age, sex, litter size, and frequency of litter. Seasonality also plays a crucial role, as some species reproduce at specific times or seasons, while others are more opportunistic. Timing influences breeding frequency and survival rates.

Nemakhavhani (2015) conducted a study on Bergplaats within the Luvhodo Nature Reserve in the Western Soutpansberg mountain range. Sherman traps were used for live trapping, and EstimateS was employed to determine species richness. The influence of various climatic variables was tested using Generalized Linear Models to analyse their combined and isolated effects on species richness. Correspondence analysis and cluster analysis were conducted to identify species habitat associations.

Trapping success was low during winter. Genus *Rhabdomys* , which has a specialized niche, was associated with specific vegetation structures. Coastal clades spanned across the Fynbos and Succulent Karoo Biome, while the Central clade was associated with the arid Nama-Karoo Biome. *Elephantulus myurus, Micaelamys namaquensis*, and *Aethomys ineptus* had broad savanna habitat distributions. *Otomys angoniensis* predominantly occurred around wetland habitats, along with *Dasymys* and *Mus minutoides*, which were also observed in grassland habitats (Nemakhavhani, 2015).

Grasslands displayed lower diversity compared to wetlands and rocky outcrops, primarily due to the high abundance of *Rhabdomys* species. *Crocidura mariquensis*, *Mastomys varius*, and *Dasymys incomtus* were dominant in wetland and rocky habitats. There was no significant influence of rainfall or temperature on species richness throughout the year.

For the four species recorded during the study, reproduction—indicated by the presence of scrotal males and lactating females—was not restricted to spring and summer but occurred throughout the

year. More males than females were trapped, possibly due to males having larger home ranges and being more active than females (Nemakhavhani, 2015).

2.6. Sampling and Altitudinal Variations in Rodent Populations on Afromontane Landscapes

Ecological sampling conducted at varied altitudinal points or transects provides valuable insights into the prevalent dynamics at both micro and macro-ecological scales (Clausnitzer & Kityo, 2001; Munyai & Foord, 2012; Taylor *et al.,* 2016). Available data generally indicate either a decrease in species richness with altitude or a mid-elevation peak, determined through sampling along altitudinal transects. At a micro scale, environmental variables such as vegetation structure, habitat complexity, and successional disturbances like fire or mass land degradation significantly influence the structure of small mammal communities along altitudinal gradients (Linden *et al.,* 2014; Taylor *et al.,* 2015).

Based on previous studies, it was hypothesized that a hump-shaped species richness pattern would be observed over the altitudinal transect, with ant species density and richness expected to peak at mid-elevation on the northern aspect of the Soutpansberg Mountain range. Additionally, it was hypothesized that seasonality would have an observable effect on species abundance, diversity, and body size. However, Taylor et al. (2015) found that seasonal effects on abundance and diversity were not significant, likely due to the mild cool season experienced in the study area.

The Luvhondo Nature Reserve in the Soutpansberg Mountain range is home to several small mammal species, including *Rhabdomys dilectus, Dasymys robertsii, Aethomyschrysophilus,* and *Aethomys ineptus*, among others. To assess species richness and distribution patterns, Taylor et al. (2015) employed various analytical methods. Species accumulation and rarefaction curves were generated using EstimateS, while Jackknife2 and Chao2 estimators were used to quantify species richness across different altitudes. Additionally, the RangeModel was applied to evaluate the mid-domain effect (MDE), a null model that predicts species richness patterns based solely on geometric constraints, excluding ecological or environmental influences (Colwell, Rahbek, & Gotelli, 2004).

The overall abundance of small mammal species did not show significant variation with altitude, season, or other environmental factors. However, *Aethomys ineptus, Micaelamys namaquensis*, and *Rhabdomys dilectus* exhibited seasonal fluctuations in abundance within specific altitudinal zones (Taylor et al., 2015). At the community level, seasonality had no significant impact on species abundance, diversity, or richness. Nonetheless, seasonal peaks in abundance for *A. ineptus, M. namaquensis*, and *R. dilectus* varied across different altitudes, highlighting the influence of local environmental conditions.

Trapping efforts were conducted in two primary vegetation types: Mountain Bushveld and Summit Sour Grassland. *Rhabdomys dilectus* and *Myosorex varius* were strongly associated with the upper grassland sites (Taylor et al., 2015). The absence of a significant seasonal effect on overall species abundance was attributed to the mild seasonal cooling in the study area. However, seasonality had a measurable impact on body mass, with *A. ineptus* and *M. namaquensis* exhibiting reduced body mass during the dry season, likely due to lower food availability, a pattern similar to that observed in *Saccostomus campestris* in northern South Africa (Ellison et al., 1993; Taylor et al., 2015).

The study also demonstrated that seasonal peaks in rodent densities varied across altitudes, cautioning against broad generalizations regarding optimal trapping times (Taylor et al., 2015).

2.7. *Rhabdomys* and *Rhabdomys dilectus dilectus*

The genus *Rhabdomys* comprises at least five mitochondrial species, characterized by distinct environmental niches and parapatric distributions, with several areas of sympatry at the margins of their ranges (Rambau *et al.,* 2003; du Toit *et al.,* 2012; Dufour *et al.,* 2015; Ganem *et al.,* 2020). This widespread *murid* genus is endemic to Africa, occurring in all African biomes except for forests, and is found throughout southern and eastern Africa (Castiglia *et al.,* 2012; Meynard *et al.,* 2012; Dufour *et al.,* 2015).

Current genetic studies group *Rhabdomys* into two main clades: a semi-arid group with four taxa—*R. bechuanae, R. intermedius, R. pumilio* coastal A (hereafter *R. pumilio*), and *R. pumilio* coastal B—and a mesic group comprising *R. dilectus chakae* and *R.d. dilectus* (Ganem *et al.,* 2020).

Rhabdomys dilectus includes several subspecies, with two occurring in South Africa and others in eastern Africa and Angola (Castiglia *et al.,* 2012; Ganem *et al.,* 2020). This study focuses on *R.d. dilectus*. Available data suggests that *R.d. dilectus* and *R.d. chakae* are sympatric at their range limits in Gauteng, as well as the North West and Free State Provinces, with *R.d. dilectus* displaying a northwestern limit in the Free State (Grange *et al.,* 2015; Ganem *et al.,* 2012). *R.d. dilectus* has a preference for denser vegetation and is mesic adapted, occurring primarily in grassland biomes (Mackay, 2011; du Toit *et al.,* 2012; Dufour *et al.,* 2015).

Despite the extensive research on *Rhabdomys*, there is still much unknown about the population demography and dynamics of *R.d. dilectus* in different habitat types and climatic conditions, or how their microhabitats influence these dynamics on a spatio-temporal basis. The lack of precise distribution data for these recently described species has implications for interpreting earlier population and epidemiological studies. For example, accurate host identification is crucial for

understanding the transmission of zoonotic agents and their potential impacts on entire ecosystems. Ongoing studies aim to better understand the distribution of the genus (Ganem *et al.,* 2020).

3. Materials And Methods

3.1. Study Area

The study was conducted in the Lajuma Research Centre (29°26'E, 23°01'S), which is located on the western Soutpansberg Mountains, forms part of the Luvhondo Nature Reserve in Limpopo province of South Africa (Fig. 1 and 2). The property covers about 430 hectares of land.

The study site is located in the subtropical region of the Soutpansberg Mountains, specifically on the western end, known as Luvhondo. This area ranges in altitude from 800 meters above sea level (a.s.l.) to a peak of 1747 meters a.s.l. (Abu Baker & Brown, 2010; Munyai & Foord, 2012; Taylor *et al.,* 2015). It is surrounded by gently rolling plains and lowlands ranging from 400 to 900 meters a.s.l., including the dry Limpopo River valley to the north.

The region experiences summer rainfall, typically occurring between October and March, with the peak rainfall months being January and February. The average annual rainfall on Luvhondo is approximately 730 mm, with precipitation increasing with altitude (Bumby *et al.,* 2002; Hahn, 2006). Across the Soutpansberg range, rainfall varies significantly, with around 400 mm on the northern slopes, 550 mm in the east, and up to 1800 mm on the central southern slopes (References Needed Here??). Much of this precipitation is orographic, resulting from moisture-laden air brought by prevailing south-easterly winds from the Indian Ocean, leading to significant rainfall on the southern scarp of the Soutpansberg (Kirchhof *et al.,* 2010).

The east-west orientation of the Soutpansberg acts as a barrier between the south-eastern maritime climate and the northern continental climate, creating distinct climatic conditions. The higher elevations, particularly on the southern and eastern slopes, are characterized by mist belt areas with frequent cloud cover and mist precipitation (Hahn, 2006).

The prevalent soil is loamy sand, resulting from the underlying sandstone geology present on Luvhondo. The soil types vary between microhabitats.

Lajuma Research Centre was identified as a suitable study area as *R.d. dilectus* was the only member of the genus that had ever been identified on the location (Ganem *et al.,* 2020). The environment type is Afromontane, comprising fragments of habitat with different characteristics; anything from grasslands, woodlands, wooded patches and montane forests (Abu Baker & Brown, 2010; Munyai &

Foord, 2012; Taylor *et al.,* 2015). This offers a variety of habitats and landscape characteristics, making it suitable to study the species in various environmental conditions.

Figure 1: Map of South Africa indicating location of study area (ArcGIS, 2023).

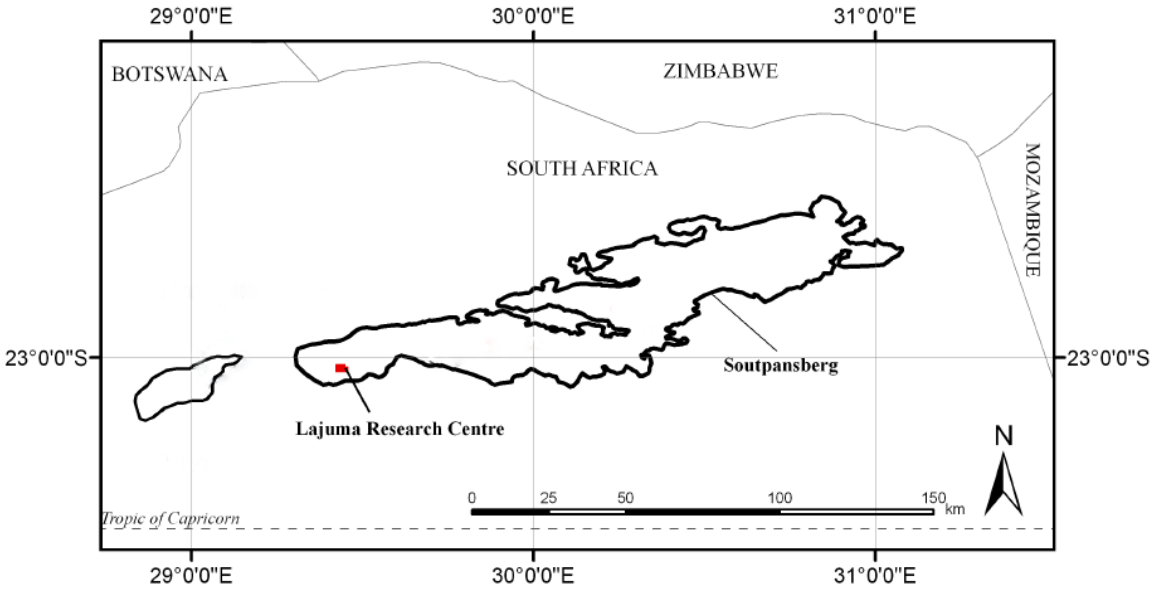

Figure 2: Trapping took place at the Lajuma Research Centre in Limpopo province, on the Southern slopes of the Soutpansberg Mountain, Makhado Municipality, approximately 50 km west of Makhado, the local town (Linden, 2010).

3.2. Sampling Sites

Sampling took place at three separate sites within the Lajuma Research Centre, namely the Wilderness Camp (Fig. 4), Wetland (Fig. 5) and the Patches (Fig. 6), with marked differences in habitat characteristics

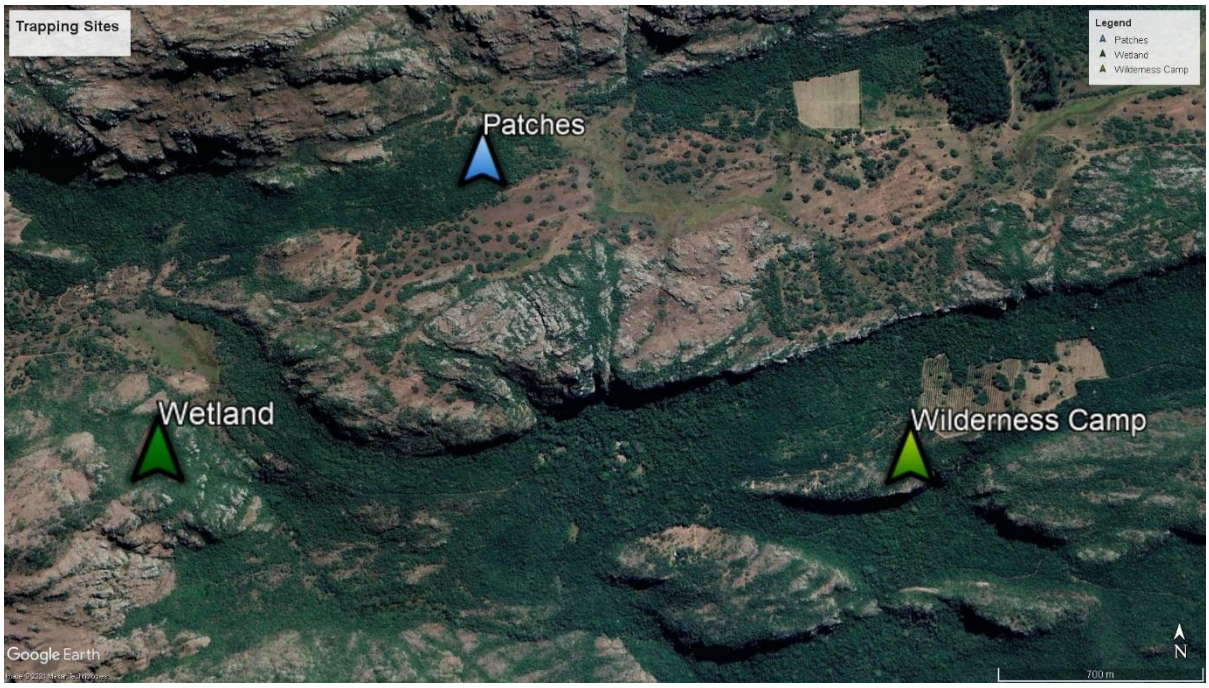

Figure 3: Location of the 3 trapping sites on the Lajuma Research Centre. (Google Maps, 2022).

Figure 4: Traps distribution in Wilderness Camp site. The site features a forested area traversed by a stream (indicated by the blue line), which influences the local habitat and small mammal activity.

3.2.1. *Wilderness Camp Site*

This trapping site has a surface area of ~0.19km^2, at an average altitude of 1297m a.s.l (Fig. 4). National vegetation units: Azonal (wetland: riparian forest); Soutpansberg Mountain Bushveld. The Study Area comprises three distinct zones. The first zone is a recently cleared (2013) area characterised by early succession of woody plants to the east of a stream and adjacent to a Macadamia orchard. This area was cleared before the 1950s but was a mature wooded savanna when cleared again in 2013 (Linden J., personal communication, July 3, 2021). The second zone is a riparian forest along the stream which has was altered because of previous site clearing. The third zone is a previously felled *Eucalyptus* plantation interspersed with woodland savanna to the west of the stream with the habitat at the western side of the stream being affected by a farm road (Linden J., personal communication, July 3, 2021).

The recently cleared area is dominated by young trees (<3 m height) including *Senegalia ataxacantha*, *Vachellia karoo*, *Ziziphus mucronata*, *Searsia chirindensis* and *Brachylaena transvaalensis* . The shrub *Ocimum labiatum* is very abundant. Other shrubs/small trees occurring include *Pavetta gardenifolia, Searsia lucida, Euclea crispa, Carissa edulis, Hyperacanthus amoenus* and *Gymnosporia harveyana*. Prevalent herbs include *Barleria sp., Cineraria sp*. and *Helichrysum sp*. The fern *Pellaea sp*. and grass *Setaria* sp. are common. The alien invasive *Senna septemtrionalis* also occurs.

The large trees (~ 8 – 10 m closed canopy) of the riparian forest are dominated by S*yzigium cordatum, Ficus sur, Searsia chirindensis, Ilex mitis* and *Podocarpus falcatus*. Less common are *Combretum kraussii* and *Schefflera umbellifera*. The *lianas Rhoicissus tomentosa* and *Rhoicissus rhomboedia* form part of the canopy. The understorey plants include *Rapanea melanophloes, Hyperacanthus amoenus* and *Gymnosporia harveyana*. Common ground layer species within the forest and along the stream include ferns*, Dietes sp., Vernonia sp., Cyperus sp.* and the grasses *Setaria* sp. Other grasses occurring within the site include *Themeda triandra, Sporobolus stapfianus, Eragrostis curvula, Setaria sphacelate*, *Digitaria eriantha, Cynodon dactylon.* The forb *Scadoxus puniceus* grows in humus on the boulders along the stream banks.

The Wilderness Camp trapping area west of the stream is composed of a felled *Eucalyptus* plantation (with subsequent regrowth; also characterised by felled trunks) and is dominated by the trees *Searsia chirindensis*, *Brachylaena transvaalensis* and *Searsia lucida*. Also occurring are *Maytenus undata, Ziziphus mucronata, Senegalia ataxacantha, Vachellia karoo, Mimusops zeyheri* and *Dovyalis zeyheri*. Several *Croton sylvaticus* saplings occur but not as mature trees. Shrubs including *Ocimum labiatum,*

Gymnosporia harveyana, Carissa edulis and *Euclea crispa*, all occur in abundance along with the woody herb *Helichrysum kraussii*. *Gerbera jamesonii* is also abundant.

3.2.2. *Wetland Site*

The surface area of the Wetland is of roughly 0.25km^2, with an average altitude of 1329m (Fig. 5). The national vegetation units are: Azonal (wetland); Northern Mistbelt Forest; Soutpansberg Summit Sourveld.

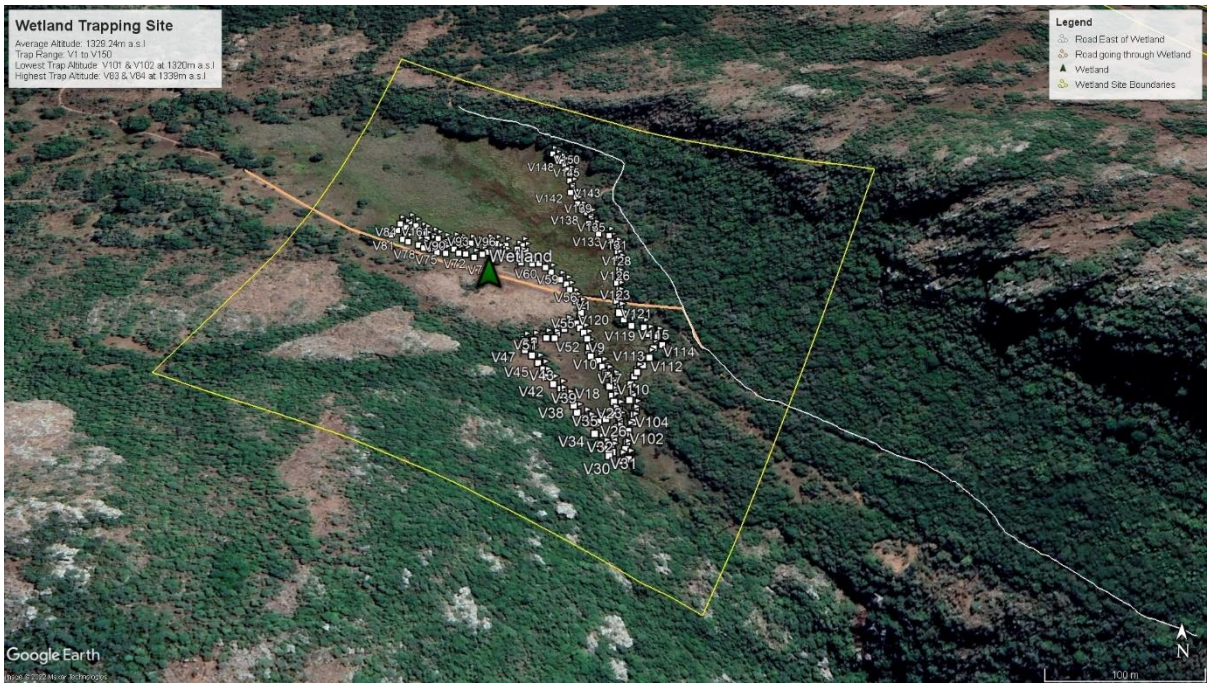

Figure 5: Traps distribution in Wetland site. The white line indicates a road towards the patches site and mount Luvhondo, while the brown line indicates a road bisecting the wetland. The green arrow indicates the site name.

The wetland is not a natural pristine habitat as it was largely cleared and drained for agriculture before the 1950s, as evidenced by historical aerial photographs. Note that the wetland area west of the road crossing (brown line) was burnt in an intense fire in July 2018, which completely removed the above-ground herb, grass, sedge, and reed cover. Many small trees and shrubs in the seasonal wetland and grassland were burnt. The fire did not burn the part of the study area east of the wetland crossing. Other regular disturbance in the wetland is by warthog and bushpig which regularly plough up substantial areas, particularly in the seasonally waterlogged zone.

The study area grades from woodland on scree in the south and clay soils in the north to grassland on deep sand and some lithosols where there is bedrock near the road crossing, dominated by the sedge *Coleochloa setifera* to seasonally waterlogged and permanently waterlogged wetland. A few traps,

however, were close to the woody vegetation. Both the permanent and seasonal wetlands have a dense layer of ferns but distinct species compositions with Kniphofia sp. in the seasonal wetland and hydrophytes, including *Gunnera perpensa* and the reed *Phragmites sp.* in the permanently waterlogged zone. Some hundred metres east of the road crossing, the drainage meets a nick point (possibly historical erosion because of anthropogenic impacts), which sees the wetland tapering to a stream incised in the sediments with a narrow seasonal wetland on the edges. A few tree ferns, *Cyathea dregei*, are scattered along the stream edges.

