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Assessing habitat selection of grassland rodents in the Cradle of Humankind

by

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9 June 2023

DECLARATION

I Catiuscia-Jade Pinto (Student number: 1706253 am a student registered for Master of Science in the school of Animal, Plant and Environmental Sciences in the between 2021 - 2023. I hereby declare that this dissertation is my own unaided work and I have followed the required conventions in referencing the thoughts and ideas of others.

Signature: _____ _____ Date: _9_June_2023_____

ABSTRACT

Habitat selection is a decision-making process undertaken by animals to select an appropriate environment suitable for fulfilling their survival and reproductive needs. These decisions are driven by a complex of biotic and abiotic factors. Habitat selection relies on how an animal interacts with its environment and is species-specific. The vegetation structure and composition influence how smaller animals, such as rodents, obtain food and cover, and are thus critical for their survival. The aim of my study was to assess the population demography and habitat selection of nocturnal rodents in two grassland sites located within the Cradle of Humankind Nature Reserve, Krugersdorp, Gauteng Province, South Africa. I obtained rodent data using Capture-Mark-Recapture (CMR) methods, and vegetation data were obtained through randomised quadrate sampling. The following six rodent species were sampled, *Gerbilliscus leucogaster, Lemniscomys rosalia, Mastomys coucha, Micaelamys namaquensis, Mus minutoides* and *Otomys angoniensis.* Rodent abundance differed between summer and winter, with winter showing a higher abundance, but richness and diversity indices did not differ significantly between sites or seasons. The three most common species, *G. leucogaster, M. coucha* and *O. angoniensis*, were selected for further population demography analyses. The demography of *G. leucogaster,* was mostly associated with the season since seasonal fluctuations were observed in their population size (higher in summer), reproductive activity (more active in summer) and body condition (higher in winter). *Mastomys coucha* was the most abundant species in the study, since it had the highest number of sampled individuals in both summer and winter, although its demography was not influenced by external factors (e.g.,, season, vegetation height, vegetation cover) recorded in both summer and winter. *Otomys angoniensis* had a positive relationship with vegetation height and rodents' body condition. The three species were able to coexist with one another due to differences in foraging strategies, reproductive strategies, spatial and dietary partitioning, which help to facilitate habitat selection and illustrate that habitat selection is species specific.

Key words: Rodents, habitat selection, *Gerbilliscus leucogaster, Mastomys coucha, Otomys angoniensis.*

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INTRODUCTION

A habitat is the space an organism occupies in order to obtain the resources necessary for survival, reproduction and persistence (Krausman, 1999; Morrison *et al.*, 2006; Montgomery and Roloff, 2017). A habitat consists of various abiotic (e.g.,, rainfall, temperature, light) and biotic (e.g.,, competition, vegetation) factors which influence the organisms' decision to occupy that space (Johnson, 2005; Montgomery and Roloff, 2017). Habitat selection is an active behavioural decision-making process which involves a series of innate and learned behaviours and is used to select an appropriate habitat with a suitable combination of resources (Krausman, 1999; Montgomery and Roloff, 2017).

The main external factors that may affect habitat selection include vegetation, ambient temperature, rainfall and competition, which are highly correlated with one another (Krausman, 1999; Vessey and Vessey, 2007; Nater *et al.*, 2016). Due to these factors being highly correlated, assessing how they interact with one another in a natural setting leads to a better understanding of habitat selection (Keesing, 1998, 2000; Cramer and Willig, 2002; Eccard and Ylönen, 2003; Johnson, 2005; Vessey and Vessey, 2007; Yarnell *et al.*, 2007; Auffray *et al.*, 2009; Nater *et al.*, 2016). Habitat selection thus involves a combination of an individual's choice and external factors including competition or predation interacting with each other (Krausman, 1999). Habitat selection is also constrained by the intensity of predation risk and intra- and inter-specific competition intensity (Krausman, 1999; Johnson, 2005). In the Namib Desert in Namibia *Gerbillurus tytanus* extends its range by inhabiting a less favourable micro-habitat in the presence of its competitor, *Rhabdomys pumilio* (Hughes *et al.*, 1994). Vibe-Petersen *et al.*, (2006) found that predation is a driving force of dispersion in *Mastomys natalensis*, which prefers the habitats with no predation risk. In these predator absent habitats, migration became density-dependent, where *M. natalensis* individuals started selecting for habitats with an increased predation risk but had a lower rodent density (intraspecific competition; Vibe-Petersen *et al.*, 2006), indicating a trade-off between predation risk and intraspecific competition.