Herbs in the grassland adjacent to the seasonal wetland include *Artemisia afra, Helichrysum setosum, Helichrysum kraussi,* which is very abundant, *Cineraria sp., Hebenstretia sp*., the fern *Pteridium aquilinum* (bracken; abundant in places and a potential encroacher) and *Vernonia sp*. The woody *Searsia rigida* grows as a very low shrub throughout much of the grasslands on the wetland edges. *Brunsvigia sp.* lilies grow in the more open sandy areas. A few scattered trees or shrubs on the deep sands include *Terminalia sericea, Vitex rehmannii, and Searsia lucida*. The bushy shrub *Seriphium plumosum* grows within the grassland to the north of the wetland downstream from the crossing. Further from the wetland, the grasslands are bordered on the northern and southern sides by dense woodland with dominant species including *Rothmannia globose, Senegalia (Acacia) ataxacantha, Olea capensis, Hyperacanthus amoenus, Maytenus undata* and a few scattered lemon trees (*Citrus sp.*; exotic).

Several very small, circular patches of forest (5 - 8 m closed canopy, distinct vegetation strata and a well-defined ecotone with the grassland) on termitaria (clay soils) are scattered along the boundary of the seasonal wetland with trees including *Searsia chirindensis* (abundant), *Senegalia ataxacantha, Dovyalis zeyheri, Ilex mitis* (rare), *Olea capensis* and *Afrocanthium mundianum*. Understorey shrubs and small trees in these patches are typical of forest habitat in Luvhondo and include *Eugenia natalitia, Gymnosporia harveyana* and *Rapanea melanophloes* with ecotone shrubs including *Euclea crispa* and *Diospyros dichrophylla*. The ground layer consists of *Dietes sp*., *Cyperus sp.* and the grasses *Setaria sp.* and *Oplismenus hirtellus*.

3.2.3. *Patches Site*

The surface area of the trapping transect was roughly 0.19km^2, with an average altitude of 1419m (Fig. 6). The national vegetation units are: Soutpansberg Mountain Bushveld; Northern Mistbelt Forest; Soutpansberg Summit Sourveld.

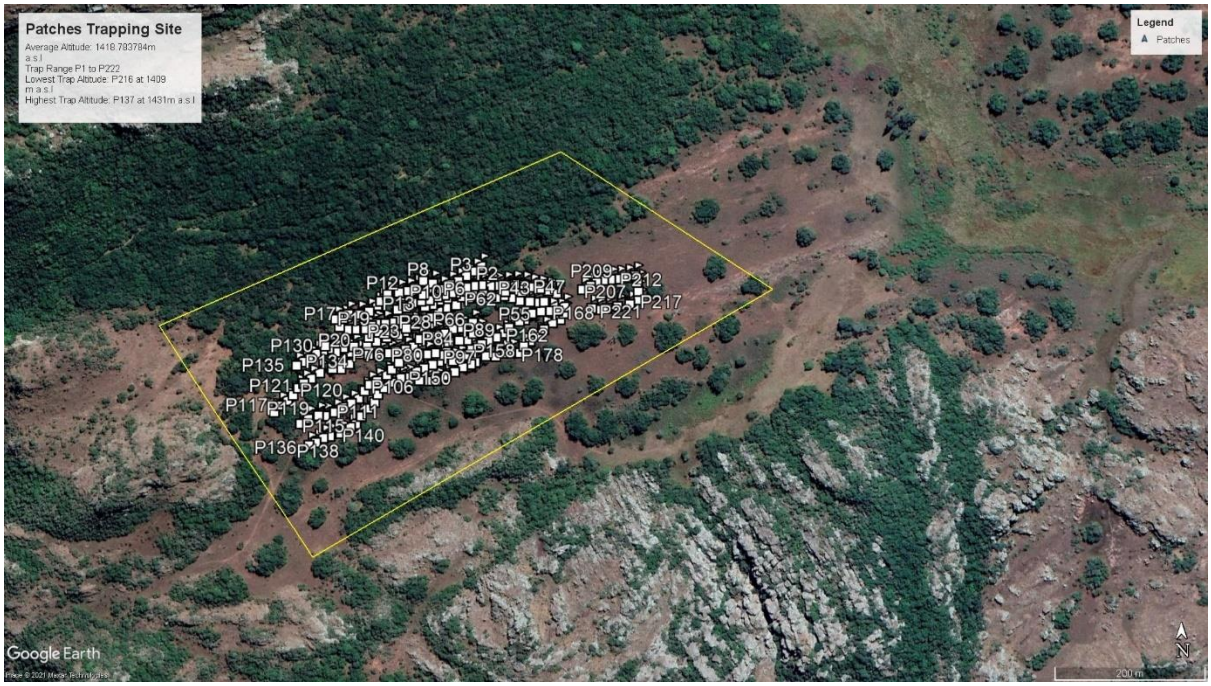

Figure 6: Traps distribution in Patches site. It is the northernmost trapping site and occurs at the highest elevation in the current study. The site is characterised by small islands of trees (Patches) on old and inactive termite mounts.

The southern part of the study area comprises a landscape of grassland on deep sand derived from erosion of the mountain quartzites interspersed with semi-circular patches of woodland or forest on termitaria characterized by clay soils. Within the grassland, the fern *Pteridium aquilinum* (bracken; abundant in places and a potential encroacher) and the herbs *Helichrysum kraussii* and *Hebenstretia sp.* occur. The woody *Searsia rigida* grows as a very small shrub and the shrub *Diospyros dichrophylla* occurs sporadically. The wooded patches have large trees (10 - 15 m) forming a closed canopy with common species including *Ekebergia capensis, Rothmannia capensis, Syzigium legati, Searsia chirindensis, Cussonia transvaalensis, Combretum kraussii, Ficus sp.* and *Olea africana. Senegalia ataxacantha* and *Vachellia karoo* occur. Main understorey and ecotone shrubs and trees include *Searsia lucida, Englerophytum magaliesmontanum, Eugenia woodii, Eugenia natalitia, Vangueria infausta, Combretum molle, Dovyalis zeyheri, Afrocanthium mundianum, Maytenus undata, Tricalaysia sp., Carissa bispinosa* and *Gymnosporia harveyana*. The ground layer consists of *Dietes sp., Cyperus sp*. and grasses *Setaria incrassata. Hyparrhenia hirta, Trichoneura grandiglumis, Themeda triandria, Eragrostis sp.,* with the exotic invasive *Opuntia ficus-indica* also occurring.

It is worth noting that the wooded patches are characterised by a moisture gradient declining from east to west (east being the source of moist maritime air) because of regular cloud immersion and subsequent precipitation from condensation. The effect of this fog precipitation is exemplified by the

presence of epiphytes including *Mystacidium sp.* orchids and *Usnea sp.* lichens and more hydrophytic plants in the understorey of the eastern edge (Linden J., personal communication, July 3, 2021).

The northern part of the study area grades into soils with high clay content derived from the basalts of the Soutpansberg and takes the form of a low canopy savanna woodland with grasses, likely regrowth from historical clearing for agriculture. Dominant tree species include *Olea africana, Afrocanthium mundianum, Senegalia ataxacantha* and *Vachellia karoo, Maytenus undata and Searsia lucida*. The shrub/creeper *Carissa edulis* is common.

3.3. Vegetation Units

Multiple vegetation units were identified across the different sites (Table 1):

Table 1: National Vegetation Units in Trapping Locations: Vegetation units at the Patches, Wetland, and Wilderness Camp where trapping took place, according to Rutherford and Mucina (2006).

National Vegetation Units		
Patches	**Wetlands**	**Wilderness Camp**
Soutpansberg Mountain Bushveld	Azonal (wetland)	Azonal (wetland: riparian forest);
Northern Mistbelt Forest	Northern Mistbelt Forest	Soutpansberg Mountain Bushveld.
Soutpansberg Summit Sourveld	Soutpansberg Summit Sourveld.	

3.4. Trapping Procedures

The sampling (Table 2) was carried out between July 7th, 2019, and November 21st, 2021, ensuring there is data for two full winter and summer seasons. Sampling was carried out bi-monthly, i.e., in July, September and November 2020, and in January, March, May, July, September and November 2021.

Table 2: Overview of trapping efforts, including site locations, trapping dates, number of trapping days, number of morning/afternoon check sessions, and total number of trap-sessions. The number of sessions indicates the frequency of trap-checking events, providing insight into the intensity and coverage of trapping activities at each site.

Site	Trapping Dates	number of trapping days	# Of morning/afternoon check sessions	Total number of trap-sessions
Wilderness Camp	Jul-20	5	9	1350
Wetland	Jul-20	5	9	1350
Patches	Jul-20	5	9	1350
Wilderness Camp	Sep-20	5	9	1350
Wetland	Sep-20	5	9	1350
Patches	Sep-20	5	9	1339
Wilderness Camp	Nov-20	5	9	1341
Wetland	Nov-20	4	7	1050
Patches	Nov-20	6	11	2090
Wilderness Camp	Jan-21	6	11	1650
Wetland	Jan-21	4	7	1050
Patches	Jan-21	6	11	1540
Wilderness Camp	Mar-21	6	11	1650
Wetland	Mar-21	4	7	1050
Patches	Mar-21	6	11	1525
Wilderness Camp	May-21	6	11	1760
Wetland	May-21	4	7	1050
Patches	May-21	6	11	1536

Wilderness Camp	Jul-21	5	9	603
Wetland	Jul-21	5	9	1260
Patches	Jul-21	5	9	711
Wilderness Camp	Sep-21	5	9	603
Wetland	Sep-21	5	9	1260
Patches	Sep-21	5	9	711
Wetland	Nov-21	5	9	1233
Patches	Nov-21	5	9	711

PVC Traps (length = 29 cm, height = 7.5 cm, width = 6cm) were used for live trapping of *R.d. dilectus* and other small mammals (other rodents and *Shrew sp.*s). Trapping took place for 4 to 6 days at every site, during every session – once in the morning and once in the evening. Wilderness Camp was not trapped in November 2021 as the neighbouring farm was using pesticides on the edges of the trapping site and trapping success had been gradually declining. The duration of sampling was determined based on the daily recapture rate of *Rhabdomys*. As a standard, trapping was conducted for five days. If the recapture rate exceeded 50% by the fourth sampling day, the trapping session concluded on that day. If it rained during the trapping week and the recapture rate was below 50% by the fifth sampling day, trapping was extended to the sixth day. The recapture rate was calculated by dividing the number of *Rhabdomys* individuals recaptured each day by the total number of *Rhabdomys* captured that day, including recaptures, with the first trapping day always excluded from this calculation. Data collection spanned 15 to 17 days per session across the three sites, over a total of nine sessions within two years. Typically, each session involved five days of trapping per site, with at least eight weeks between successive trapping sessions at the same site.

Generally, 150 PVC traps were set per site in a transect with parallel running transects, with ~10m x 15m transect dimensions. The traps were placed well within vegetation cover to protect and enhance *Rhabdomys* trapping success. Two traps were generally set 10 metres apart; however, priority was given to parts along the transect that offered the most vegetation cover rather than the distance between each trap. Each trap was taped with masking tape and given a number. The location of each trap was then recorded using a handheld GPS (Dakota 10, Garmin International, Kansas, USA). Red and white marker tape was used to indicate the position of each trap. The tape was tied on anything

from branches, fences, or a bunch of grass. The traps were baited with a mixture made of peanut butter, sunflower seeds, oats and coarse salt in variable 10g to 15g quantities (Dufour et al., 2015), along with cotton wool to insulate the mice and serve as an additional bait (Perrin et al, 2012; Dufour et al., 2015).

The traps were checked twice daily. In the morning, the standard checking time was 8:30 AM; however, if weather conditions were unfavourable, they were checked at 9:00 AM. In the afternoon, traps were typically checked at 2:30 PM, and if the weather was bad, they were checked at 3:00 PM. Traps containing animals were taken to a convenient location within the trapping site for processing. A foldable 1.5m x 1m table was used at each site for this purpose. Captured individuals were identified visually using the ECORAT guide (Kirsten *et al.,* 2010). Body and tail lengths were measured with a twenty-centimetre metal ruler to the nearest millimetre. Three Pesola Spring balances (10g, 100g, and 300g maximum) were used to weigh the animals to the nearest 0.5 grams. New individuals were marked with a numbered metal tag on each ear (National Band & Tag Co., USA). Re-trapped individuals were identified during each session and accounted for when recording the number of individuals trapped per session. Individuals previously trapped were considered recaptures.

Body and tail length, mass, sex, and reproductive status were measured in the initial and subsequent captures, where applicable. Tail length was not measured in *Rhabdomys* recaptures since they were cut at the first capture.

The reproductive state of each animal was recorded as follows: males were noted as TA (testes abdominal) if their testes were not visible and TD (testes descended) if their testes were descended. Females were categorized as NR (non-reproductive), VO (vagina open), Lac (lactating), or Preg (pregnant). After recording this information, the animal was returned to the trap with some food and placed back at the original trap location. The traps were then rebaited and reset. All data were documented on a datasheet and subsequently transferred to an Excel spreadsheet.

A standardised capturing procedure was established to prevent inducing excessive animal stress and to establish an optimised, efficient processing procedure (Table 3). This procedure was followed as is every time:

Table 3: The table outlines the detailed procedure for handling and measuring small mammals during both initial capture and recapture events. Each step is crucial for collecting consistent and accurate data on the animals.

	Measurements	Initial Capture	Recapture
	Remove the animal from the trap into plastic 'handling' bag	Y	Y
	Weigh (in bag)	Y	Y
	Record trap number, time, and date	Y	Y
	Restrain the animal by the skin over the scapulae	Y	Y
	Apply ear tag and record number, if unmarked	N	Y
	Record ear tag number, if already marked	Y	N
	Record sex and inspect the reproductive state	Y	Y
	Measure body size from the tip of the nose to just below the anal opening.	Y	Y
	Measure tail length	Y	N
	Collect tissue (nail clipping)	Y	N

For analysis, the initial weight and body length of each individual per session were used as measurement parameters. Additionally, the weight recorded for individuals recaptured in the afternoon session was used to assess the accuracy of readings based on the recordings made each trapping month.

3.5. Habitat Characterisation

Vegetation cover, vegetation composition, and state were characterised for each site at each session. Vegetation cover was determined within a 1x1m metal square placed at the left and right side of a trap line at every second trap (Dufour *et al.*, 2015). Within these 1x1m quadrats, the percentage of grass cover, shrub cover, bare soil, leaf litter, and bare rock, was estimated. Moreover, mouse visibility (an index ranging from 1, completely visible, to 5, completely hidden) was determined by placing a dummy mouse (a hand GPS) across the four corners of the 1x1m transect, taking four separate estimates of the mouse visibility on each corner and averaging the visibility (Dufour *et al.*, 2015). For example, if the quadrat consisted of 50 % bare soil, half of the quadrat was utterly devoid of vegetation. If the remaining cover was a mix of grass and woody plants, the plant type providing most of the cover would be first identified, and the approximate contribution of each plant type (wood/ grass) would be estimated in percentage. The sum of the proportions of every vegetation type along with the bare soil/rock/leaf cover, always equalled 100%. This approach was used to determine if there is a correlation between vegetation type, cover, and the trapping success.

Vegetation samples were collected at every second trap along each transect, resulting in a minimum of 75 samples per site in a typical 150-trap setup. Exceptions to this are noted in Table 4. To ensure accurate identification, the vegetation across the transects was thoroughly surveyed, with assistance from J. Linden, the manager of the Lajuma Research Centre.

Table 4: Number of traps deployed at Wetland, Patches, and Wilderness Camp across the different trapping sessions. The table provides a detailed overview of the number of traps deployed at Wetland, Patches, and Wilderness Camp during various trapping sessions from July 2020 to November 2021. It highlights the total number of traps sampled at each site and across different time periods, reflecting the effort and coverage of trapping activities aimed at capturing small mammals in these locations.

Site	**Trapping Sessions**	**Total Number of Traps sampled**
Wetland	July 2020 - November 2021	75
Patches	July 2020 - September 2020	75

Patches	November 2020	95
Patches	January 2021 - May 2021	70
Patches	July 2021 - November 2021	62
Wilderness Camp	July 2020 - March 2021	75
Wilderness Camp	May 2021	90
Wilderness Camp	July 2021 - September 2021	38

3.6. Weather

The weather data was collected at the Luvhondo Nature Reserve Weather Station, at 1278m a.s.l, which is lower than the altitude of the three sites. It is 0.53 km from the Wilderness Camp site, 1.41 km from the Patches site and about 1.71 km from the Wetland site. Parameters of interest for the present study were the maximum, minimum and average temperatures; and average precipitation measured in millimeters on the capture days. We used data collected in the course of three years from 2019 to 2021 as that range was most relevant to the study.

3.7. Data Preparation

The study has different elements which were analysed to characterise and determine the general behaviour of the studied populations of *Rhabdomys*. Study variables included analysing demographic parameters, such as the number of individuals caught across different sessions, the variability of sex ratios across the different sessions, the number of reproductively active males and females and how that varies across the three sites, in all sessions. Trapping success was also determined across all sites by assessing the percentage of captured individuals versus the number of traps set out during any of the trapping days. Community composition is also an element of the study, for which data was prepared and analysed.

3.8. Age Determination

In the context of demographic parameters, the determination of age classes was key as it provides insight into the age composition of the populations across the three sites, i.e., to determine the

number of adults, sub-adults etc. or to get an understanding of the distribution of age classes across the trapping sessions. Not having access to the actual age of the animal body length was used as a proxy. Because length and mass were measured on live animals and accuracy of measurements was variable, we chose to categorise our population into two classes, i.e., adult and non-adult classes. The criterion selected from for the females was based on their reproductive status. It was determined the distribution of body lengths of reproductive females, i.e., mostly lactating females or females with visibly open vaginas, and identified that the most petite reproductive female body length was 80mm. Two classes were considered: the not yet matured animals (hereafter non-adults) with body sizes smaller than 80mm and the matured and potentially reproducing animals with body sizes equal to or larger than 80mm. Similarly, males with body sizes equal to or larger than 80mm were considered adults as all reproductively active individuals measured ≥ 80mm.

3.9. Data Analysis

3.9.1. *Statistical Analyses:*

R Studio version 4.0.5 (2021-03-31) was used for all data analyses. Ggplot (Wickham, 2009) was used to represent the data in boxplots, stacked bar plots, scatterplots and line graphs.

3.9.2. *Trapping Success*

The package dplyr (Wickham *et al.,* 2021) was used to generate summary statistics, including the mean, standard deviation, median and interquartile range of the trapping success rates for the dataset. For trapping success, the Pairwise Wilcoxon Signed-Ranks Test (Kruskal, 1957) was used to determine if there were differences in trapping success between morning and afternoon trapping activity. Trapping success was calculated by dividing the total captures by the number of traps set daily. The Kruskal-Wallis (KW) test was used to determine the effects of the site on the trapping success of *Rhabdomys* and other observed species in the communities. A non-parametric post-hoc Dunn Test from the FSA package (Ogle *et al.,* 2022) was used to assess the differences between pairs of sites in KW tests. The non-parametric tests were used because they can handle non-normally distributed data, making them suitable for this analysis.

3.9.3. *Influence of Weather Variables on the Trapping Success of Rhabdomys dilectus*

General Linear Mixed Models (Lmer's) were used to determine the influence of continuous weather variables observed over the course of the study, i.e., min, max, and mean temperatures, rainfall, and wind on the trapping success of *R.d. dilectus.* A series of diagnostic tests were conducted to assess homoscedasticity and normality of residuals. A plot of residuals vs. fitted values was performed to

visually determine homoscedasticity. Additionally, the normality of residuals was evaluated using the Shapiro-Wilk test and Q-Q plots.

3.9.4. *Vegetation and Rhabdomys trapping success.*

General Linear Mixed Models (Lmer's) were used to assess the influence of ground cover characteristics (bare ground, grass cover, shrub cover and mouse visibility) on the trapping success of *R.d. dilectus* with trapping success as the response variable. Trapping success was not normally distributed, so a log transformation was used to make the distribution standard. To assess the influence of the four vegetation cover variables on *Rhabdomys* trapping success, generalised linear models (GLM), were carried out.

3.9.5. *Sex ratio variation across seasons and sites*

To assess the population dynamics and reproductive activity of the small mammal community at the Wetland site, we conducted a series of trapping sessions across different months. The number of males and females captured during each session was recorded to calculate various demographic and reproductive ratios.

Sex Ratio Calculation:

The sex ratio for each trapping session was determined by dividing the number of males by the number of females. This ratio provided insights into the relative abundance of males and females within the population.

Reproductive Activity of Females:

The ratio of reproductively active females was calculated by dividing the number of reproductively active females by the total number of females captured in each session. This ratio indicated the proportion of females that were reproductively active at the time of sampling.

Lactating Females:

Similarly, the ratio of lactating females was determined by dividing the number of lactating females by the total number of females. This measurement provided an understanding of the reproductive output and maternal investment within the population.

Reproductive Activity of Males:

The ratio of reproductively active males (scrotal) to total males was calculated by dividing the number of males with descended testes by the total number of males captured in each session. This ratio served as an indicator of the reproductive readiness of the male population.

Data collection occurred over a series of trapping sessions from July 2020 to November 2021. These sessions included specific months: July 2020, September 2020, November 2020, January 2021, March 2021, May 2021, July 2021, September 2021, and November 2021. For each session, the total number of males and females, along with their reproductive states, were recorded and used to compute the aforementioned ratios. These calculations were performed to analyse seasonal variations in population structure and reproductive activity, providing a comprehensive understanding of the demographic and reproductive dynamics at the Wetland site.

To statistically analyse the variations in sex ratios and reproductive states, the Wilcoxon rank-sum test was employed to assess variations in the sex ratio of *R.d. dilectus* populations across different sessions and sites. This non-parametric test was suitable because it compared two independent groups, making it appropriate for examining differences in sex ratios between pairs of sessions or sites.

In addition, the Friedman rank-sum test was applied to investigate whether the ratios of adult to non-adult *R.d. dilectus* differed across sites and sessions. This test compared three unrelated groups—Wetland, Wilderness Camp, and Patches—with non-normally distributed data. The Friedman test was chosen for its ability to handle multiple related samples, allowing for a robust analysis of the variations in age structure across different environmental contexts.

3.9.6. *Body Size*

Three separate one-way ANOVAs were used to determine whether there was a difference in body size across sites, sessions, and sex for all captured *Rhabdomys* individuals and whether these variables interact. The data was also analysed to check for significant differences in size between reproductively active and non-reproductively active males and females across all sessions and sites.

3.9.7. *Community Composition*

The iNext R package (Chao *et al.*, 2014) was used to analyse the species richness, species diversity and species evenness of the ecological community by using rarefaction and extrapolation Hill numbers.

The Jaccard Similarity Index was used to determine the extent to which the three sites were similar in vegetation composition (Ivchenko & Honov, 1998).

3.9.8. Rarefaction Analysis

Rarefaction curve analysis was conducted to evaluate species diversity across three sites. Three diversity indices were employed to provide a comprehensive assessment. The first index (q=0), or species richness, emphasizes the presence of rare species by giving them greater weight. The second index (q=1), known as Shannon's entropy, considers species frequency without bias towards rare or common species, thus providing a balanced view of diversity. The third index (q=2), Simpson's concentration, integrates both species richness and abundance, giving more weight to common species. These indices, as described by Jost (2006), allow for a nuanced understanding of species diversity by accounting for both the presence and frequency of species within each site.

4. Results

4.1. Small Mammal Community Composition Across Wetlands, Patches, and Wilderness Camp

The trapping period for this study spanned 133 days, from July 2020 to November 2021. During this time, a total of 596 individuals of *R.d. dilectus* (including recaptures) were captured, alongside 295 captures of other species which were identified (appendix I). The most commonly occurring species across the sites were *R.d. dilectus* (confirmed through genotyping of tissue samples in the laboratory at Montpellier University by G. Ganem), *Aethomys ineptus*, *Lemniscomys rosalia*, and *Mus minutoides*. Over the study period, eight species of rodents and two species of *Shrew sp.*s were captured across the sites (appendix I).

R.d. dilectus was the most abundant species, with 596 individuals caught, followed by *A. ineptus* (129), *L. rosalia* (90), and *M. minutoides* (32) (Fig. 7). The *Shrew sp.*s, *Dasymys incomtus*, *Otomys angoniensis*, *Dendromus sp*., and *Elephantulus myurus* had the lowest abundances. The different *Shrew sp.* species were identified later in the study as *Crocidura mariquensis* and *Myosorex varius*, consistent with previous findings (Nemakhavhani, 2015) which occurred within proximity of the current study's site.

Remarkably, considering the total numbers trapped over the entire study period, *R.d. dilectus* dominated the small mammal community in the Wetland site. In contrast, two species co-dominated in the Patches (*R.d. dilectus* and *L. rosalia*) and in the Wilderness Camp (*R.d. dilectus* and *A. ineptus*) (Fig. 7).

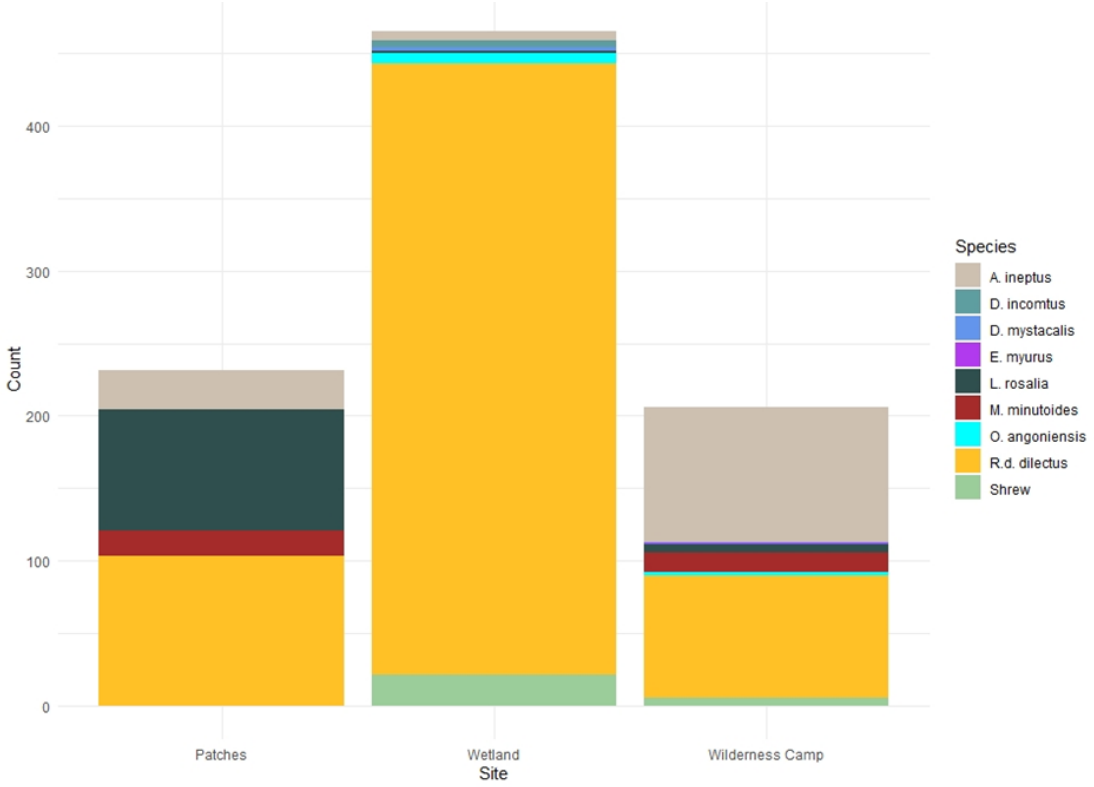

Figure 7: Abundance of small mammal species sampled across three habitat types (Patches, Wetland, Wilderness Camp) at Luvhondo Nature Reserve, Western Soutpansberg Mountains.

The composition of the small mammal community showed clear variation across the three sites and between different trapping sessions. *R.d. dilectus* consistently dominated in the Wetland site, particularly during certain seasons, while the Wilderness Camp and Patches exhibited greater species diversity but lower overall captures of this species (Fig. 7). There was significant site-specific and seasonal differences in species abundance and composition, highlighting the influence of habitat characteristics and temporal variation (see Figs. 7, 8, 9, and corresponding statistical analyses below):

4.1.1. Patches

At the Patches site, four species were recorded, with *R.d. dilectus* and *L. rosalia* being the most dominant, accounting for 45% and 36% respectively, along with *A. ineptus* and *M. minutoides* trapped in lower numbers (Fig. 8; Appendix I). The captures of *L. rosalia* peaked in January 2021, while *M. minutoides* peaked in July 2021, and *R.d. dilectus* in September 2021. Notably, most captures of *R.d. dilectus* occurred in areas with dense grass and ferns. The trapping transect was modified in May 2021, where unproductive traps were replaced and new traps were added about 30 meters from the old line, targeting areas with higher grass density. This modification led to an increase in *R.d. dilectus* captures and a significant decrease in *L. rosalia* and other species from July to November (Fig. 8).

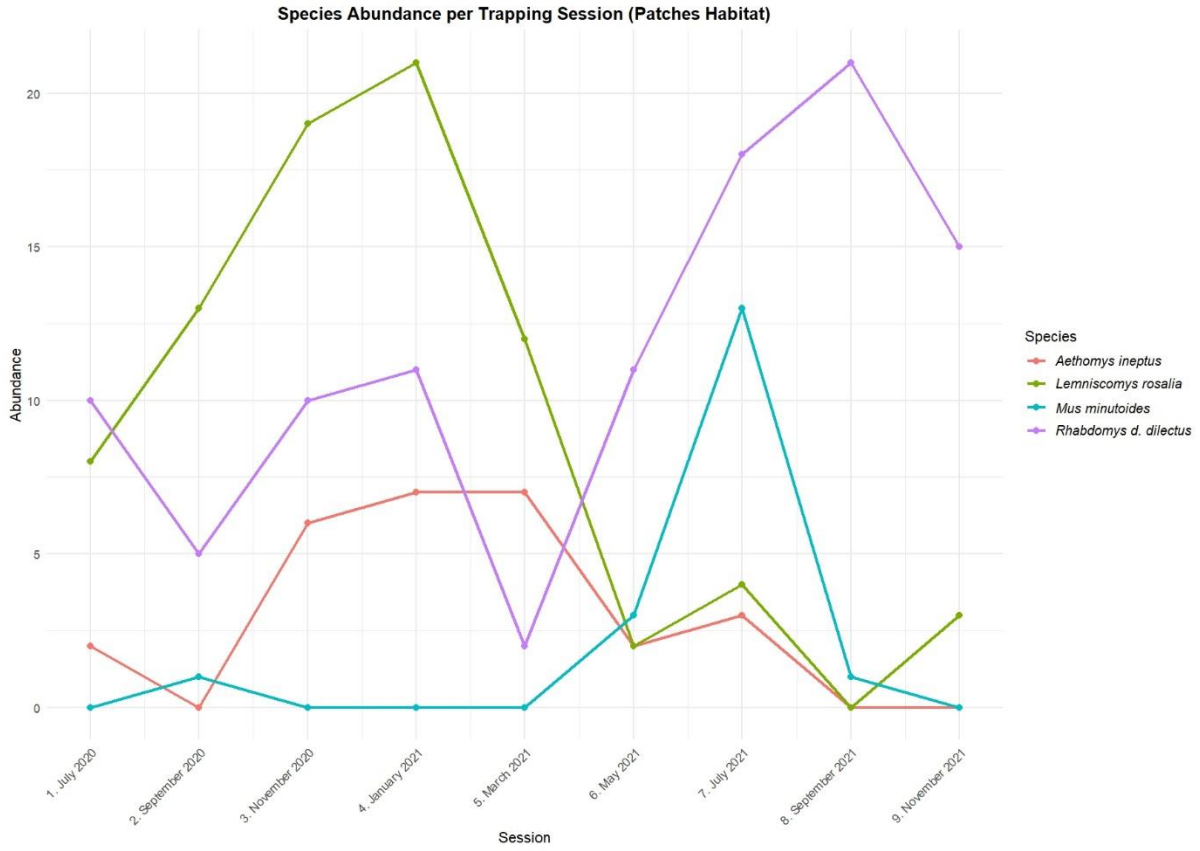

Figure 8: Seasonal variation in the observed number of individuals and species at the Patches. Recaptures are included. The legend indicates the comprehensive list of species identified at the three studied sites.

4.1.2. Wetland

The Wetland site recorded the highest species diversity with nine species observed. *R.d. dilectus* was dominant across the study period, despite fluctuations in numbers across sessions, accounting for 90% of all captures. *Shrew sp.*s were the second most captured species, accounting for 4% (Fig. 9). *R.d. dilectus* was captured throughout the Wetland. Both years showed a decline in capture rates during spring (September-November 2020 and 2021). Captures of *Shrew sp.*s and *O. angoniensis* peaked in July 2021, while their numbers were low in July 2020. In contrast, captures of *R.d. dilectus* were highest in July 2020, with *Shrew sp.*s also appearing to be abundant in July 2020 (Fig. 9).

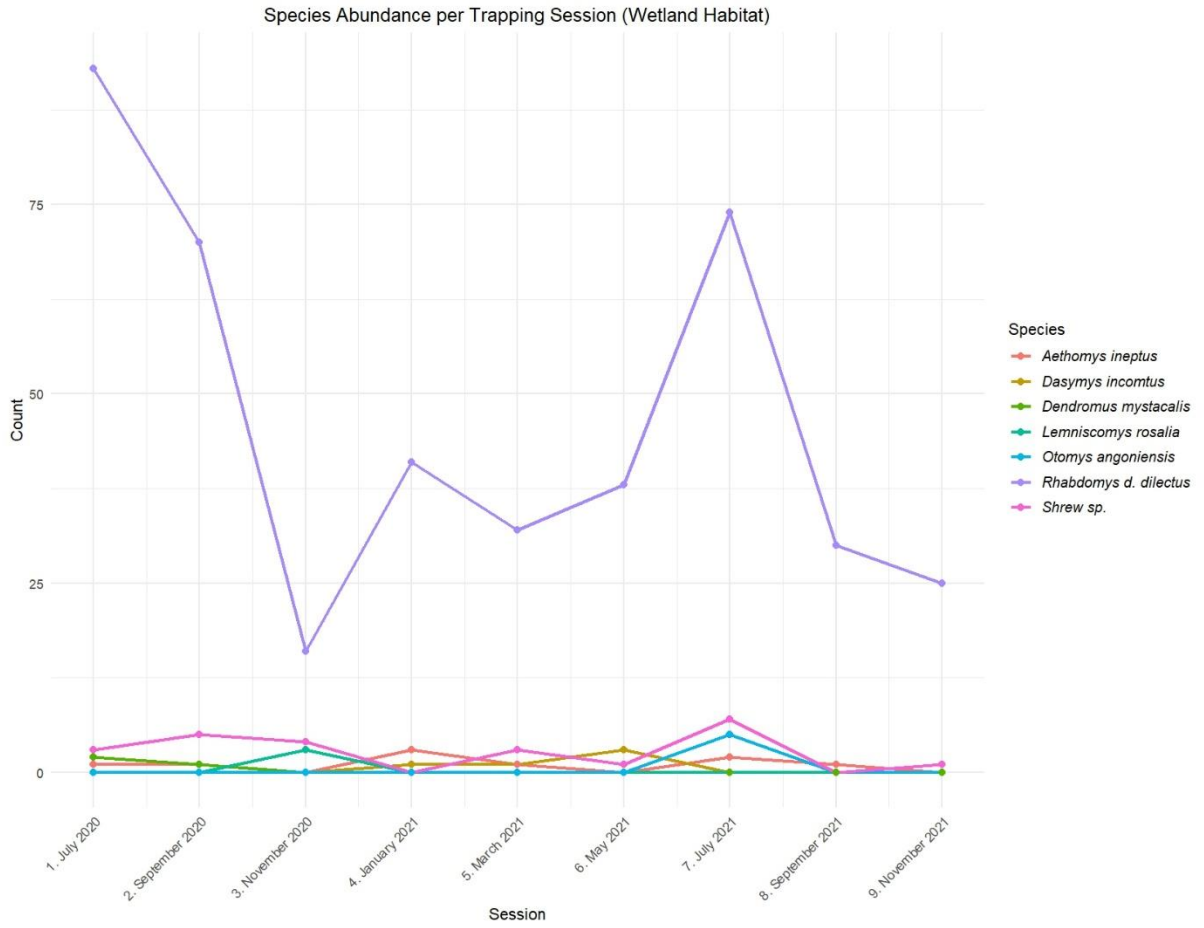

Figure 9: Seasonal variation in the observed number of individuals and species at the Wetland. Recaptures are included. The legend indicates the comprehensive list of species identified at the three studied sites.

At the Wilderness Camp, *A. ineptus* accounted for 45% of all captures, while *R.d. dilectus* accounted for 41% (Fig. 10). *R.d. dilectus* dominated from July to September 2020, while *A. ineptus* dominated from January to July 2021 (Fig. 10). *R.d. dilectus* was most captured during the first two sessions, with a marked decline afterward. Conversely, *A. ineptus* became the most abundant species from the third trapping session onwards. *M. minutoides* accounted for less than 1% of captures, peaking in May 2021. The Wilderness Camp trapping transect was divided into three parts: a riparian forest, a felled *eucalyptus* plantation, and a recently cleared area characterized by early woody plant succession. *R.d. dilectus* was primarily captured in the riparian forest understory where grass was abundant, while *A. ineptus* was mostly found in early succession woody plant areas. From January 2021, the distribution of *A. ineptus* extended to the riparian areas, maintaining a fairly stable population (Fig. *10).*

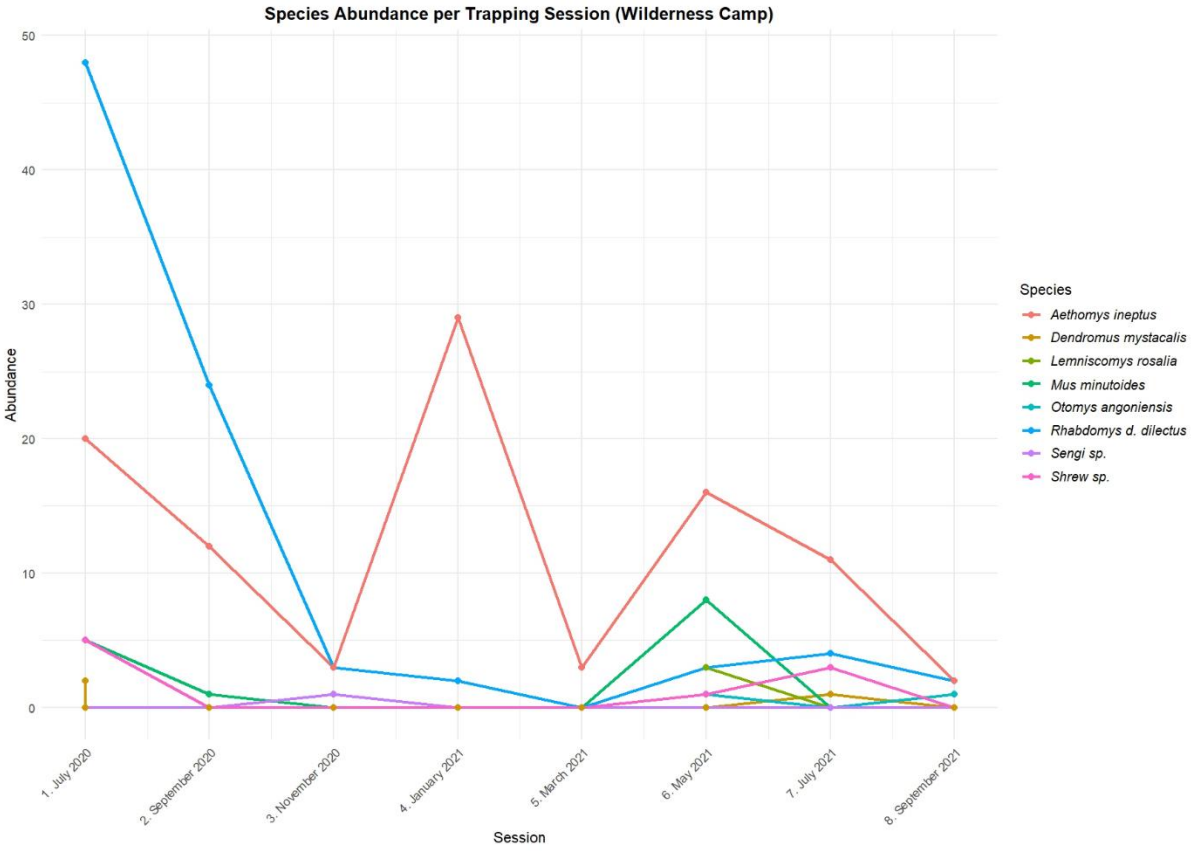

Figure 10: Seasonal variation in the observed number of individuals and species at the Wilderness Camp. Recaptures are included. The legend indicates the comprehensive list of species identified at the three studied sites.

4.1.3. **Estimates of small mammals' diversity in the three study areas**

The rarefaction curve analysis (Figure 11) assessed species diversity across the three distinct sites using three diversity indices: species richness (q = 0), Shannon's diversity index (q = 1), and Simpson's index (q = 2).

Species Richness (q = 0):

Wetland and Wilderness Camp exhibited the highest species richness, whereas Patches displayed the lowest. Despite relatively wide confidence limits for Wilderness Camp and Wetland estimates, the overall trend showed these sites as more species-rich (Fig. 11).

Shannon's Diversity Index (q = 1):

This index, which reflects species frequency, identified Wetland as the least diverse site due to the dominance of *R.d. dilectus*. In contrast, Wilderness Camp demonstrated diversity values similar to those of Patches.

Simpson's Index (q = 2):

Simpson's index, reflecting species richness and abundance, supported the pattern observed with Shannon's index. Patches emerged as the least diverse site, while Wilderness Camp and Wetland exhibited comparable and higher species diversity, surpassing that of Patches (Fig. 11).

These indices collectively highlight the dominance of *R.d. dilectus* at the Wetland site, which significantly impacts its overall diversity metrics, while Wilderness Camp and Wetland both show higher species diversity compared to Patches.

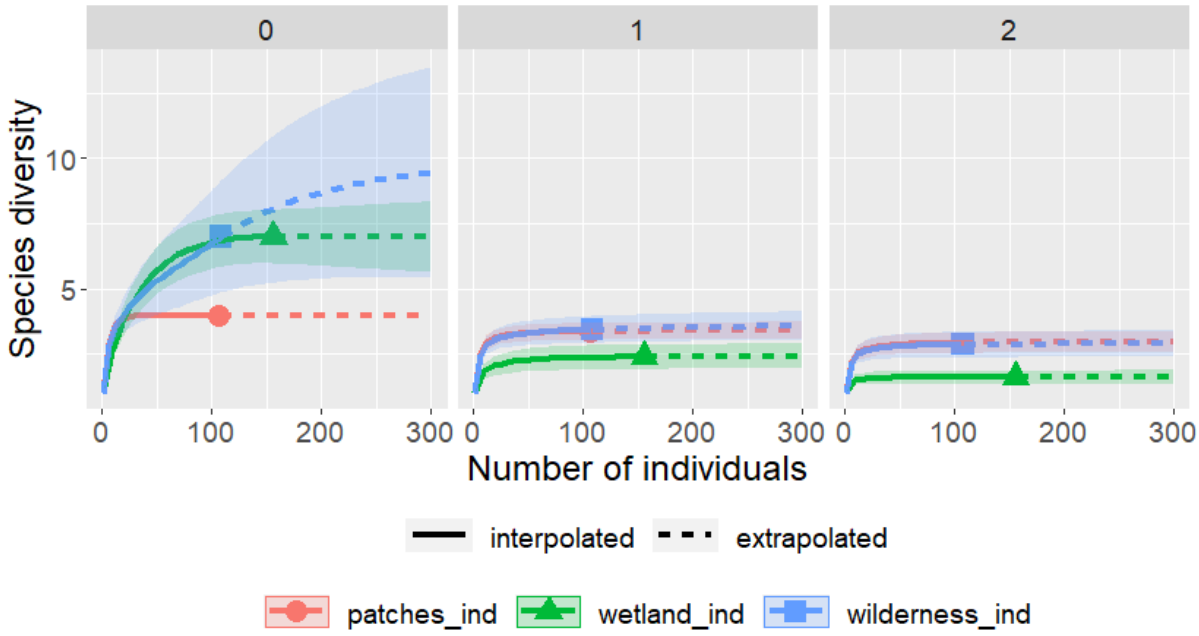

Figure 11: Individual Based Rarefaction and extrapolation curves for each site, with q = 0 (species richness), q =1 (Shannon's entropy) and q = 2 (Simpson's concentration) diversity indices.