My study involves the ecology of rodents, which will be the focus of the introduction below. Rodents are good models for diversity and population demographic studies since they have fast life histories and are sensitive to environmental change (Vessey and Vessey, 2007; Auffray *et al.*, 2009; Krebs, 2014; Nater *et al.*, 2016). Rodents are the most diverse order of

mammals, comprising of 42% of all mammal diversity, occurring in a large variety of habitats worldwide (Auffray et al., 2009; Krebs, 2014). Most rodents have comparatively short life spans and high mortality rates (Vessey and Vessey, 2007; Auffray et al., 2009). In order to offset the high mortality rates, sexual maturity occurs comparatively early in life and fecundity rates are generally high (Vessey and Vessey, 2007). The reason for their success may be due to their phenotypic plasticity (Auffray *et al.*, 2009). Behavioural plasticity allows rodents to quickly adjust to changes in their environment (Vessey and Vessey, 2007; Auffray *et al.*, 2009; Nater *et al.*, 2016). Such phenotypic adjustments are important for survival since rodents are less able to disperse over large distances due to their small size (Auffray *et al.*, 2009). Therefore, to persist, rodents can adjust to prevailing changes in their environment (Schradin and Pillay, 2006). Behavioural adjustments may include, for example, shifting home ranges with seasonal changes (Bronner and Meester, 1988; Schradin and Pillay, 2006; Vessey and Vessey, 2007). Furthermore, the type and degree of behavioural adjustments may differ among rodent species (Auffray *et al.*, 2009). Generalist species are highly opportunistic and are usually able to adapt relatively quickly in comparison to specialist species (Wywialowski, 1987; Auffray *et al.*, 2009). The ease of adaptability gives generalists a competitive advantage over specialists (Auffray *et al.*, 2009) and allows generalists to gain dominance in most habitats, especially new or changing habitats (Morris, 1996; Johnson, 2005).

Vegetation provides resources such as cover, shelter and food, especially for small herbivorous animals (Monadjem and Perrin, 1998; Johnson, 2005; Morrison *et al.*, 2006). Thus, vegetation has a significant influence on habitat selection and habitat selection is highly dependent on the forage quality and quantity, the level of cover and the availability of nesting or resting sites (Krausman, 1999; Johnson, 2005; Morrison *et al.*, 2006). Monadjem and Perrin (1998) found that *M. natalensis* prefers areas with a high a proportion of vegetation cover, but would still occupy areas with reduced cover if there was an abundance of food.

Vegetation cover is especially important to rodents since reduced cover causes several negative effects such as reduction of food availability and an increase in predation risk (Bowland and Perrin, 1989; Jensen *et al.*, 2003; Yarnell *et al.*, 2007). The presence of large mammal grazers reduces cover for rodents, especially in open grasslands (Bowland and Perrin, 1989; Nyako-Lartey and Baxter, 1995; Saetnan and Skarpe, 2006; Yarnell *et al.*, 2007). By reducing cover, these grazers decrease habitat quality for rodents, thereby

negatively affecting rodent densities and diversity (Nyako-Lartey and Baxter, 1995; Saetnan and Skarpe, 2006; Yarnell *et al.*, 2007). Vegetation cover and diversity influence habitat complexity, where increased complexity is positively associated with rodent diversities and densities (Utrera *et al.*, 2000; Horváth *et al.*, 2001).