4.2. *Rhabdomys* Population Ecology

4.2.1. *Trapping success across sites and sessions*

Differences in trapping success were investigated across all species recorded, across all sites. There

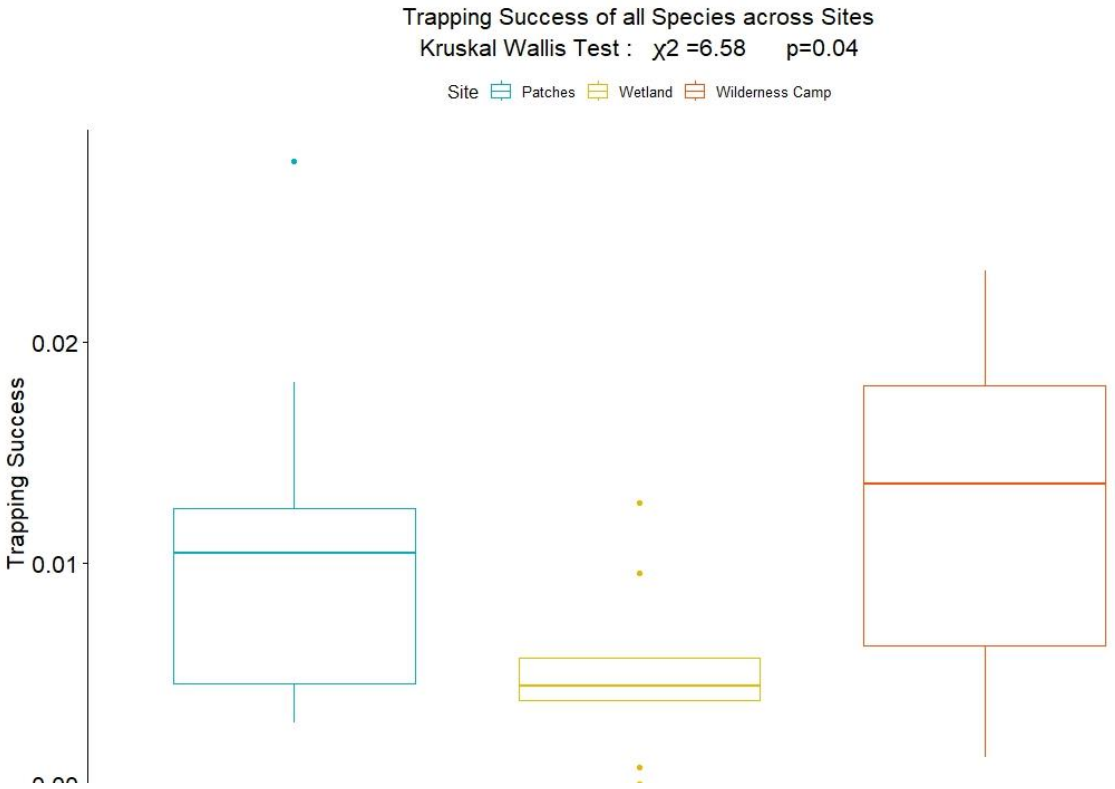

Figure 12: Comparative trapping success rates across Patches, Wetland, and Wilderness Camp sites, showing significant differences in species capture efficiency (Kruskal-Wallis test: $\chi^2 = 6.58$, $p = 0.04$).

was a significant difference in overall trapping success among the three sites, with the Wetland exhibiting the highest trapping success (Kruskal-Wallis $\chi^2 = 6.58$, df = 2, p = 0.04; Fig. 12).

When analysing the trapping success of *R.d. dilectus* separately (Fig. 13), it became clear that this species was the primary driver of the observed differences between sites. The trapping success of *R.d. dilectus* was significantly higher in the Wetland compared to the Patches and the Wilderness Camp (Kruskal-Wallis $\chi^2 = 13.34$, df = 2, p = 0.001). In contrast, the trapping success for other species did not show statistically significant differences between the sites (Kruskal-Wallis $\chi^2 = 5.17$, df = 2, p = 0.08).

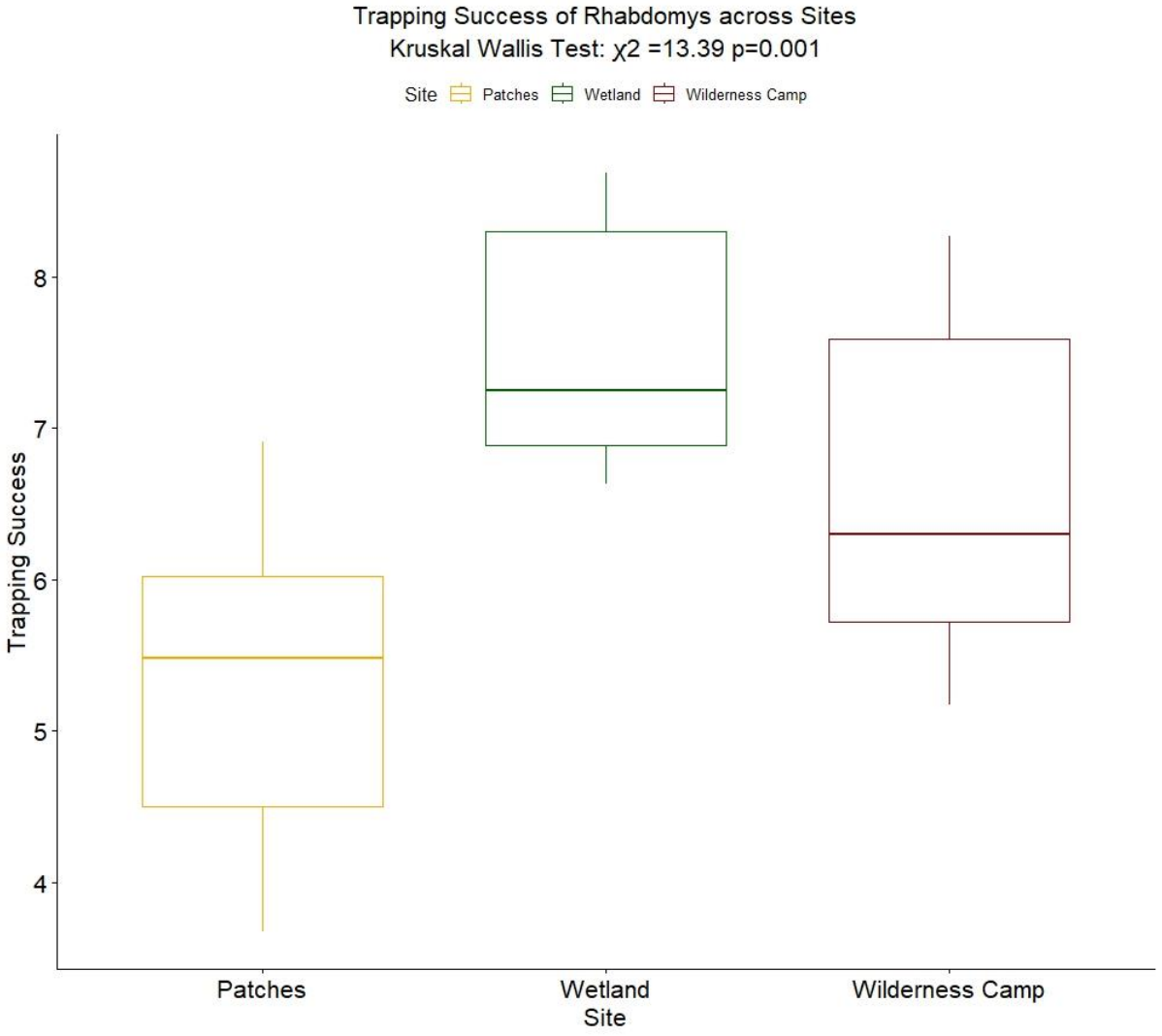

Figure 13: This figure illustrates the trapping success rates of Rhabdomys at three distinct sites—Patches, Wetland, and Wilderness Camp. The data shows significant variations in capture efficiency across these sites, as indicated by the Kruskal-Wallis test ($\chi^2 = 13.39$, p =0.001)

Pairwise comparisons revealed that the trapping success was significantly higher in the Wetland compared to the Patches (Z = -2.64, p = 0.01) and the Wilderness Camp (Z = 3.49, p < 0.01) after adjustment. There was no significant difference in trapping success between the Patches and

Wilderness Camp sites (Z = 0.93, p = 0.35). This indicates that the high trapping success observed at the Wetland site is a significant factor in the overall trapping success differences among the sites.

It was also tested whether trapping success differed between the morning and afternoon trapping sessions. For *Rhabdomys dilectus*, there was no significant difference in trapping success between the two periods across all three sites (Wilcoxon's test, V = 25, p = 0.82). Similarly, no difference was observed in the trapping success of *Lemniscomys rosalia* between the morning and afternoon sessions across all sites. However, for *Aethomys ineptus*, there was a significant difference in trapping success at the Patches (Wilcoxon's test, V = 21, p = 0.04) and the Wilderness Camp (Wilcoxon's test, V = 36, p = 0.01), with higher captures in the morning sessions. No significant difference was observed at the Wetland site.

4.2.2. The influence of weather and vegetation on *Rhabdomys* trapping success

Trapping success of *Rhabdomys* showed varying responses to precipitation trends across habitats (Figure 14). Total rainfall peaked in January and gradually declined, with the last recorded rain in March. Interestingly, trapping success in the wetland site peaked in July, despite low precipitation, suggesting that factors other than immediate rainfall, such as residual moisture or vegetation growth, may have influenced *Rhabdomys* activity. In contrast, as precipitation started increasing in January, trapping success in the Wilderness camp initially peaked but then declined by March, potentially indicating a lag effect or changes in habitat suitability. The patches site exhibited consistently low capture rates, with minor increases in November, and January, and peaking in July, reinforcing the idea that habitat structure plays a critical role in determining population activity. Notably, as rainfall ceased after March, trapping success patterns diverged, suggesting that *Rhabdomys* responses are influenced by a combination of seasonal habitat changes and moisture availability rather than rainfall alone.

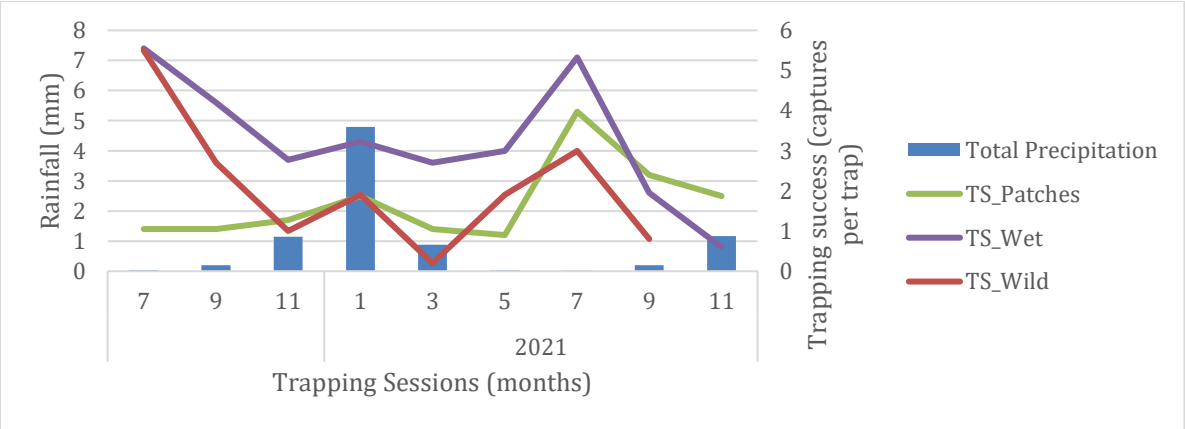

Figure 14: Variation of rainfall and trapping success (TS) of R.d. dilectus at the Patches, Wetland, and Wilderness Camp.

Since no clear pattern could be derived from Fig. 14, Pearson correlation coefficients and their corresponding p-values were calculated to determine if there was a correlation between precipitation and trapping success at the three sites. The p-values were greater than 0.05 across all sites, indicating no significant correlation. The Pearson correlation coefficients were -0.21 for Wilderness Camp, -0.01 for Patches, and -0.22 for the Wetland, suggesting that there is no positive correlation between trapping success and rainfall at any of the sites during the study period.

Linear mixed models revealed that trapping success was significantly influenced by site, minimum, maximum, and mean temperatures, as well as rainfall events occurring 5 and 6 months prior to trapping (Table 5). In contrast, wind, rainfall events, and trapping sessions at the time of capture were tested but did not show significant effects on trapping success.

Wind and rainfall (Table 5) recorded during each trapping session did not have a significant impact on trapping success. Additionally, rainfall events occurring 1 to 4 months prior to a trapping event were also not found to significantly affect trapping success.

Table 5: Summary table from simple linear mixed models using the 'cftest' command in R, showing significant relationships between weather variables and Rhabdomys trapping success with site as the constant factor. Models where the response variables were not significant are not included. These include rainfall of the same month of capture and previous one to four months, and wind speed. The weather data used was recorded on the day of capture.

Response Variable: Trapping Success				
	Estimate	Std. Error	Z Value	Pr (> |z |)
Minimum Temp.				
(Intercept)	0.048	0.009	5.181	1.48e-05
MinT	-0.002	0.000	-3.241	0.003
Maximum Temp.				
(Intercept)	0.0875	0.0237	3.681	0.001
MaxT	-0.002	0.001	-2.572	0.016
Mean Temperature				
(Intercept)	0.084	0.0157	5.364	8.15E-08
MeanT	-0.003	0.001	-3.974	7.06E-05
Rainfall 5 months previously				
(Intercept)	2.09E-02	7.82E-03	2.669	0.007
Rain_5mth	1.12E-04	3.81E-05	2.954	0.003
Rainfall 6 months previously				
(Intercept)	2.25E-02	7.51E-03	2.988	0.002
Rain_6mth	1.38E-04	3.97E-05	3.47	0.001

Rainfall events occurring five and six months prior to the capture month significantly influenced trapping success (Table 5). There was a positive correlation between the amount of rainfall observed five months prior to a trapping event and the trapping success (Figure 15). This correlation is most pronounced in the Wetland site, indicating that early rainfall may stimulate reproduction, leading to a delayed increase in the population due to the gestation period and early development of young until they become trappable.

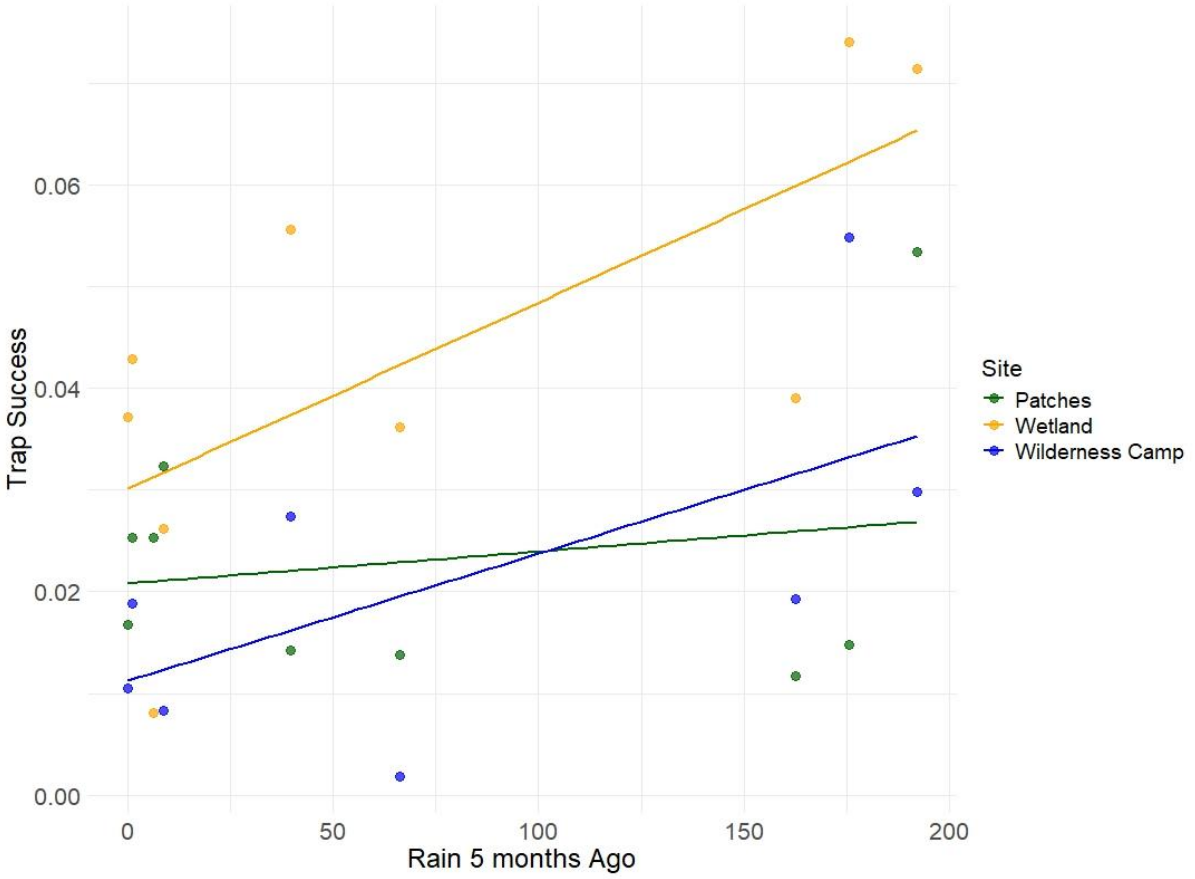

Figure 15: Effects of rain observed 5 months prior to a trapping event (in mm) on the trapping success of R.d. dilectus, determined using linear mixed models. The figure shows that as rainfall increases five months prior, trapping success tends to increase across all sites, with the Wetland site showing the strongest positive correlation. This suggests that higher rainfall during this period may result in higher trapping success, potentially due to its effects on reproduction and population growth.

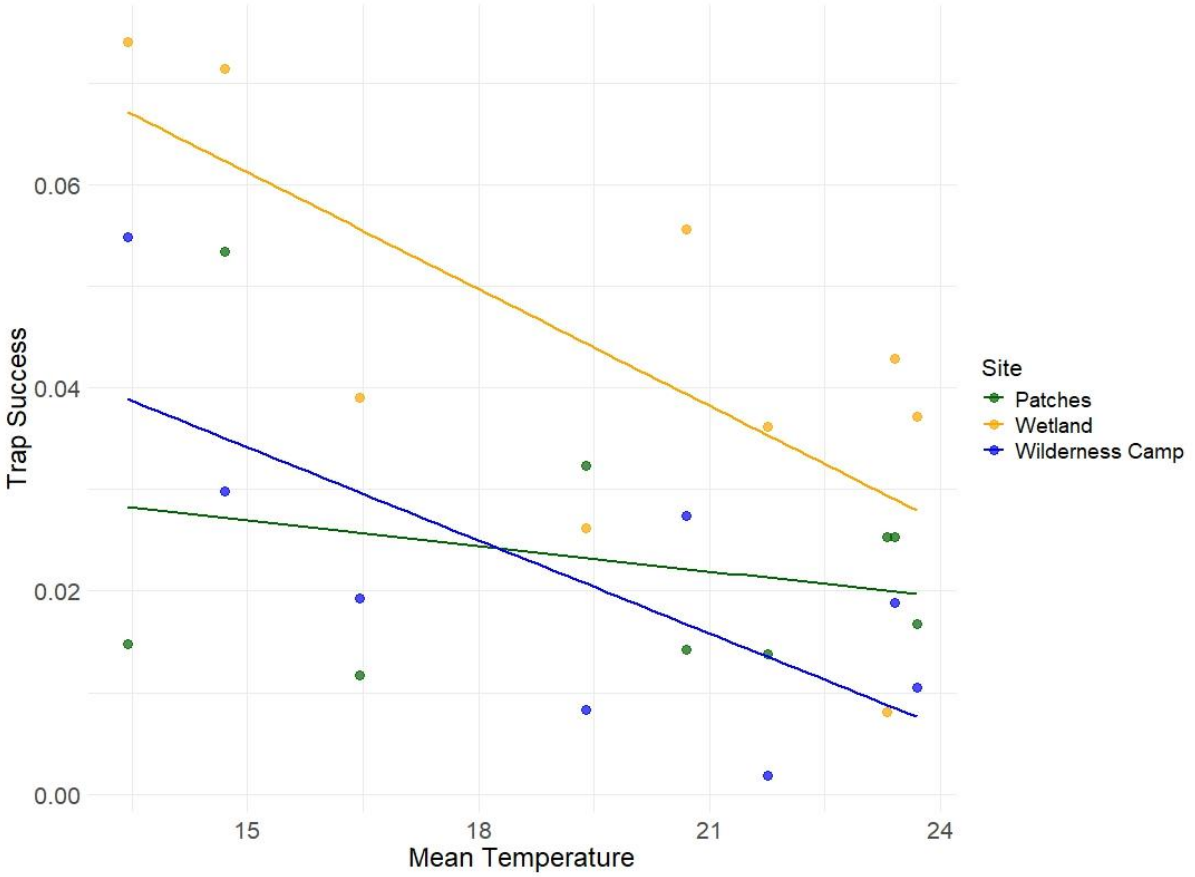

Figure 16: Patterns of variation of mean temperature (◦C) with trapping success. Linear mixed models were used to determine the effect of temperature on the trapping success of R.d. dilectus.

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Although habitat structure differed between sites, with the Wetland dominated by open grassland and the other sites being progressively more dominated by thicket woodland in the Patches and Wilderness Camp sites, habitat variables considered together showed no significant effect on trapping success of *Rhabdomys* (Table 6). Similarly, when model estimates were considered for each variable separately, no significant relationship was shown (Table 6). The coefficient for mouse visibility was estimated at 0.032 with a standard error of 0.191, resulting in a z-value of 0.170 and a p-value of 0.865 (Table 6). This indicates that mouse visibility did not have a statistically significant effect on trapping success.

The coefficient for shrub cover was -0.006 with a standard error of 0.038, a z-value of -0.178, and a p-value of 0.858, indicating that shrub cover did not have a significant impact on trapping success.

The coefficient for grass cover was -0.002 with a standard error of 0.020, a z-value of -0.087, and a p-value of 0.933, showing that grass cover did not significantly affect trapping success.

The coefficient for bare soil itself was 0.001 with a standard error of 0.021, a z-value of 0.028, and a

p-value of 0.977, suggesting that bare soil cover did not have a significant effect on trapping success.

Table 6: Generalized linear regression models with a Poisson distribution were used to examine the relationship between Rhabdomys trapping success and four different vegetation variables. The model considering all habitat variables was not significant. Using the 'cftest' command in R, the effects of mouse visibility, shrub cover, grass cover, and bare soil on trapping success are presented for each variable. The data used for the analysis was pooled from all sites.

Response Variable: Trapping Success				
	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	0.769	0.408	1.884	0.059
Mouse visibility	0.032	0.191	0.170	0.865
Shrub Cover				
(Intercept) == 0	0.867	0.478	1.811	0.070
Shrub == 0	-0.006	0.038	-0.178	0.858
Grass Cover				
(Intercept) == 0	0.868	0.794	1.093	0.275
Grass == 0	-0.002	0.020	-0.087	0.933
Model 4: Bare Soil				
(Intercept) == 0	0.802	0.369	2.173	0.029
Soil == 0	0.001	0.021	0.028	0.977

4.3. *R.d. dilectus* Demography across the three Sites

4.3.1. Sex ratio

. In Patches, the number of males fluctuated with a notable peak in July 2020 (7), while the number of females peaked in September 2021 (9), See Table 7. The sex ratio showed significant variation, with the highest value of 3.50 in July 2020 and the lowest value of 0.50 in September 2020. Reproductively active females were consistently observed, particularly in January 2021 and November 2021 when the ratio reached 1.00. Lactating females were present in several sessions, with the highest ratio of 0.60 in November 2021. The proportion of scrotal males was generally low, with notable activity only in a few sessions. In the Wetland, the number of males and females varied across sessions, with males peaking at 21 in July 2020 and females at 18 in July 2021. The sex ratio ranged from 0.33 in November 2021 to 2.71 in May 2021.

The reproductive activity of females was high, especially in September 2020 and November 2021 (Table 7). Lactating females were present in most sessions, with the highest ratios observed in January 2021. The reproductive activity of males was moderate, with peaks in September 2020 and November

2021. In Wilderness Camp, the number of males and females was generally low, with significant fluctuations in sex ratios. The reproductive activity of females was sporadic, with notable peaks in November 2020 and January 2021. Lactating females were observed in several sessions, particularly in November 2020 and January 2021. The reproductive activity of males was minimal, with scrotal males observed only in September 2021 (Table 7).

Table 7: Demographic Parameters of Rhabdomys dilectus Across Trapping Sessions and Sites. The table below presents the demographic parameters of Rhabdomys dilectus across various trapping sessions and sites. These parameters include the number of males and females, sex ratio, ratio of reproductively active females, ratio of lactating females to total females, and ratio of reproductively active males (scrotal) to total males. See the methods section for detailed explanations on how these ratios were calculated.

PATCHES									
	Jul-20	Sep-20	Nov-20	Jan-21	Mar-21	May-21	Jul-21	Sep-21	Nov-21
No. of males	7	1	6	3	5	5	2	8	3
No. of females	2	2	2	2	3	3	1	9	5
Sex ratio	3.50	0.50	3	1.50	1.67	1.67	2	0.89	0.60
Ratio of reproductively active females	0	0.50	0	1	0.33	0.33	0	0	1
Ratio of lactating females to total females	0	0	0	0.50	0.33	0.3	0	0	0.60
Ratio of reproductively active males (scrotal) to total males	0	0	0.17	0.33	0	0	0	0	0.33
WETLAND									
	Jul-20	Sep-20	Nov-20	Jan-21	Mar-21	May-21	Jul-21	Sep-21	Nov-21
No. of males	21	13	7	14	9	19	16	11	4
No. of females	14	11	14	9	6	7	18	6	12
Sex ratio	1.50	1.18	0.50	1.56	1.50	2.71	0.89	1.83	0.33
Ratio of reproductively active females	0.14	0.64	0.89	0.89	0.83	0.43	0.17	0.33	1
Ratio of lactating females	0	0.64	0.50	0.78	0.50	0.43	0.17	0.33	0.58
Ratio of reproductively active males (scrotal) to total males	0	0.46	0.14	0.07	0.33	0	0	0.09	0.25
WILDERNESS CAMP									
	Jul-20	Sep-20	Nov-20	Jan-21	Mar-21	May-21	Jul-21	Sep-21	Nov-21
No of males	12	12	1	0	0	2	10	1	NA
No. of females	18	2	2	1	0	1	6	0	NA
Sex ratio	0.67	6	0.50	0	0	2	1.67	0	NA

Ratio of reproductively active females	0.06	0	1	1	0	1	0	0	NA
Ratio of lactating females to total females	0	0	1	1	0	1	0	0	NA
Ratio of reproductively active males (scrotal) to total males	0	0	0	0	0	0	0	1	NA

4.3.2. Reproductive patterns and activity

Over the entire study period, 41.15% (158 individuals) of all captured *Rhabdomys dilectus* females were reproductively active, identified by their reproductive status of VO (perforate), lactating, or pregnant. The reproductive ratios varied across different study sites, with the lowest ratios observed in Patches and Wilderness Camp, and the highest in the Wetland.

Reproductive Activity Across Sites

Effective breeding, indicated by the presence of lactating females (Fig. 17), was observed throughout the year in Luvhondo but varied among the three study areas. In the Wetland, breeding was noted in eight out of nine sessions, peaking in September 2020 and March 2021, and being lowest in September 2021. In contrast, no reproductively active females were trapped in the Patches and Wilderness Camp during July and September of both 2020 and 2021.

At the Patches, lactating females were identified during three distinct periods: one individual in September 2020, and two individuals in May and July 2021. In the Wilderness Camp, the presence of lactating females was only noted in July 2020. No reproductively active females were observed in the

Wilderness Camp from September 2020 to September 2021.

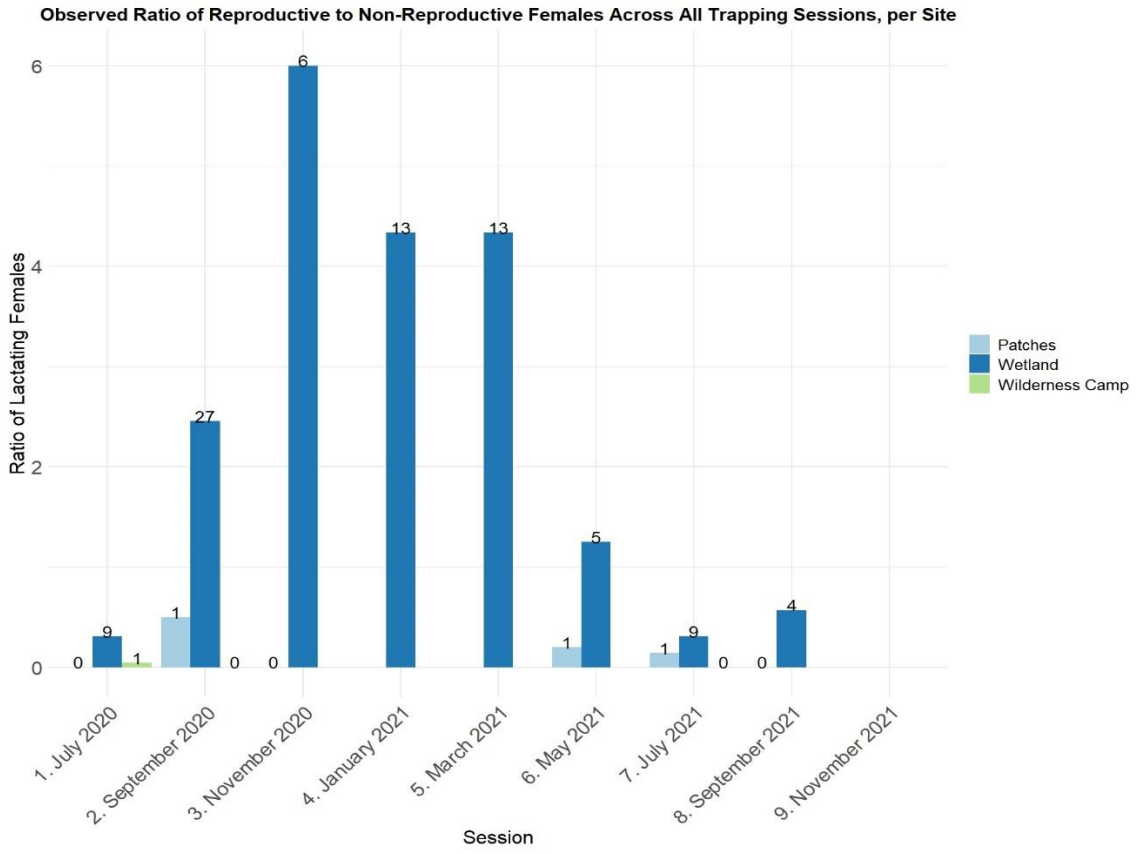

Figure 17: The observed ratio of lactating R.d. dilectus - defined as the number of lactating females/total adult females - across all trapping sessions and sites (the numbers refer to total number of adult females trapped at a given session/site).

Male Reproductive Activity

On average, the presence of scrotal males was infrequent, indicating a shorter reproductive period compared to females. Scrotal males with descended testes (TD) were recorded in July 2020, September 2020, January 2021, and March 2021 at the Wetland site. No reproductive males were found during the dry winter months of May and July 2021, despite the presence of lactating females during the same periods. Scrotal males were observed again in September 2021, but none were recorded in November 2021, with the lowest number recorded in November with just one scrotal male (Fig. 18).

At the Patches, scrotal males were only recorded during the wet summer months of November 2020, January 2021, and November 2021. In contrast, the only scrotal male observed at the Wilderness Camp was in September 2021.

This suggests that reproductive activity in Luvhondo primarily occurs from September to November, with a notable decrease in July, indicating a seasonal pattern in male reproductive readiness (Fig. 18).

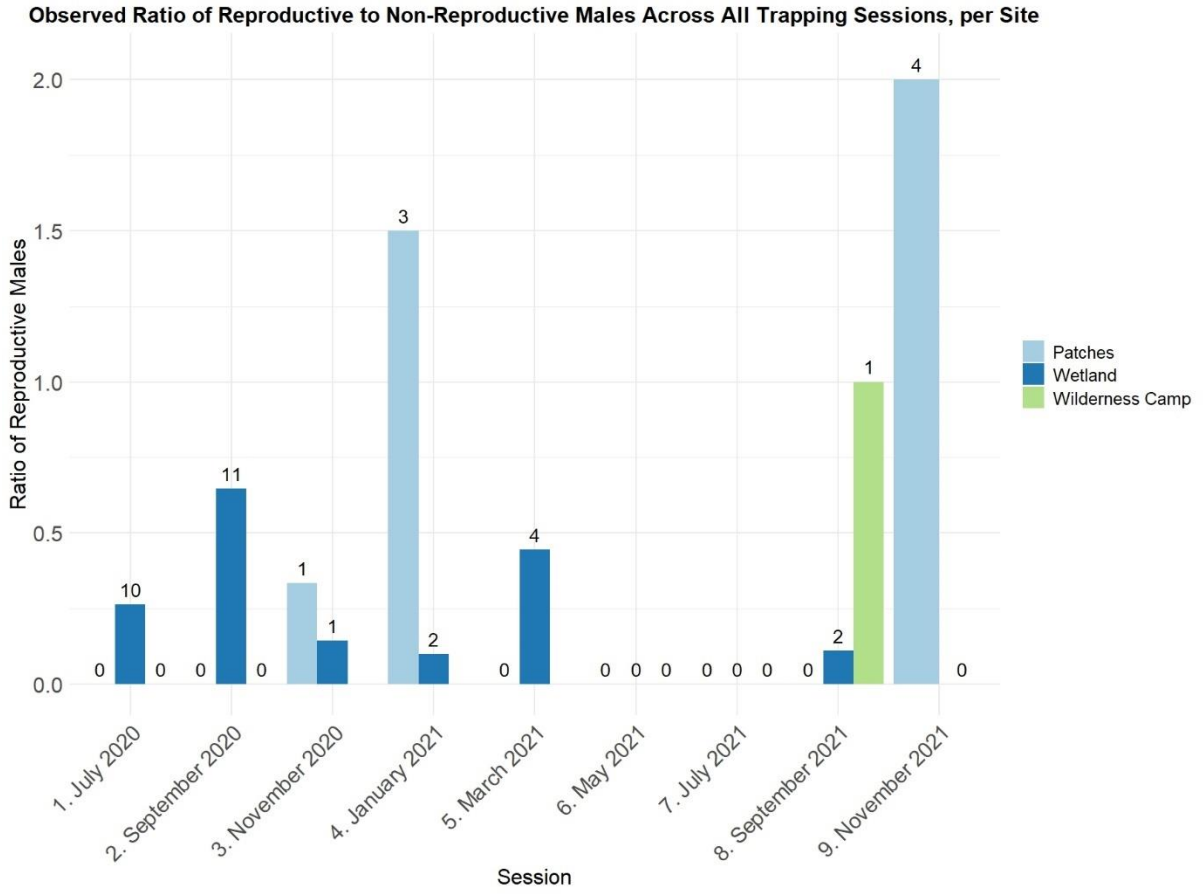

Figure 18: The observed ratio of reproductive R.d. dilectus males - defined as the number of reproductive males/total adult males - across all trapping sessions and sites (the numbers refer to total number of adult males trapped at a given session/site).

In the Wetland (Fig. 18), female reproductive activity peaked in September 2020 and March 2021, while male activity peaked in September 2020 and January 2021. Females showed no reproductive activity in July 2020, and males were inactive during the dry winter months of May and July 2021, and in November 2021.

At the Patches, females were most reproductively active in May and July 2021, whereas males peaked in November 2020, January 2021, and November 2021. There was no reproductive activity for females in July and September 2020, and September 2021, and males showed no activity in July and September of both 2020 and 2021 (Fig. 18).

In the Wilderness Camp, female reproductive activity was noted only in July 2020, with no activity from September 2020 to September 2021. For males, reproductive activity was recorded only once in September 2021 (Fig. 18).

Overall, females exhibited broader peaks in reproductive activity, while males showed more sporadic activity, primarily during the wetter months. This suggests a longer reproductive period for females compared to males, with both sexes showing reduced activity during the winter months (Fig. 18)

One-Way ANOVA:

The one-way ANOVA was performed to compare the reproductive ratios across different sites. The results indicated that there were no significant differences in the reproductive ratios across the three sites ($F(2, 49) = 0.614$, $p = 0.545$).

Two-Way ANOVA:

A two-way ANOVA was conducted to evaluate the interaction effects of site and session on the reproductive ratios. The two-way ANOVA results showed that neither the main effect of site ($F(2, 26) = 0.593$, $p = 0.5601$) nor the interaction effect between site and session ($F(15, 26) = 0.357$, $p = 0.9795$) were statistically significant. However, the main effect of the session approached significance ($F(8, 26) = 1.995$, $p = 0.0876$), suggesting a possible influence of seasonality on reproductive ratios that warrants further investigation.

Sex Ratio Analysis

A Friedman rank sum test was employed to determine if the ratios of males to females differed significantly across sites. The test revealed no significant differences in the ratios between sites ($\chi^2 = 2.5161$, $df = 2$, $p = 0.2$).

4.3.3. Variations in Body Condition: Understanding Differences Across Sites

The analysis of body condition in *Rhabdomys dilectus* across the study sites revealed significant differences, despite the overall similar trends in body length and mass. A multivariate analysis of variance (MANOVA) confirmed these differences were statistically significant ($p = 4.548e-07$).

Figure 19 illustrates the relationship between body length and mass for *Rhabdomys dilectus* across Wilderness Camp, Wetland, and Patches. Across all sites, there is a clear positive correlation between body length and mass, indicating that as body mass increases, so does body length. Site-Specific Findings:

- Wilderness Camp: The data points from Wilderness Camp, represented in green, show a strong correlation between body length and mass, with the fitted curve (R^2 = 0.6188) indicating a substantial increase in body length with increasing mass.
- Wetland: Represented in blue, the Wetland site also exhibits a strong positive correlation, with an even higher R^2 value of 0.6748. This suggests that body length increases reliably with mass in this environment.
- Patches: The orange data points for Patches indicate a positive correlation, though with more variability (R^2 = 0.5545) compared to the other sites. This variability suggests that while the general trend of increasing body length with mass holds, there are other influencing factors at this site.

Figure 19: Regression plot of body length versus mass in Rhabdomys dilectus. N=348 mice from 3 sites sampled between July 2020 and November 2021.

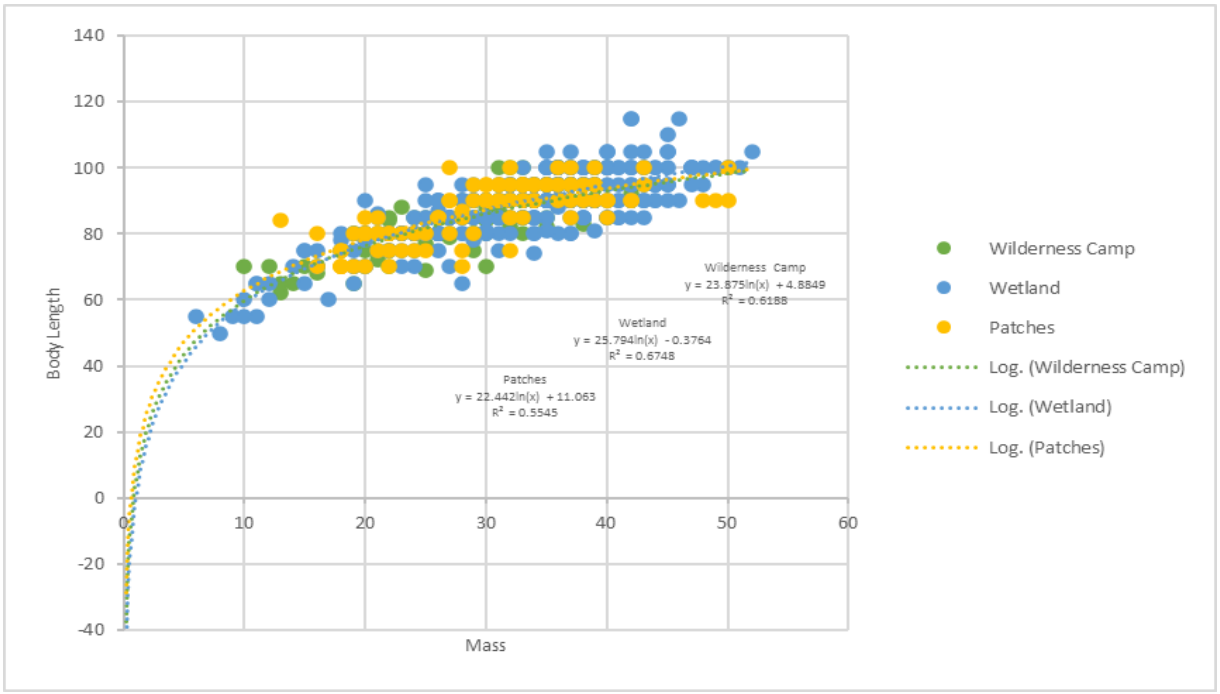

Figure 20 illustrates the distribution of *Rhabdomys dilectus* across two primary age classes (Adult and Non-Adult) for each trapping session at the three study sites: Wetland, Wilderness Camp, and Patches. The number of captured individuals is represented with adults (blue) and non-adults (green), providing insight into demographic fluctuations over time.

Across all sampling periods, adult individuals consistently dominated captures, with the highest numbers recorded in the Wetland site, particularly in July 2020, September 2020, and July 2021. The Wilderness Camp site exhibited lower capture rates overall, with sporadic increases in adult counts, particularly in January and July 2021. Patches consistently had the lowest number of captures across all sessions, with minimal fluctuations in both age classes.

A potential third demographic group was observed, consisting of individuals measuring between 70 mm and 80 mm in body length and weighing between 9 g and 28 g. These individuals were non-reproductive across both sexes and may represent juvenile mice transitioning between non-adult and adult stages. Their presence, particularly in higher-density periods, suggests a possible recruitment pattern following peaks in adult population size.