The season can influence vegetation complexity (Yarnell *et al.*, 2007). During the dry season, food availability and cover are reduced (Schradin and Pillay, 2006), while during the wet season, food is abundant and protein rich (Vessey and Vessey, 2007) and vegetation cover increases (Jacob, 2008). This seasonal variation in vegetation can cause rodents to make behavioural adjustments to the altered vegetation (Auffray et al., 2009; Hall and Chalfoun, 2019; Ribeiro et al., 2019). Behavioural adjustments can occur both spatially and temporally (Gockel and Ruf, 2001; Auffray et al., 2009; Hall and Chalfoun, 2019). Spatial adjustments include shifts in home ranges in search for better quality food, avoiding predation by shifting home range to a habitat with increased cover and shifts in breeding season or reproductive activity (Brown *et al.*, 1988; Brown, 1989b; Schradin and Pillay, 2006; Auffray *et al.*, 2009). Temporal adjustments may include shifts in foraging activity to avoid predation (Beier, 2013) or high ambient temperatures (Levy *et al.*, 2016; Hall and Chalfoun, 2019). Weather plays a major role in rodent survival, with small variations in mean precipitations resulting in a significant decrease in population size (Reed *et al.*, 2007). *Peromyscus maniculatus* in the mixed-grass prairies of Kansas, USA, experienced significant population declines with the decrease in annual precipitation (Reed *et al.*, 2007). Reproduction of *M. natalensis* and *M. coucha* is onset by sprouting vegetation, which is linked to the onset of the rainy season in Tanzania (Leirs, 2013).

The season also affects both intra- and inter-specific competition (Morris, 1996; Cramer and Willig, 2002; Vessey and Vessey, 2007). In summer when vegetation is abundant, competition is weaker, while in winter, when vegetation is scarce competition increases (Cramer and Willig, 2002). This affects habitat selection since dominant rodent species will often outcompete subordinate species by excluding subordinate species from habitats (Morris, 1996). Specialist species tend to be weaker competitors (subordinates) that require specific resources which may limit their competitive abilities when conditions are not optimal for them (Morris, 1996). This leads to dominant species, which usually are generalist, occupying the better quality areas (Morris, 1996; Cramer and Willig, 2002; Eccard and Ylönen, 2003; Johnson, 2005). In addition, specialists often occupy only one type of micro-

habitat which limits their competitive ability, especially when their population sizes are small and there are multiple species occupying the same area (Morris, 1996; Eccard and Ylönen, 2003). In contrast, generalists can exploit unoccupied habitats or habitats with low rodent densities to avoid competition with specialists (Morris, 1996). Competition is often density-dependent (Morris, 1996; Nater *et al.*, 2016; Schradin *et al.*, 2010). When rodent densities are high, species will compete for resources, while low rodent densities are associated with coexistence with competing species (Morris, 1996; Schradin *et al.*, 2010).

Coexistence can occur at high population densities if resources are abundant (Brown, 1989b; Morris, 1996). Competition between coexisting species may occur when resources are not abundant or predation is high (Perrin, 1980; Hughes et al., 1994; Vessey and Vessey, 2007). This may result in a subordinate species extending its habitat to increase its foraging needs (Hughes *et al.*, 1994). Coexistence with a dominant species may result in morphological changes, as in *Rhabdomys pumilio* where individuals are significantly smaller in areas where it co-occurs with *Lemniscomys griselda* in the southern savannah woodland (Yom-Tov, 1993). Coexistence may differ temporarily due to seasonal fluctuations in population densities of coexisting species (Brown *et al.*, 1988). For example, *M. natalensis* has seasonal cyclical fluctuation in population sizes, having population spikes after the wet season (Massawe *et al.*, 2011). These fluctuations allow for density dependent habitat selection, where more species can coexist at low densities, but competition increases in high densities (Shenbrot et al., 2006). Seasonal variation affects the vegetation types, percentage of cover and presence of certain predators, and as a consequence, rodents can adopt various foraging strategies that facilitate coexistence (Brown, 1989b).