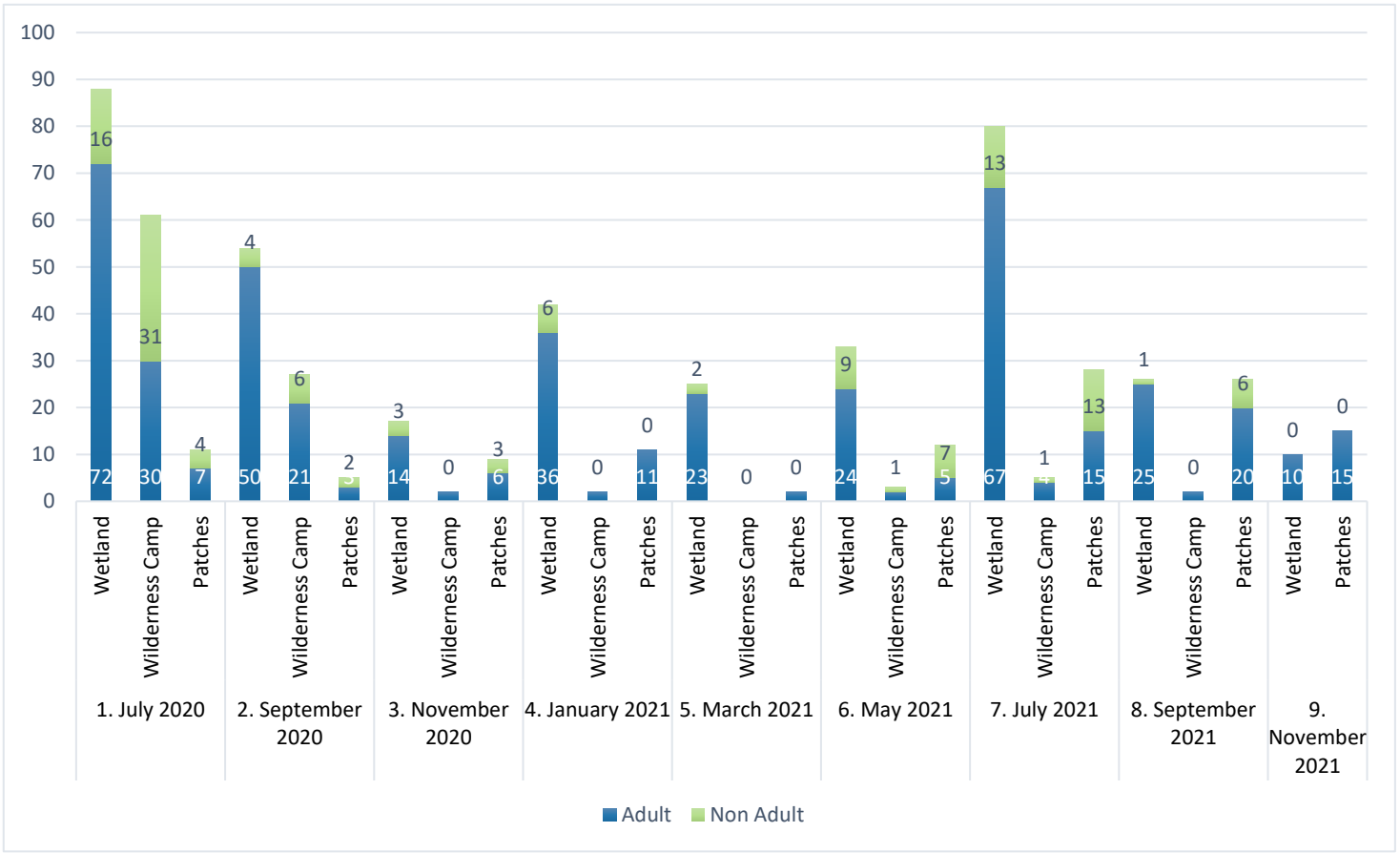

Figure 20: Distribution of R.d. dilectus age classes (adults and non-adults) observed across all sessions and sites.

The ratios statistically differed between trapping sessions, with more adult mice being captured across all sessions (χ^2 =6.23, df = 2, p = 0.04). Adult *R.d. dilectus* occurred far more consistently across the different sites and sessions than the non-adult individuals (Fig. 19). Non-adult individuals were

generally more frequent during the dry seasons across all sites (May and July, Fig. 19) which may coincide with a seasonal decline in food availability.

4.4. Variation of Body Length across Sites, Seasons, and Sessions in *R.d. dilectus*.

Differences in body length of *Rhabdomys dilectus* were detected between sites. The analysis showed that the site had a significant effect on body length ($F(2, 592) = 32.31$, $p < .001$. This suggests that environmental factors associated with different sites contribute to variations in body length.

Table 8 shows the standard deviation and averages of net mass and body length of *Rhabdomys* dilectus captured in patches, wetlands, and the wilderness camp from July 2020 to November 2021.

Significant differences in body length and net mass of *Rhabdomys dilectus* were observed across different sessions and sites (Table 8). In the Patches site, the highest average net mass for males was recorded in September 2020 at 37.00g, while females showed a peak average net mass of 35.33g in November 2021. The highest average body length for males in Patches was 97.50mm in March 2021, and for females, it was 92.50mm in November 2020 (Table 8).

In the Wetland site, the highest average net mass for males was 37.25g in November 2021, with females peaking at 36.97g in September 2020. The maximum average body length for males was 92.00mm in March 2021, and for females, it was 91.53mm in September 2020 (Table 8).

At the Wilderness Camp, the highest average net mass for males was 42.50g in September 2021, while females had their peak at 36.50g in January 2021. The highest average body length for males was 91.67mm in July 2021, and for females, it was 90.00mm in May 2021 (Table 8).

Table 8: Comparison of Mass and Length Variability by Site and Session, along with the sample size. The table is based on data obtained at first capture for each session and not at recapture and including both adult and non- adult mice.

Session	StdDev of Net Mass		StdDev of Body Length		Average of Net Mass ± StdDev		Average of Body Length		Sample Size	
	F	M	F	M	F	M	F	M	F	M
	Patches									
1. July 2020		6.69	8.49	10.23	24.50±4.95	30.56	81.00	85.00	2	8
2. Sep 2020	8.72	0.00	5.77	0.00	22.00	37.00	78.33	97.50	3	2
3. Nov 2020	0.00	13.04	3.54	13.73	34.00	31.14	92.50	87.86	2	7
4. Jan 2021	4.54	2.30	4.52	2.24	35.17	31.40	91.67	96.00	6	5
5. March 2021		4.24		0.00		30.00		97.50		2
6. May 2021	6.70	7.84	4.49	11.73	28.71	21.00	79.14	75.00	7	5
7. July 2021	1.25	4.55	1.29	6.89	21.87	24.92	79.67	81.54	15	13
8. Sep 2021	7.42	8.10	4.08	2.05	24.40	36.55	81.67	90.64	14	11
9. Nov 2021	3.16	4.07	0.83	1.71	35.33	35.83	89.44	93.33	9	6
	Wetland									

1. July 2020	8.46	8.42	10.33	8.71	31.21	32.69	86.04	88.08	35	51
2. Sep 2020	6.11	8.39	8.12	8.68	36.97	35.23	91.53	91.73	36	30
3. Nov 2020	7.72	9.43	6.36	10.06	31.00	34.50	87.86	92.00	7	10
4. Jan 2021	9.08	10.11	10.58	9.82	35.13	32.73	86.56	89.68	16	26
5. March 2021	8.43	8.63	6.00	13.47	35.50	32.27	89.44	92.00	16	15
6. May 2021	6.97	7.73	7.75	9.74	27.25	25.50	85.42	79.72	12	32
7. July 2021	6.71	7.26	7.43	4.86	27.98	32.08	84.68	89.58	37	31
8. Sep 2021	5.68	4.34	6.78	3.33	28.33	32.90	87.08	91.50	12	20
9. Nov 2021	2.40	3.20	3.16	2.04	36.83	37.25	95.00	92.50	6	4
					Wilderness Camp					
1. July 2020	8.48	7.72	11.99	6.84	25.95	26.69	82.95	80.14	22	25
2. Sep 2020	0.58	4.50	2.89	5.90	26.33	27.29	81.67	84.44	3	19
3. Nov 2020	2.83		3.54		34.00		87.50		2	
4. Jan 2021	2.12		0.00		36.50		80.00		2	
6. May 2021	0	7.07	0	10.61	35.00	21.00	90.00	77.50	1	2
7. July 2021	0.00	2.08	0.00	5.77	19.00	37.33	80.00	91.67	2	3
8. Sep 2021		0.71		0.00		42.50		90.00		2

4.4.1. Site-Specific Variations in Body Length of *Rhabdomys dilectus*

The analysis of variance (ANOVA) was conducted to assess differences in body length among the three sites: Wetland, Wilderness Camp, and Patches. The results indicated no overall significant differences in body length across these sites (F-statistic: 2.0253, p-value: 0.1345). However, a detailed pairwise comparison revealed specific site differences.

In comparing Wetland and Patches, the Wetland site exhibited a significantly higher body length (difference = 3.66 units, confidence interval: 0.70 to 6.63 units, p adj = 0.01), indicating that mice in Wetland are generally larger. Conversely, the comparison between Wilderness Camp and Patches showed a slightly lower body length at Wilderness Camp (difference = -1.30 units), but this difference was not statistically significant (p adj = 0.720126).

A more pronounced difference was observed between Wilderness Camp and Wetland. Mice in Wilderness Camp had significantly shorter body lengths compared to those in Wetland (difference = -4.97 units, confidence interval: -8.19 to -1.74 units, p adj = 0.000932), highlighting a substantial size difference.

The mean differences in body length between the groups were also examined. On average, mice in the Wetland site were 0.8631 units longer than those in the Patches site. However, this difference was not statistically significant.

The data underscore the presence of site-specific variations in body length among R. dilectus, with Wetland consistently showing larger sizes (Table 10).

Table 9: Tukey HSD test results for the site variable, indicating where significant differences in body length occurred between sites for the complete dataset (including adults and non-adults). The "diff" column shows the mean differences in body length between sites, "lwr" and "upr" represent the lower and upper bounds of the confidence interval, and "p adj" indicates the adjusted p-value for multiple comparisons.

	diff	lwr	upr	p adj
Wetland-Patches	0.863	-3.497	5.223	0.887
Wilderness Camp-Patches	-3.219	-8.735	2.297	0.354
Wilderness Camp-Wetland	-4.082	-8.876	0.711	0.112

The effect of sex on body length across the three locations (Wetlands, Patches, and Wilderness Camp) was analyzed. The results indicated that there was no significant difference in the average body length between sexes. The F-statistic was 0.5549, and the p-value was 0.4572. Since the p-value is greater than the typical significance level of 0.05, it suggests that the differences in body length between male and female *Rhabdomys dilectus* are not statistically significant across the three locations in this dataset.

4.4.2. Impact of Sex and Site on Body Length of Adult *Rhabdomys dilectus*

The analysis of adult *Rhabdomys dilectus* revealed significant differences in mean body length based on sex and site (Table 10). This analysis excluded non-adults to avoid confounding results due to growth variations.

Sex was found to have a statistically significant effect on body length, with males being larger than females ($F(1, 496) = 14.85$, $p < .001$). Site also significantly affected body length ($F(2, 496) = 12.79$, $p < .001$), indicating environmental influences on growth.

Table 10: ANOVA results comparing the mean body length of adult Rhabdomys dilectus across sex and site, showing significant effects of sex, site, and their interaction.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Sex	1	518	517.90	14.85	0.002
Site	2	892	446	12.79	3.84E-06
Sex: Site	2	725	362.31	10.39	3.80E-05
Residuals	496	17297	34.90		

Additionally, there was a significant interaction between sex and site ($F(2, 496) = 10.39$, $p < .001$), suggesting that the effect of sex on body length varied across different locations (Table 11).

The body length of *Rhabdomys dilectus* showed significant variations based on sex and site. Females in the Wetland site had significantly longer body lengths compared to females in the Patches site ($p = 0.0056$). Additionally, males in the Patches site exhibited significantly longer body lengths than females in the same site ($p < 0.0001$), as did males in the Wetland site compared to females in the Patches site ($p < 0.0001$).

Notable differences were also observed among males from different sites. Males in the Wilderness Camp had significantly shorter body lengths than those in the Patches and Wetland sites ($p < 0.0001$ for both comparisons). Furthermore, females in the Wetland site had significantly longer body lengths compared to males in the Wilderness Camp ($p = 0.003$).

Table 11: Post hoc Tukey HSD Test for the Interaction Between Sex and Site, Assessing Their Influence on the Body Length of Adult Rhabdomys dilectus.

	diff	lwr	upr	p adj
F: Patches - F: Wetland	37.347	0.7248	67.446	0.0056
F: Patches - F: Wilderness Camp	3.469	-1.255	81.929	0.2885
F: Patches - M: Patches	62.239	25.299	9.918	0.0
F: Patches - M: Wetland	58.917	29.286	88.548	0.0
F: Patches - M: Wilderness Camp	0.0015	-3.712	37.149	1.0
F: Wetland - F: Wilderness Camp	-0.2657	-4.359	38.275	1.0
F: Wetland - M: Patches	24.892	-0.3541	53.326	0.1247
F: Wetland - M: Wetland	2.157	0.3629	39.511	0.0083
F: Wetland - M: Wilderness Camp	-37.332	-66.018	-0.8647	0.003
F: Wilderness Camp - M: Patches	2.755	-18.647	73.746	0.5284
F: Wilderness Camp - M: Wetland	24.227	-16.362	64.817	0.5274
F: Wilderness Camp - M: Wilderness Camp	-34.675	-81.027	11.677	0.2684
M: Patches - M: Wetland	-0.3322	-3.126	24.615	0.9994
M: Patches - M: Wilderness Camp	-62.225	-98.023	-26.426	0.0
M: Wetland - M: Wilderness Camp	-58.902	-87.097	-30.708	0.0

Another ANOVA model (Table. 12) factoring session and its influence on the body length of adult *R.d. dilectus* mice was carried out; it showed that body length varied significantly across trapping session ($F (8, 495) = 7.49$, $p < .001$).

Table 12:ANOVA Results for Assessing the Effect of Different Sessions on the Body Length of Rhabdomys dilectus. The analysis shows significant differences in body length across sessions.

	df	Sum of Sq	F value	Pr(>F)
Session	8	2115.14	7.49	1.90e-09
Residual	495	17480.41		

The Tukey HSD test results for the effect of session on the body length of *Rhabdomys dilectus* revealed several significant pairwise differences (Table 13). There was a significant difference in body length between September 2020 and May 2021 (p = 0.0014), with May 2021 having shorter body lengths. Similarly, a significant difference was observed between September 2020 and July 2021 (p = 0.0003), with July 2021 also having shorter body lengths. November 2020 vs. May 2021 (p = 0.0007) and November 2020 vs. July 2021 (p = 0.0009) comparisons showed May 2021 and July 2021 having shorter body lengths, respectively.

Further, January 2021 vs. May 2021 (p = 0.0016) and January 2021 vs. July 2021 (p = 0.0010) comparisons indicated shorter body lengths in May 2021 and July 2021. March 2021 vs. May 2021 (p = 0.0003) and March 2021 vs. July 2021 (p = 0.0002) comparisons showed shorter body lengths in May 2021 and July 2021. Lastly, significant differences were found between May 2021 and November 2021 (p = 0.0074) and between July 2021 and November 2021 (p = 0.0122), with November 2021 showing longer body lengths in both comparisons.

Table 13: Tukey test done for sessions, to determine where the significant differences in body length were recorded between sessions for the adult dataset.

	diff	lwr	upr	p adj
1. July 2020 - 2. September 2020	1.921	-0.704	45.461	0.3563
1. July 2020 - 3. November 2020	38.921	-0.4074	81.917	0.112
1. July 2020 - 4. January 2021	23.538	-0.7927	55.003	0.3257
1. July 2020 - 5. March 2021	35.798	-0.1568	73.165	0.0725
1. July 2020 - 6. May 2021	-32.266	-69.633	0.51	0.1539
1. July 2020 - 7. July 2021	-21.012	-47.005	0.4981	0.2255
1. July 2020 - 8. September 2021	-0.4226	-34.841	26.389	1.0
1. July 2020 - 9. November 2021	26.831	-13.933	67.594	0.5086
2. September 2020 - 3. November 2020	19.711	-24.524	63.946	0.902
2. September 2020 - 4. January 2021	0.4328	-28.811	37.466	1.0
2. September 2020 - 5. March 2021	16.588	-22.198	55.374	0.9212
2. September 2020 - 6. May 2021	-51.477	-90.263	-12.691	0.0014
2. September 2020 - 7. July 2021	-40.223	-68.218	-12.227	0.0003
2. September 2020 - 8. September 2021	-23.436	-55.768	0.8895	0.3698
2. September 2020 - 9. November 2021	0.762	-34.448	49.688	0.9997
3. November 2020 - 4. January 2021	-15.383	-62.898	32.132	0.985
3. November 2020 - 5. March 2021	-0.3123	-54.736	4.849	1.0

3. November 2020 - 6. May 2021	-71.188	-12.28	-19.575	0.0007
3. November 2020 - 7. July 2021	-59.934	-104.016	-15.851	0.0009
3. November 2020 - 8. September 2021	-43.148	-90.104	0.3809	0.1005
3. November 2020 - 9. November 2021	-12.091	-66.214	42.032	0.9988
4. January 2021 - 5. March 2021	1.226	-30.229	54.749	0.993
4. January 2021 - 6. May 2021	-55.804	-98.293	-13.315	0.0016
4. January 2021 - 7. July 2021	-4.455	-77.485	-11.615	0.001
4. January 2021 - 8. September 2021	-27.764	-64.456	0.8928	0.3101
4. January 2021 - 9. November 2021	0.3293	-42.212	48.797	1.0
5. March 2021 - 6. May 2021	-68.065	-115.091	-21.038	0.0003
5. March 2021 - 7. July 2021	-5.681	-95.423	-18.198	0.0002
5. March 2021 - 8. September 2021	-40.024	-81.888	0.1839	0.0737
5. March 2021 - 9. November 2021	-0.8968	-58.736	40.801	0.9998
6. May 2021 - 7. July 2021	11.254	-27.358	49.866	0.9925
6. May 2021 - 8. September 2021	2.804	-13.823	69.903	0.4835
6. May 2021 - 9. November 2021	59.097	0.9328	108.865	0.0074
7. July 2021 - 8. September 2021	16.786	-15.337	4.891	0.7891
7. July 2021 - 9. November 2021	47.843	0.5935	89.751	0.0122
8. September 2021 - 9. November 2021	31.057	-13.865	75.978	0.4378

4.4.3. Impact of Sex, Site and Session on Body Length of non-Adult *Rhabdomys dilectus*

The results of the two-way ANOVA (Table 14), investigating the influence of sex and site on the body length of *Rhabdomys*, indicate the following: There was no significant effect of sex on body length, F (1,123) = 3.64, p = 0.059F(1, 123) = 3.64, p = 0.059F(1,123) = 3.64, p = 0.059. This suggests that male and female *Rhabdomys* did not significantly differ in their body lengths. Similarly, the main effect of site was not significant, F (2,123) = 1.28, p = 0.280, F(2, 123) = 1.28, p = 0.280, F(2,123) = 1.28, p = 0.280, indicating that body length did not significantly vary across the different sites sampled. Furthermore, the interaction effect between sex and site was also not significant, F (2,123) = 1.20, p = 0.303F(2, 123) = 1.20, p = 0.303F(2,123) = 1.20,p = 0.303, suggesting that the combined influence of sex and site did not affect the body length of the specimens. These results imply that neither sex nor site, nor their interaction, significantly contribute to variations in body length in this sample of *Rhabdomys*.

Table 14: ANOVA Comparing the Mean Body Length of Rhabdomys dilectus Across Sex and Site for the Non-Adult R. dilectus Population.

	Df	Sum Sq	F value	Pr(>F)
Sex	1	160.74	3.644	0.059
Site	2	113.32	1.285	0.280
Sex: Site	2	107.01	1.205	0.303
Residuals	123	5425.46		

A one-way ANOVA was conducted to investigate the effect of different sessions on the body length of *Rhabdomys dilectus* (Table 15). The analysis revealed a significant effect of session on body length, F (7,121)=5.59,p<0.001F(7, 121) = 5.59, p < 0.001F(7,121)=5.59,p<0.001. This indicates that the body length of *R. dilectus* significantly varies.

Table 15: ANOVA Comparing the Mean Body Length of Rhabdomys dilectus Across Different Sessions.

	Df	Sum Sq	F value	Pr(>F)
Session	7	1428.76	5.59	<0.001
Residuals	121	4418.24		

The Tukey test (Table 16) revealed several significant differences in the mean body length of non-adult *Rhabdomys dilectus* across different sessions. The body length in the 7. July 2021 session was significantly greater than that in the 1. July 2020 session (mean difference = 5.67, p = 0.006). Additionally, the body length in the 5. March 2021 session was significantly greater than that in the 3. November 2020 session (mean difference = -15.83, p = 0.035). The 7. July 2021 session also exhibited significantly greater body lengths compared to the 4. January 2021 session (mean difference = 10.83, p = 0.003) and the 8. September 2021 session compared to the 4. January 2021 session (mean difference = 11.79, p = 0.014). Furthermore, the 6. May 2021 session had significantly greater body lengths compared to the 5. March 2021 session (mean difference = 14.11, p = 0.037), and the 7. July 2021 session had significantly greater body lengths compared to the 5. March 2021 session (mean difference = 18.33, p = 0.002). Lastly, the 8. September 2021 session exhibited significantly greater body lengths compared to the 5. March 2021 session (mean difference = 19.29, p = 0.003). These findings indicate that significant variations in body length occurred predominantly in sessions from March 2021 onwards, suggesting temporal factors may have contributed to the observed differences in body length among the non-adult *R. dilectus* population.

Table 16: Tukey test done for session variable, to determine where the significant differences in body length were detected between session for the non-adult dataset.

	diff	lwr	upr	p adj
1. July 2020 - 2. September 2020	10.915	-50.263	72.093	0.9993
1. July 2020 - 3. November 2020	31.748	-49.726	113.222	0.9299

1. July 2020 - 4. January 2021	-51.585	-13.306	29.889	0.5177
1. July 2020 - 5. March 2021	-126.585	-261.565	0.8394	0.0831
1. July 2020 - 6. May 2021	14.486	-31.212	60.184	0.9768
1. July 2020 - 7. July 2021	56.748	1.055	102.946	0.0056
1. July 2020 - 8. September 2021	66.272	-0.9957	142.501	0.1384
2. September 2020 - 3. November 2020	20.833	-72.365	114.032	0.9971
2. September 2020 - 4. January 2021	-6.25	-155.699	30.699	0.4411
2. September 2020 - 5. March 2021	-13.75	-279.863	0.4863	0.0664
2. September 2020 - 6. May 2021	0.3571	-60.742	67.885	1.0
2. September 2020 - 7. July 2021	45.833	-18.836	110.503	0.3674
2. September 2020 - 8. September 2021	55.357	-33.293	144.007	0.5359
3. November 2020 - 4. January 2021	-83.333	-19.095	24.283	0.2564
3. November 2020 - 5. March 2021	-158.333	-310.526	-0.614	0.0352
3. November 2020 - 6. May 2021	-17.262	-101.116	66.592	0.9983
3. November 2020 - 7. July 2021	2.5	-59.128	109.128	0.9839
3. November 2020 - 8. September 2021	34.524	-69.178	138.226	0.9695
4. January 2021 - 5. March 2021	-7.5	-227.193	77.193	0.7952
4. January 2021 - 6. May 2021	66.071	-17.783	149.926	0.2364
4. January 2021 - 7. July 2021	108.333	24.206	192.461	0.003
4. January 2021 - 8. September 2021	117.857	14.155	221.559	0.0144
5. March 2021 - 6. May 2021	141.071	0.4642	27.75	0.0372
5. March 2021 - 7. July 2021	183.333	46.736	319.931	0.0016
5. March 2021 - 8. September 2021	192.857	43.407	342.308	0.0029
6. May 2021 - 7. July 2021	42.262	-0.8014	92.538	0.1687
6. May 2021 - 8. September 2021	51.786	-26.982	130.553	0.4676
7. July 2021 - 8. September 2021	0.9524	-69.535	88.582	1.0

Notably, the non-adult animals exhibited significantly smaller lengths in September and November 2020 compared to March 2021. This difference may potentially be attributed to age-related factors such as the developmental stage of the individuals.

5. Discussion

This study provides new insights into the population dynamics of *Rhabdomys dilectus dilectus* at the Lajuma Research Station in the Soutpansberg, Limpopo Province, with a focus on local ecology and population structure. Previous research on the genus *Rhabdomys* has largely concentrated on the genetic diversity and evolutionary history of its species and subspecies (Rambau & Robinson, 2003; Castiglia *et al.,* 2012; du Toit *et al.,* 2012). However, this investigation shifts focus towards

understanding the ecological factors shaping the population characteristics of *R.d. dilectus* in its natural habitat. By building on earlier ecological studies (Abu Baker & Brown, 2010; Dufour *et al.,* 2015; Dufour *et al.,* 2019; Ganem *et al.,* 2012), the current research aimed to provide a more comprehensive understanding of how *R.d. dilectus* interacts with its environment.

This study explores the small mammal community across three distinct ecological sites over multiple seasons, assessing the population structure and demographics of *R.d. dilectus*. It also examines how both abiotic factors, such as rainfall, and biotic factors, such as competition, influence the population. Furthermore, the research evaluates the role of habitat characteristics and vegetation structure in shaping the distribution and abundance of *R.d. dilectus*, offering a broader ecological context to its population dynamics.

Through the detailed analysis of these factors, this research contributes significantly to our understanding of *R.d. dilectus* in a localized geographical setting. These findings are particularly relevant for conservation efforts, especially in the face of environmental changes, and highlight the importance of understanding species responses to ecological pressures in shaping population resilience.

5.1. Community composition and estimates of small mammal diversity across the three sites.

The composition and distribution of small mammal species across the three study sites provide key insights into habitat preferences and community structure. *Rhabdomys dilectus dilectus*'s dominance at the Wetland site underscores its adaptation to mesic environments with dense vegetation and consistent water availability. This observation aligns with previous research (Ganem *et al.,* 2012; Dufour *et al.,* 2015), which highlights the species' dependence on such habitats for food and shelter. The high abundance of *R.d. dilectus* at the Wetland likely reflects reduced competition for resources, as fewer species were able to thrive in the wetter conditions.

At the Wilderness Camp, the higher diversity of small mammals suggests that habitat heterogeneity plays a critical role in supporting a broader range of species. Nemakhavhani (2015) made similar observations, highlighting how varied habitat structures can influence species richness. This aligns with findings from Magige (2013), who reported that species richness in the Serengeti ecosystem was higher in woodlands compared to grasslands, as woodlands provide a greater variety of microhabitats that support diverse rodent communities. Woodlands act as safe havens, offering structural complexity, shelter, and food resources that facilitate the coexistence of multiple species (Salvatori et al., 2001).

Additionally, Magige (2013) found that cropland habitats also supported high species richness due to their diverse food resources and the presence of microhabitats created by agricultural activities. This suggests that heterogeneous landscapes, whether natural or human-modified, contribute to small mammal diversity by creating niches that different species can exploit. Similarly, the habitat complexity at the Wilderness Camp likely provides multiple ecological niches, allowing *R. d. dilectus* and other small mammals to coexist despite competition. This reinforces the idea that structural diversity within habitats plays a crucial role in shaping species distributions and community composition in small mammal populations.

The habitat preferences of *Mus minutoides* and *Lemniscomys rosalia* also reflect the influence of vegetation structure on species distribution. *M. minutoides* was found in areas with dense grass and shrubs, likely benefiting from the shelter and foraging opportunities these microhabitats offer, similar to patterns observed in Swaziland and Uganda (Long *et al.,* 2013; Ssuuna *et al.,* 2020). Likewise, *L. rosalia*'s affinity for dry grasslands and areas with specific trees such as *Searsia chirindensis* highlights the importance of vegetative diversity in supporting a variety of small mammals (Perrin, 1997; Saanya *et al.,* 2022). These findings suggest that maintaining habitat heterogeneity is crucial for promoting species diversity in the region.

A noteworthy observation was the expansion of *Aethomys ineptus* into more mesic habitat areas between March 2021 and September 2021. This shift contrasts with its typical preference for habitats with shrub and rocky coverage, as reported by Linzey et al. (2003), who examined its distribution across South Africa. Their study indicated that *A. ineptus* is primarily found at higher elevations in north-central South Africa but has been observed expanding into lower-elevation habitats towards the southern part of its range. While typically associated with drier environments, its presence in more mesic habitats suggests ecological plasticity, potentially driven by environmental gradients or shifting habitat conditions. The observed expansion in this study further supports the notion that *A. ineptus* can occupy a broader range of habitats than previously assumed. This expansion may be driven by resource partitioning or competition mitigation, suggesting a dynamic interplay between *A. ineptus* and *R.d. dilectus*. The proximity of different habitat types within the trapping transect likely facilitates such interactions, as previously documented in studies of spatiotemporal resource partitioning among rodent species in the southern Cape mountains (Bond *et al.,* 1979).

The comparison of community dynamics with Nemakhavhani (2015) reveals notable differences. Her study found *Rhabdomys dilectus dilectus, followed by Crocidura mariquensis* to be the most common species in the wetlands, followed by *Myosorex varius*. However, in the present study, only 21 *Shrew sp.*s were recorded, which included both *Myosorex varius* and *Crocidura mariquensis*. This discrepancy

could be attributed to changes in the site's ecology since 2015, including a fire in July 2018, and differences in study design, as the present study was optimized for capturing *R.d. dilectus*.

The rarefaction analysis, coupled with curve extrapolation, provided valuable insights into sample completeness across different sites. The Wetland demonstrated high sample completeness, as indicated by narrow confidence limits, suggesting that the trapping efforts likely captured a significant portion of the small mammal community. This high completeness can be attributed to the homogeneous habitat, where reduced niche diversity leads to a higher likelihood of capturing a representative sample (Chao *et al.,* 2014; Henriksen *et al.,* 2019).

Henriksen *et al.* (2019) explored the effects of habitat structure on the completeness of species sampling within ecological networks. Their study highlighted that homogeneous environments, such as those characterized by consistent vegetation cover and fewer microhabitats, allow for more efficient sampling efforts. In these environments, species interactions and distributions tend to be less complex, resulting in higher sampling completeness with less effort. This contrasts with more heterogeneous habitats, where the complexity of microhabitats and greater species diversity can lead to under-sampling unless significant efforts are made. The findings from Henriksen *et al.* (2019) align with the results observed at the Wetland site in this study, where the uniformity of the habitat likely contributed to the success of capturing a representative portion of the mammal community. In contrast, the Wilderness Camp, characterized by habitat heterogeneity, presented a rarefaction curve with wide confidence limits, suggesting the potential for additional species with increased trapping effort.

The divergent outcomes between the Wetland and the Wilderness Camp emphasize the profound impact of habitat characteristics on sample completeness. Homogeneous habitats like the Wetland tend to exhibit higher completeness due to fewer rare or elusive species and more efficient sampling of the existing species. Conversely, heterogeneous habitats like the Wilderness Camp allow for greater species diversity, which may be unveiled with further sampling.

Patches, despite having the lowest species richness, showcased the highest species diversity when analysed with Simpson's concentration diversity index (q = 2) and the second highest with Shannon's entropy diversity index (q = 1). This heightened diversity is likely due to the habitat's heterogeneity, like the Wilderness Camp. The notable disparity in sample completeness between Patches and the Wilderness Camp, despite both being heterogeneous, suggests potential influences from anthropogenic factors, such as herbicides and flooding, as well as variations in habitat quality and micro-habitat elements.

The differences in plant compositions between habitats significantly impact habitat quality and ecological dynamics, influencing overall diversity (Mengist *et al.,* 2021). Variations in vegetation structure, nutrient availability, and plant species composition directly affect the abundance and distribution of various organisms. For instance, specific plant species may provide resources or microhabitats favouring certain animal species. In the context of this study, the divergent plant compositions between Patches and the Wilderness Camp result in varying levels of food availability, shelter, and suitable breeding sites for different organisms, thereby influencing species diversity and abundance.

5.2. Trapping Success

Trapping success varied significantly across the three study sites, reflecting the distinct habitat preferences of the four prevalent species: *Rhabdomys dilectus dilectus*, *Aethomys ineptus*, *Lemniscomys rosalia*, and *Mus minutoides*. The Wetland site, characterized by its mesic habitat and extensive grass cover, proved to be particularly conducive to *R.d. dilectus*, aligning with previous research highlighting this species' preference for such environments (Abu Baker & Brown, 2010; Dufour *et al.,* 2015; Mackay, 2017). The dense vegetation at this site not only provided ample food resources but also offered protection from predators, contributing to the high abundance and trapping success of *R.d. dilectus*.

In contrast, the Wilderness Camp site exhibited greater habitat heterogeneity, facilitating the coexistence of eight different species. Notably, a distinct spatial segregation was observed, with *R.d. dilectus* primarily occupying the mesic grassland areas along the stream, while *A. ineptus* and *M. minutoides* were more frequently captured in areas with old pine plantations and woody vegetation. This pattern aligns with the niche partitioning theory, suggesting that species within the community have evolved to utilize different resources or habitats to minimize competition.

The flooding event caused by tropical cyclone Eloise in January 2021 provided a unique opportunity to examine the resilience and adaptability of these small mammal populations to environmental disturbances. The decline in *R.d. dilectus* captures at the Wilderness Camp and the subsequent expansion of *A. ineptus* into previously occupied territories underscore the dynamic nature of ecological communities and the potential for shifts in species distributions in response to changing conditions.

The Patches site, with its lower trapping success and limited captures of *R. d. dilectus* predominantly in areas with ferns, shrubs, and grasses, highlights the importance of predation risk in habitat selection. The presence of predators like black mambas in wooded patches may deter *R. d. dilectus*

from fully utilizing these areas, even if they offer potential foraging opportunities (Pillay et al., 2003). This aligns with findings by Pillay et al. (2003), who demonstrated that *Rhabdomys pumilio* exhibits a graded anti-predator response to snake faeces, particularly from *Hemachatus haemachatus* (rinkhals). Their study showed that *R. pumilio* reduced exploratory behaviour, increased inactivity, and actively avoided areas containing snake faeces, with heightened responses when the faeces contained conspecific remains. These behavioural adaptations suggest that *Rhabdomys* species, including *R. d. dilectus*, may rely on olfactory cues to assess predation risk and avoid high-risk habitats, such as the wooded patches where black mambas are present in this study.

The study also revealed seasonal fluctuations in trapping success, aligning with patterns observed in other *Rhabdomys* species, where breeding activity and natural food availability influence the attractiveness of supplementary food in traps (David & Jarvis, 1985; Jackson & Bernard, 2006). Additionally, the introduction of new traps at the Patches site led to increased captures of *R.d. dilectus*, emphasizing the influence of spatial factors and potential competitive interactions on trapping data.

5.2.1. The Influence of Weather and Vegetation on the trapping success of *R.d. dilectus*

Population ecology and trapping success are both influenced by extrinsic and intrinsic factors, including but not limited to temperature and food availability (Van Hensbergen & Martin, 1993; Turchin, 2013). These factors have also been implicated in the differentiation of environmental niches within the *Rhabdomys* genus (du Toit *et al.,* 2012; Ganem *et al.,* 2012; Meynard *et al.,* 2012). This study investigated these complex relationships in *Rhabdomys dilectus dilectus* within the diverse habitats of the Lajuma Research Station. The findings illuminate a nuanced interplay of factors shaping the distribution, abundance, and interspecific interactions of this species.

5.2.1.1. Habitat Preferences and Trapping Success

Trapping success varied significantly across the three study sites, underscoring the importance of habitat preferences in shaping small mammal populations. The Wetland site, characterized by its mesic habitat and extensive grass cover, including species like *Coleochloa setifera, Gunnera perpensa, Phragmites* sp., and *Setaria incrassata*, proved to be the most suitable for trapping *R.d. dilectus*. This aligns with previous research (Abu Baker & Brown, 2010; Dufour *et al.,* 2015; Mackay, 2017) highlighting this species' preference for grasslands with dense vegetation, providing both ample food and shelter from predators. The low average mouse visibility at this site (1.74 out of 5) further supports the hypothesis that habitat structure plays a crucial role in predator avoidance and, consequently, population density.

Conversely, the Wilderness Camp site exhibited greater habitat heterogeneity, encompassing grasslands, old pine plantations, and areas with woody vegetation. This diversity supported a wider range of species, with eight different small mammals recorded. Notably, a distinct spatial segregation was observed, reflecting niche partitioning among species. *R.d. dilectus* was predominantly captured in the mesic grassland areas along the stream, consistent with its documented preference for such habitats (du Toit *et al.,* 2012; Meynard *et al.,* 2012). In contrast, *A. ineptus* and *M. minutoides* were more frequently found in areas with woody vegetation and dense undergrowth, aligning with their reported habitat affinities (Linzey *et al.,* 2003; Long *et al.,* 2013; Ssuuna *et al.,* 2020).

The Patches site, characterized by a mix of ferns, shrubs, and grasses interspersed with wooded patches, yielded the lowest trapping success. The absence of *R.d. dilectus* captures in wooded areas suggests that these habitats may be perceived as less suitable due to predation risk or lack of preferred food sources.

5.2.1.2. Environmental Influences and Interspecific Interactions

Environmental factors, both abiotic and biotic, play a crucial role in shaping small mammal populations. The impact of rainfall, while not immediately evident in trapping success during individual sessions, could have delayed effects on population dynamics, as documented in other rodent studies (Dickman *et al.,* 1999; Brown & Ernest, 2002; Yarnell *et al.,* 2007). The observed correlation between rainfall and trapping success in high-density populations underscores the complex interplay between environmental variables and population-level processes such as resource competition, territorial behaviour, disease dynamics, and social structures.

Temperature also emerged as a significant factor influencing trapping success, with a general trend of decreased captures at higher average temperatures. This finding aligns with previous research (Van Hensbergen & Martin, 1993) and suggests that *R.d. dilectus* may exhibit behavioural adaptations to thermal stress, such as reduced activity or altered foraging patterns, at higher temperatures.

The flooding event at the Wilderness Camp provided a natural experiment to examine the impact of environmental disturbances on small mammal communities. The decline in *R.d. dilectus* captures and subsequent expansion of *A. ineptus* into previously occupied territories highlight the dynamic nature of ecological systems and the potential for shifts in species distributions in response to changing conditions.

Interspecific interactions, particularly competition, also play a role in shaping community structure. The observed spatial segregation of species at the Wilderness Camp suggests that niche partitioning

may be a mechanism for minimizing competition and facilitating coexistence. Furthermore, the increased capture rate of *R.d. dilectus* in newly established trap lines at the Patches site, away from areas with high *L. rosalia* abundance, suggests that competitive exclusion or spatial avoidance may influence the distribution of these species.

5.2.1.3. Seasonal Variations and Future Directions

Seasonal fluctuations in trapping success, aligning with patterns observed in other *Rhabdomys* species, were also evident in this study. The decline in captures during September could be attributed to increased breeding activity and natural food abundance, reducing the reliance on supplementary food in traps.

5.2.1.4. Rainfall and Trapping Success: A Complex Relationship

Rainfall can influence rodent populations through both direct and indirect mechanisms, affecting food availability, vegetation growth, water sources, resource distribution, and predator-prey dynamics (Dickman *et al.,* 1999; Brown & Ernest, 2002; Yarnell *et al.,* 2007). However, the relationship between rainfall and trapping success in *R.d. dilectus* proved to be more nuanced than a simple correlation.

While single rainfall events did not directly impact trapping success, a significant relationship was observed between rainfall occurring five to six months prior and increased trapping success, particularly at the Wetland site (Previtali *et al.,* 2009; Barros *et al.,* 2018). This suggests a delayed response, potentially due to the time required for vegetation growth and subsequent increase in food availability to manifest. Such delayed responses have been documented in other rodent studies, with lags ranging from 2 to 10 months (Previtali *et al.,* 2009; Yarnell *et al.,* 2007).

Yarnell *et al.* (2007) investigated how rainfall patterns influenced small mammal populations in various habitats, particularly in the semi-arid regions. They found that species such as *Saccostomus campestris* and *Mastomys natalensis* demonstrated strong positive correlations with rainfall events, but with varying time lags depending on the species and environmental conditions. Their study revealed that the abundance of certain species peaked 4 to 6 months after significant rainfall, which allowed sufficient time for vegetation regrowth and increased availability of resources such as seeds and insects. This aligns with the results observed in this study, where small mammal species at the Wetland site exhibited increased trapping success following a similar time lag after rainfall events. Yarnell (2007)'s findings emphasize the importance of rainfall in driving population dynamics through indirect effects on habitat productivity, a factor that also likely played a role in the observed abundance of *R.d.*

dilectus and other species in my study. The delayed response highlights the complex interplay between rainfall, vegetation recovery, and small mammal ecology in mesic environments.

This observed lag aligns with the understanding that ecological processes often have temporal dynamics. In the case of *R.d. dilectus*, rainfall may stimulate vegetation growth and increase food availability, but the benefits may not be immediately available to the population. Increased food availability could lead to improved body condition, higher reproductive success, and subsequent population growth, all of which could contribute to increased trapping success after a certain time lag.

A hypothesis could be that isolated rainfall events may not be sufficient to trigger significant population responses. A sustained period of increased rainfall, leading to consistent vegetation growth and resource abundance, may be necessary to initiate observable changes in population dynamics. This hypothesis is supported by the lack of correlation between single rainfall events and trapping success in this study, as well as by observations in other studies where rodent populations respond more robustly to cumulative or prolonged rainfall (Letnic & Dickman, 2006).

The varying responses to rainfall across the three study sites highlight the importance of habitat heterogeneity in shaping population dynamics (Price *et al.,* 2010). The Wetland site, with its consistent vegetation cover and relatively stable microclimate, may be more resilient to short-term fluctuations in rainfall compared to the Wilderness Camp and Patches sites, which are characterized by greater variability in vegetation structure and microclimatic conditions.

5.2.1.5. Alternative Hypotheses and Future Directions

While the delayed response to rainfall in *R. d. dilectus* appears to be primarily driven by resource-mediated mechanisms, other factors could also contribute. As Pech *et al.* (2000) explain regarding mouse population dynamics, "social behaviour, predation pressure, and disease dynamics may interact with rainfall patterns to influence population dynamics in complex ways." In the case of mice, the availability of food resources is a primary driver of population growth, but the impact of these resources is also mediated by density-dependent factors like predation and disease (Pech *et al.,* 2000). Similarly, for *R.d. dilectus*, the delayed response to rainfall may be influenced by a combination of resource availability and other ecological factors. Further research is needed to disentangle these various factors and their relative contributions to the observed patterns.

Additionally, exploring the potential for individual variation in responses to rainfall, both within and between populations, could provide valuable insights into the adaptive mechanisms that enable *R.d. dilectus* to thrive in a fluctuating environment. Investigating the physiological and behavioural

responses of individuals to rainfall events, as well as their reproductive strategies, could shed light on the underlying mechanisms driving the observed population dynamics.

5.2.2. *Vegetation Influence, Habitat Preferences and Trapping Success of Rhabdomys dilectus dilectus*

The influence of habitat properties on the trapping success of *Rhabdomys dilectus dilectus* reveals a complex interplay of factors beyond simple correlations with individual habitat variables. While the initial hypothesis predicted a direct relationship between grass cover and trapping success, the findings suggest a more nuanced understanding.

Although individual habitat variables like grass cover, shrub cover, bare soil, and mouse visibility did not significantly predict trapping success on their own, the broader habitat composition played a crucial role. The Wetland site, characterized by its homogeneous grassland habitat and low mouse visibility, consistently yielded the highest trapping success, aligning with the species' preference for dense vegetation and lower predation risk (Abu Baker & Brown, 2010; Dufour *et al.,* 2015). This suggests that a combination of factors, rather than a single variable, contributes to creating optimal conditions for *R.d. dilectus*.

In contrast, the Patches and Wilderness Camp sites, with their more heterogeneous habitats comprising a mix of grasses, shrubs, and woody plants, exhibited lower and more variable trapping success. This variability may be attributed to the presence of diverse microhabitats within these sites, each potentially catering to different ecological niches and influencing the distribution of *R.d. dilectus* and other small mammal species. The higher mouse visibility in these sites could also contribute to increased predation risk, further affecting the abundance and distribution of the target species.

The findings highlight the importance of considering the broader ecological context when investigating habitat preferences and trapping success. The complex interplay of vegetation structure, microclimatic conditions, and interspecific interactions likely shapes the distribution and abundance of *R.d. dilectus* in a way that cannot be fully captured by examining individual habitat variables in isolation.

These results have important implications for conservation and management efforts. They suggest that preserving a diversity of habitat types, including both grasslands and areas with varying vegetation structure, may be crucial for supporting diverse small mammal communities and ensuring the long-term persistence of species like *R.d. dilectus*. Furthermore, the findings emphasize the need for a nuanced understanding of habitat preferences, as well as the potential for species to adapt their

habitat use in response to changing environmental conditions and competitive pressures. This aligns with Avenant's (2011) findings in South African grasslands, where a variety of factors, including habitat structure, rainfall, predation, and disturbance history, were found to influence the composition and diversity of small mammal communities.