The composition of species in a particular habitat can be represented by the species diversity, which is a measure of the variability of species present within a certain area (Kiester, 2013). Species diversity is calculated by using the measures of species richness and abundance (Kiester, 2013). Species richness is a count of species found within an area and is either represented as a list of the species or the number of those species (Kiester, 2013). The abundance is the number of individuals per species found within a specific area (Kiester, 2013). The importance of species diversity is that it can be used to identify certain habitat selection factors, as well as identifying competing species within a region by comparing the abundances of the different species (Kiester, 2013). Species diversity also provides an indication of habitat quality since higher species diversities usually occur in more complex

habitats (Utrera *et al.*, 2000; Horváth *et al.*, 2001). Degrading habitats have small or declining species richness and diversity (Avenant, 2011). Certain species, such as *M. coucha*, are indicators of poor quality habitats, since these species usually occur in habitats exposed to disturbances such as fire, overgrazing, drought and cultivation (Avenant, 2011; Kneidinger *et al.*, 2014). The decline of *M. coucha* (an indicator species of disturbance) is also an indicator of improving habitat (Avenant, 2011). In contrast, the presence of certain specialist species, such as *Otomys irroratus,* indicates a good quality or improving habitats (Avenant, 2011).

Since habitat selection is a combination of push and pull factors influencing an individual's choice to occupy a space, habitat selection can also be described by the population dynamics of a species (Krausman, 1999). Population dynamics is a description of how a population of a species changes over time, which include population increases, maintenance and declines (Hastings, 2013). Population demographics are statistical measures used to describe a population by its specific characteristics (Tarsi and Tuff, 2012) and includes the study of size, distribution, composition (including age and sex structure), changes and the factors causing changes in a population (Xie, 2000).

Population demography studies considers a variety of demographic parameters to accurately describe populations (Xie, 2000). These parameters can be used to assess current populations and make predictions about future populations (Lebreton *et al.*, 1992; Tarsi and Tuff, 2012). The parameters considered usually include population size, population density, age structure, fecundity, mortality and sex ratios (Xie, 2000; Odhiambo et al., 2008; Shilereyo et al., 2020). Population size is the number of individuals of the same species co-occurring within the population based on direct counts (Udevitz and Gould, 2002; Tarsi and Tuff, 2012). Population size is one of the most important and most common parameters used to assess habitat selection, since abundance has a direct link to habitat quality (Krausman, 1999; Udevitz and Gould, 2002; Johnson, 2005). The size of the population can predict future population dynamics (Tarsi and Tuff, 2012). For example, small population sizes increase the probability of inbreeding, whereas large populations increase the probability of competition (Tarsi and Tuff, 2012). Population size may also indicate a preference for a particular habitat; in the absence of competition, if the population sizes differ between two habitats, the bigger population may indicate the preferred habitat for a species (Cramer and Willig, 2002).

Population density is the number of individuals within a population found within a specific area and is expressed as the population size per unit area (Lebreton *et al.*, 1992; Tarsi and

Tuff, 2012). Much like population size, density is an important and common parameter in population demography studies since it can be used as a proxy for population size when the population exceeds its spatial boundaries (Udevitz and Gould, 2002; Tarsi and Tuff, 2012; McArdle, 2013). Unlike population size, density itself may influence habitat selection, since density may provide pressures from the population itself (endogenous factors) that may influence habitat quality. Density dependent factors are the environmental responses to the density of the population, which intensify as density increases (Tarsi and Tuff, 2012; McArdle, 2013). These density dependent factors include competition, predation and migration (Tarsi and Tuff, 2012). Density can be a predictor of interactions, since higher densities equate to higher probabilities of competition, but higher densities also lead to lower probabilities of predation due to the predator saturation effect (McArdle, 2013; Nater *et al.*, 2016).

The age structure of a population determines the reproductive potential of the current population and will predict the growth pattern of the population (Tarsi and Tuff, 2012). Individuals in the population can be divided into age categories, which will determine the potential growth of the population, since each cohort represents a different contribution to population growth (e.g.,, too old or young to reproduce, Tarsi and Tuff, 2012; Hastings, 2013). Therefore, the occurrence of many reproductively active adults will predict rapid population growth (Tarsi and Tuff, 2012). Similarly, the sex ratio may influence population growth. To predict population growth using sex ratios, the importance is placed on the females because of their relatively high reproductive investment (Hastings, 2013). Therefore, a ratio favouring females is likely to result in increased population growth (Tarsi and Tuff, 2012). Fecundity and mortality are the number of births and deaths per unit time. The rates of these will determine the growth or decline of a population, since more births will result in growth and more deaths will result in population decline (Tarsi and Tuff, 2012).