5.3. Demographic variability across sites.

The number of traps deployed across the three sites was initially standardized at 150 traps per site. However, when trapping success was low or insufficient numbers of *R.d. dilectus* were being captured, the number of traps was increased to improve capture rates. The highest number of traps used was 190 at the Patches, 150 at the Wetland, and 160 at the Wilderness Camp. This variation in the number of traps was necessary to account for factors such as flooding, anthropogenic influences, and differing microhabitat conditions, including temperature variations, community composition, and habitat diversity. Consequently, these factors resulted in differing trapping dynamics, sample sizes, and measured variable effects across the sites.

5.3.1. Trapping Success and Reproductive Patterns

The Wetland consistently exhibited the highest number of captures, suggesting a unique breeding pattern characterized by continuous reproduction with seasonal peaks. The favourable habitat conditions in the Wetland, offering a uniform environment suitable for *R. d. dilectus*, likely contribute to this species being the most abundant rodent in the area. This pattern may be linked to the stable and reliable environment for breeding provided by the Wetland. This coincides with Dufour et al. (2015), who found that *R. dilectus* is primarily associated with wetter, grassland-dominated regions, suggesting that its ecological success may be driven by adaptation to mesic environments. The high capture rates observed in the Wetland further support the idea that *R. d. dilectus* thrives in stable, moisture-rich habitats, reinforcing the link between habitat suitability and species abundance.

At the Wilderness Camp, there was a notable variation in the ratio of males to females across different trapping sessions. For instance, the sex ratio fluctuated significantly, with a higher number of males captured in some sessions (e.g., July 2020 and September 2020) and a higher number of females in others (e.g., July 2021 and November 2020). Interestingly, reproductive activity among females was high in some sessions, particularly in January 2021 and May 2021, where the ratio of lactating females to total females was 1. This suggests a sporadic pattern of reproductive activities, possibly influenced by environmental factors such as food availability and habitat conditions.

5.3.2. Influence of Social Dynamics and Interspecies Interactions

Social dynamics at the Patches, potentially influenced by interactions with *L. rosalia*, may have prompted social flexibility in *R. d. dilectus* breeding behaviour (Schradin & Pillay, 2005; Rymer *et al.,* 2013). The data indicates a fluctuating sex ratio and varying reproductive activity, suggesting complex interactions between environmental conditions and reproductive strategies. For instance, the presence of lactating females was notably high in January 2021 and May 2021, highlighting the role of food availability and habitat conditions in reproductive success.

5.3.3. Seasonal Reproductive Activity

Reproductive activity for females at the other sites appeared seasonal rather than continuous. At the Wilderness Camp, reproductively active females were observed from November 2020 until May 2021, transitioning from wet summer conditions and abundant vegetation in November to dry and cold winter conditions with limited food sources by mid-May. Similarly, reproductively active females at the Patches were recorded between January and May 2021 and again in November 2021. In contrast, *R. d. dilectus* females in the Wetland were reproductively active across all sessions, aligning with conditions that support extended breeding seasons up to seven months (Rymer *et al.,* 2013).

5.3.4. Adaptive Reproductive Strategies

The observed reproductive patterns in *R.d. dilectus* across the three sites may be attributed to the species' capacity for flexible social and reproductive behaviour, as highlighted by Kinahan & Pillay (2008). This flexibility is considered an adaptive strategy in response to varying environmental and social conditions. Notably, *R.d. dilectus* employs flexible reproductive behaviours and adaptive strategies to cope with challenges such as limited food resources, intraspecific competition, and the dominance of adults over juveniles (Rymer *et al.,* 2013; Schradin *et al.,* 2012; Nemakhavhani, 2015).

Drawing parallels with *R. pumilio,* known for opportunistic reproductive behaviours triggered by unexpected rainfall and subsequent vegetation growth in semi-arid environments (Schradin & Pillay, 2005; Jackson & Bernard, 2006; Rymer *et al.,* 2013), there is a possibility that *R. d. dilectus* employs similar strategies in response to its specific habitat conditions. However, the opportunistic behaviour observed in *R. pumilio* may not precisely align with the circumstances of this study. Given the shared climatic conditions across the three sites, albeit with microclimatic differences, it is apparent that *Rhabdomys* as a genus may exhibit breeding behaviours in response to resource availability. In this study, the Wetland's consistent reproductive activity suggests more continuous resource availability compared to the Patches and the Wilderness Camp.

Identifying descended testes as a marker for male reproductive activity is not challenging, but the position of testes can vary, especially during colder temperatures when testes may ascend into the body. This variability might explain the inconsistency in identifying males with descended testes, particularly in colder conditions. The limited number of males identified with descended testes (11.78% of 331), primarily from the Wetland, raises questions about the reliability of this marker and prompts closer examination of potential variables at play.

Handling stress can affect reproductive parameters, potentially leading to an overrepresentation of scrotal individuals (Brehm *et al.,* 2020). Additionally, males may not necessarily be scrotal during female lactation, aligning with established biological knowledge. Lactation typically commences three weeks after copulation, suggesting that the scrotal state may not persist beyond this timeframe. The discrepancy in timing may factor into the relatively low proportion of males with scrotal characteristics among captured individuals.

Reproductive activity for scrotal males seemed to begin in August/September each year at the Wetland, when conditions are dry with scarce food resources. Previous studies also recorded scrotal *Rhabdomys* males in August, although the species studied was *R. pumilio* and environmental conditions differed (Jackson & Bernard, 2006). Scrotal males were trapped at the Patches from November 2020 to January 2021 and again in November 2021, while only one scrotal male was trapped at the Wilderness Camp across all sessions. Studies found that *Rhabdomys* males regress their testes in winter and begin reproductive activity in September (David & Jarvis, 1985).

5.3.5. Microhabitat Conditions and Growth in *Rhabdomys dilectus*.

The influence of microhabitat conditions on the growth and development of *Rhabdomys dilectus dilectus* was examined to understand the species' ecological adaptations. Body weight and length, crucial for survival and reproduction, were analyzed across three distinct sites within the Lajuma Research Station.

Contrary to expectations, no significant differences in body length and weight were found among the three sites or between sexes within each site. This suggests a degree of phenotypic plasticity in *R.d. dilectus*, allowing for consistent growth patterns despite varying environmental conditions. These findings align with a previous study on *Rhabdomys bechuanae* in a semi-arid grassland region, which also reported no sexual dimorphism in body size (Kotze, 2019). This contrasts with studies on *Rhabdomys pumilio*, where males were found to be significantly heavier than females (Schradin & Pillay, 2005; Jackson & Bernard, 2006).

However, a notable exception emerged in the comparison of body weight between the Wetland and Wilderness Camp sites. Individuals from the Wilderness Camp exhibited significantly lower body weights, potentially reflecting ecological pressures such as food scarcity or environmental stressors. This suggests that while body length may be relatively consistent across habitats, body weight may be more sensitive to microhabitat variations, offering a potential indicator of resource availability and environmental quality.

The study also delved into the classification of age classes based on body length, weight, and reproductive activity. Two distinct groups were identified: adults and non-adults. The adult class, characterized by individuals exceeding specific weight and length thresholds, was present throughout the year, peaking during winter. This peak aligns with findings on the social flexibility of striped mice, suggesting that dominant females may suppress the reproductive activity of subordinate individuals (Schradin & Pillay, 2005b; Jackson & Bernard, 2006; Kinahan & Pillay, 2008; Schoepf & Schradin, 2012; Rymer *et al.,* 2013).

The decline in the non-adult population observed in July, following a peak, may coincide with the breeding season when food availability increases, potentially reflecting a shift in resource allocation towards reproduction rather than growth (Giulia *et al.,* 2022). Alternatively, this decline could be attributed to a lack of recruitment of new individuals into the population, highlighting the importance of considering demographic processes in interpreting population fluctuations (Nater *et al.,* 2016).

Overall, this study provides valuable insights into the growth and development patterns of *R.d. dilectus* in relation to microhabitat conditions. While body length appears to be relatively stable across different habitats, body weight may serve as a more sensitive indicator of environmental quality and resource availability. The observed seasonal variations in age class distribution further emphasize the dynamic nature of population ecology and the importance of considering both intrinsic and extrinsic factors in understanding the life history of this species.

6. Conclusion

The exploration of the population dynamics, habitat preferences, and ecological interactions of *Rhabdomys dilectus dilectus* within the Lajuma Research Station in the Soutpansberg of Limpopo Province has filled a critical gap in ecological knowledge. While previous studies primarily focused on genetic aspects (Rambau & Robinson 2003; Castiglia *et al.,* 2012; du Toit *et al.,* 2012), this investigation emphasizes the local ecology and population structure of *R.d. dilectus*.

6.1. Population Dynamics and Community Composition

The identification of four common small mammal species across all sites—*R.d. dilectus*, *Aethomys ineptus*, *Lemniscomys rosalia*, and *Mus minutoides*—highlights the diverse community composition. Notably, *R.d. dilectus* exhibited a high abundance in the Wetland, reflecting its preference for mesic conditions with substantial vegetation cover, as supported by previous research (Ganem *et al.,* 2012; Dufour *et al.,* 2015). The Wilderness Camp, characterized by greater habitat heterogeneity, supported a higher overall species richness and distinct spatial segregation among species, suggesting niche partitioning and habitat-specific preferences.

6.2. Environmental Influences on Trapping Success

Environmental factors, particularly temperature and habitat characteristics, significantly impacted trapping success. The Wetland site, with its homogeneous grassland habitat and lower predation risk, exhibited the highest trapping success, aligning with findings from Abu Baker & Brown (2010), Dufour *et al.* (2015), and Mackay (2017). In contrast, the more heterogeneous habitats at the Wilderness Camp and Patches showed variable trapping success, influenced by the presence of different microhabitats and ecological pressures. Higher trapping success at lower temperatures suggests behavioural adaptations to thermal stress and highlights the complex interplay between environmental conditions and small mammal activity (Van Hensbergen & Martin, 1993).

The reproductive activity of *R.d. dilectus*, as indicated by the presence of reproductive males and lactating females, showed distinct seasonal patterns across the three study sites (Patches, Wetland, and Wilderness Camp). In the Wetland, peak reproductive activity for males (Fig. 18) was observed in September 2020, January 2021, and November 2021, while females (Fig. 17) peaked in September 2020, January 2021, and March 2021. Reproductive activity for both genders was notably absent during the cooler winter months of May and July 2021. Similarly, at the Patches, peak reproductive activity for males (Fig. 18) occurred in January 2021 and November 2021, and for females (Fig. 17) in November 2020, January 2021, and May 2021, with no reproductive activity from July 2020 to July 2021. In the Wilderness Camp, reproductive males (Fig. 18) were recorded only in November 2021, and reproductive females (Fig. 17) in September 2020 and May 2021.

These reproductive patterns align with mean temperature trends (Fig. 16), as shown by the scatter plot illustrating the relationship between mean temperature and trap success. Higher mean temperatures were generally associated with increased reproductive activity, with breeding seasons starting around September, peaking during the warmer months (September to March), and declining during the cooler months (May to July). The stronger negative correlation between mean temperature

and trap success in the Wetland and Wilderness Camp sites suggests that temperature significantly influences reproductive success in these areas. Overall, the data indicate that the reproductive activity of *R.d. dilectus* is closely tied to seasonal temperature variations, with higher temperatures facilitating greater reproductive success and activity.

6.3. Impact of Rainfall and Seasonal Variations

The relationship between rainfall and trapping success proved complex and non-linear. Immediate rainfall did not directly affect trapping success, but a significant delayed response was observed, particularly at the Wetland site. This delayed response likely reflects the time required for vegetation growth and subsequent increases in food availability, influencing population dynamics and trapping outcomes. Seasonal variations in trapping success were also evident, with declines observed during peak breeding periods due to reduced reliance on supplementary food in traps as natural food availability increased.

6.4. Microhabitat Conditions and Growth

The influence of microhabitat conditions on the growth and development of *R.d. dilectus* revealed no significant differences in body length and weight among the three sites or between sexes, suggesting phenotypic plasticity that allows for consistent growth patterns despite varying environmental conditions. However, individuals from the Wilderness Camp exhibited lower body weights, potentially reflecting ecological pressures such as food scarcity. The classification of age classes based on body length, weight, and reproductive activity provided further insights into growth patterns, emphasizing the importance of considering both intrinsic and extrinsic factors in understanding the life history of this species.

6.5. Conservation and Management Implications

These findings have significant implications for the conservation and management of *R.d. dilectus* and similar small mammal species. The high trapping success and species abundance at homogeneous sites like the Wetland highlight the need to preserve such habitats to support stable populations. Conversely, the greater species richness and habitat diversity observed at heterogeneous sites like the Wilderness Camp underscore the value of maintaining diverse habitat types to support broader ecological communities.

7. Future research on the population dynamics of *Rhabdomys dilectus dilectus*

Based on the findings and limitations of this study, several avenues for future research emerge to deepen the understanding of the population ecology of *Rhabdomys dilectus dilectus* and other small mammals in similar environments. Conducting long-term monitoring of *R.d. dilectus* populations across multiple seasons and years would provide valuable insights into the species' responses to environmental fluctuations, including rainfall patterns, temperature changes, and resource availability. This approach would allow for a more comprehensive assessment of population trends, reproductive cycles, and survival rates, ultimately contributing to more effective conservation and management strategies.

Experimental manipulations of habitat features, such as vegetation density, ground cover, and food availability, could help elucidate the specific mechanisms by which these factors influence *R.d. dilectus* populations. For example, altering grass cover in different areas could reveal its direct impact on trapping success and population density, while modifying food availability could shed light on its influence on reproductive behaviour and body condition.

Detailed dietary analyses of *R.d. dilectus* across different seasons and habitats would provide valuable insights into the species' feeding ecology and its relationship with resource availability. This could involve analysing stomach contents, faecal samples, or stable isotopes to determine the relative importance of different food sources and how they vary across time and space.

Utilizing radio telemetry to track individual movements and home ranges would offer a more comprehensive understanding of *R.d. dilectus* behaviour and habitat use. This technique could reveal how individuals navigate their environment, select specific microhabitats, and interact with conspecifics and other species. Such information would be invaluable for assessing the impact of habitat fragmentation and identifying critical areas for conservation.

Conducting genetic analyses of *R.d. dilectus* populations across different sites could uncover patterns of gene flow, genetic diversity, and local adaptation. This information is crucial for understanding the evolutionary potential of the species and its ability to adapt to changing environmental conditions. Additionally, genetic analyses could help identify potential barriers to dispersal and inform management strategies aimed at maintaining genetic connectivity among populations.

Investigating the interactions between *R.d. dilectus* and other small mammal species, particularly potential competitors like *A. ineptus* and *L. rosalia*, would shed light on the mechanisms of coexistence

and resource partitioning. This could involve observational studies, experimental manipulations of resource availability, or behavioural experiments to assess competitive interactions directly.

Given the projected changes in temperature and rainfall patterns due to climate change, assessing the potential impacts on *R.d. dilectus* populations is crucial. This could involve modelling the species' distribution under different climate scenarios, investigating its physiological tolerance to thermal stress, and evaluating its ability to adapt to changing resource availability.

Finally, expanding the research focus to encompass the entire small mammal community would provide a more holistic understanding of ecological dynamics within the Luvhondo Research Station. This could include investigating the interactions among different species, their responses to environmental fluctuations, and their roles in ecosystem functioning. By addressing these research avenues, a deeper and more integrated understanding of the ecological dynamics of *R. d. dilectus* and other small mammals can be acquired, informing conservation efforts and enhancing the ability to manage these species in the face of environmental change.

8. References

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Appendix I: Individuals Observed Per Site: This appendix presents the total number of unique individuals captured per species across the three study sites: Patches, Wetland, and Wilderness Camp. The dataset highlights species diversity and distribution, with *Rhabdomys dilectus dilectus* being the most frequently recorded species, particularly in the Wetland. *Aethomys ineptus* showed the highest occurrence in the Wilderness Camp, while *Lemniscomys rosalia* was more abundant in Patches. The Wetland site exhibited the greatest species diversity, including *Dasymys incomtus* and *Otomys angoniensis*, which were absent from Patches. The presence of *Shrew sp.*s and *Elephantulus myurus* at Wilderness Camp further underscores habitat heterogeneity.

Site	Species	Total Number of unique individuals
Patches	*Rhabdomys dilectus dilectus*	103
Patches	*Aethomys ineptus*	27
Patches	*Lemniscomys rosalia*	83
Patches	*Mus minutoides*	18
Wetland	*Rhabdomys dilectus dilectus*	408
Wetland	*Dasymys incomtus*	5
Wetland	*Otomys angoniensis*	6
Wetland	*Aethomys ineptus*	9
Wetland	*Shrew sp. (A&B)*	20
Wetland	*Lemniscomys rosalia*	2
Wetland	*Dendromus mystacalis*	3
Wilderness Camp	*Rhabdomys dilectus dilectus*	85
Wilderness Camp	*Aethomys ineptus*	93
Wilderness Camp	*Lemniscomys rosalia*	5
Wilderness Camp	*Dendromus mystacalis*	1
Wilderness Camp	*Mus minutoides*	14
Wilderness Camp	*Shrew sp.*	5
Wilderness Camp	*Elephantulus myurus*	1
Wilderness Camp	*Otomys angoniensis*	2

Appendix II: Trapping efforts and trapping success across sites and sessions with details on number of trapped small mammals.

Trapping session / Dates	site	Number of trapping days	Number of sessions	Number of traps used	*Rhabdomys* captures	*Dendromus mystacalis* captures	*Mus minutoides* captures	*Shrew sp.* captures	*Otomys angoniensis* captures	*Elephantulus myurus* captures	*Aethomys ineptus* captures	*Lemniscomys rosalia* captures
Jul-20	Wilderness	5	9	1350	48	0	5	1	0	0	20	0
Jul-20	Wetland	5	9	1350	93	2	0	5	0	0	0	0
Jul-20	Patches	5	9	1350	10	0	0	0	0	0	2	8
Sep-20	Wilderness	5	9	1350	24	0	1	0	0	0	12	0
Sep-20	Wetland	5	9	1350	69	1	0	4	0	0	1	0
Sep-20	Patches	5	9	1339	5	0	1	0	0	0	0	13
Nov-20	Wilderness	5	9	1341	5	0	0	0	0	1	1	0
Nov-20	Wetland	4	7	1050	29	0	0	0	0	0	0	2
Nov-20	Patches	6	11	2090	10	0	0	0	0	0	6	19
Jan-21	Wilderness	6	11	1650	2	0	0	0	0	0	29	0
Jan-21	Wetland	5	7	1050	41	0	0	0	0	0	3	0
Jan-21	Patches	6	11	1540	11	0	0	0	0	0	7	21
Mar-21	Wilderness	6	11	1650	0	0	0	0	0	0	3	0
Mar-21	Wetland	4	7	1050	32	0	0	3	0	0	1	0
Mar-21	Patches	6	11	1525	2	0	0	0	0	0	7	12
May-21	Wilderness	6	11	1760	3	0	8	1	1	0	16	5
May-21	Wetland	4	7	1050	38	0	0	1	0	0	1	0
May-21	Patches	6	11	1536	11	0	3	0	0	0	2	2
Jul-21	Wilderness	5	9	603	4	1	0	3	0	0	11	0
Jul-21	Wetland	5	9	1260	74	0	0	7	6	0	2	0
Jul-21	Patches	5	9	711	18	0	13	0	0	0	3	4
Sep-21	Wilderness	5	9	603	2	0	0	0	1	0	1	0
Sep-21	Wetland	5	9	1260	30	0	0	0	0	0	1	0
Sep-21	Patches	5	9	711	21	0	1	0	0	0	0	1
Nov-21	Wetland	5	9	1233	10	0	0	0	0	0	0	0
Nov-21	Patches	5	9	711	15	0	0	0	0	0	0	3

Appendix III: Vegetation identified across sites. This appendix presents the tree and shrub species identified across the Patches, Wetland, and Wilderness Camp sites, highlighting habitat differences that may influence small mammal distribution. The Wilderness Camp exhibited the highest tree diversity, while the Wetland and Patches supported a mix of tree and shrub species suited to their respective environments. Some vegetation types, particularly certain shrubs, were present across all sites, while others were restricted to specific locations, reflecting differences in habitat structure. These variations in vegetation contribute to habitat complexity, which can affect species distribution, resource availability, and predator avoidance strategies among small mammals.

	Species	Site		
Trees		Patches	Wetland	Wilderness Camp
	Afrocanthium mundianum	x	x	
	Brachylaena transvaalensis			x
	Combretum kraussi	x		
	Combretum molle	x		
	Cussonia transvaalensis	x		
	Cyathea dregei		x	
	Dovyalis zeyheri	x	x	
	Ekebergia capensis	x		
	Englerophytum magaliesmontanum	x		
	Eugenia woodii	x		
	Eugenis natalitia	x		
	Ficus sp	x		
	Ficus sur			x
	Hyperacanthus amoenus	x	x	
	Ilex mitis			x
	Maytenus undata	x	x	
	Mimusoos zeyheri	x		
	Mimusops zeyheri			x
	Olea africana	x		
	Olea capensis		x	
	Podocarpus falcatus			x
	Rothmannia capensis	x		
	Rothmannia globosa		x	
	Searsia chirindensis	x		
	Searsia chirindensis		x	
	Senegalia (Acacia) ataxacantha	x	x	x
	Syzigium cordatum			x
	Syzigium legati	x		
	Terminalia sericea		x	
	Vachellia (Acacia) karoo	x		x
	Vangueria infausta	x		
	Ziziphus mucronata			x
Shrubs	*Artemisia afra*		x	
	Carissa edulis			x
	Carissa edulis	x		
	Diospyros dichrophylla		x	
	Euclea crispa			x
	Euclea crispa		x	
	Eugenia natalitia		x	
	Fadogia homblei	x		
	Gerbera jamesonii			x
	Gymnosporia harveyana	x	x	x

	Hebenstretia sp	x	x	
	Helichrysum kraussi	x	x	x
	Helichrysum setosum		x	
	Helichrysum sp			x
	Hyperacanthus amoenus			x
	Ocimum labiatum			x
	Pavetta gardenifolia			x
	Pellaea (fern) sp			x
	Pteridium aquilinum	x		