RATIONALE OF MY STUDY

My project assesses the habitat selection of small nocturnal rodents in grasslands within the Cradle Nature Reserve, Krugersdorp, Gauteng Province, South Africa. Assessing the habitat selection of grassland rodents in an area of paleoanthropological significance may give some insight into the rodent ecology of both the past and the present. The location of the study site was on the doorstep of the City of Johannesburg, South Africa's largest metropolitan area and

therefore understanding the population biology of grassland rodents may contribute to future conservation efforts of indigenous species in peri-urban locations. Conservation of rodents is important since they occupy low trophic levels in the food chain which supports a wide range of predatory species (Happold and Happold, 1986). This study may highlight the factors leading to habitat selection for several rodent species in a natural habitat with little human disturbance.

AIMS, OBJECTIVES AND PREDICTIONS

My overall aim was to assess the population demography and habitat selection of rodents in two grassland sites approximately 1.3 km apart from one another in the Cradle Nature Reserve. The sites were selected based on their similarities such as their gradient, their south facing slopes and general grass cover. They did differ slightly in that one site was rockier while the other had more trees.

Objective 1: To investigate whether rodent species richness, abundance and diversity were varied by site and season.

Prediction 1: Diversity parameters will differ significantly from one another, although sites are in close proximity to one another and are exposed to the same environmental conditions, the habitats differ.

Prediction 2: Overall, the rodent diversities will vary seasonally, with higher diversities occurring in the warm wet season (summer).

Objective 2: To investigate whether the rodent population demography (population size, sex ratio, age, reproductive activity, body condition) were varied by site and season.

Prediction 1: Demographics between the sites will differ because of habitat differences.

Prediction 2: Population size, reproductive activity and body condition will be greater in the summer. Population sizes will decrease during the dry season (winter). The sex ratios will not differ between seasons. The age structure will favour adults in both seasons, but a significant

increase of juveniles in the winter season. The ratio of potentially reproductive rodents was expected to be higher in summer than in winter. Body conditions are expected to be higher in summer.

Objective 3: To investigate vegetation characteristics (plant cover, height, density) in each site by season.

Prediction 1: Vegetation characteristics should differ due to the differences between the sites. The rockier site is expected to have less cover and shorter vegetation than the site with more trees.

Prediction 2: I expected that there would be a higher percentage of plant cover, density and taller grass species in the wet summer season compared to the dry winter season.

Objective 4: To determine the relationships between vegetation characteristics, rodent diversities and population demography.

Prediction: Vegetation characteristics that favour higher ratios of cover will have positive relationships with diversity and demography parameters. High diversity parameters will be positively linked to demography measures such as larger population sizes, high ratio of reproductive activity and better body conditions. Poor vegetation characteristics such as short plant heights and low percentage of cover are expected to be associated with low diversity scores and demography measures.

MATERIALS AND METHODS

GENERAL STUDY AREA

The study took place at the Cradle Nature Reserve (25° 55' 17.28" S; 27° 51' 1.86"E), Krugersdorp, South Africa which occurs on the borders between the North West and Gauteng Provinces (Figure 1). The Cradle Nature Reserve (hereinafter referred to as the Reserve) falls within the Magaliesberg biosphere reserve, made up of the sub-Saharan savanna and highveld grassland (Bredenkamp and Brown, 2003). The ecoregion of the Reserve is the Bankenveld that is characterised by alternating ridges and valleys covered by high altitude grasslands and patches of woody vegetation usually found in sinkholes and valleys (Rogers, 1944; Bredenkamp and Brown, 2003). The study area falls under the '*Monocymbium ceresiforme – Loudetia* simplex grassland' vegetation type, which is dominated by mixed short grasses and scattered dwarf shrubs (Bredenkamp and Brown, 2003). Two study sites were selected based on their ecological similarity; both sites were south facing slopes with similar gradients and general grass cover (Figure 2 and Figure 3). They were separated by a distance of 1.3 km (Figure 1). Although similar, the northern site (Figure 2) had more bare ground patches, fewer trees and was comparatively rockier than the southern site (Figure 3). The southern site was located at the bottom of a hill, while the northern site was located at the top of a hill side.

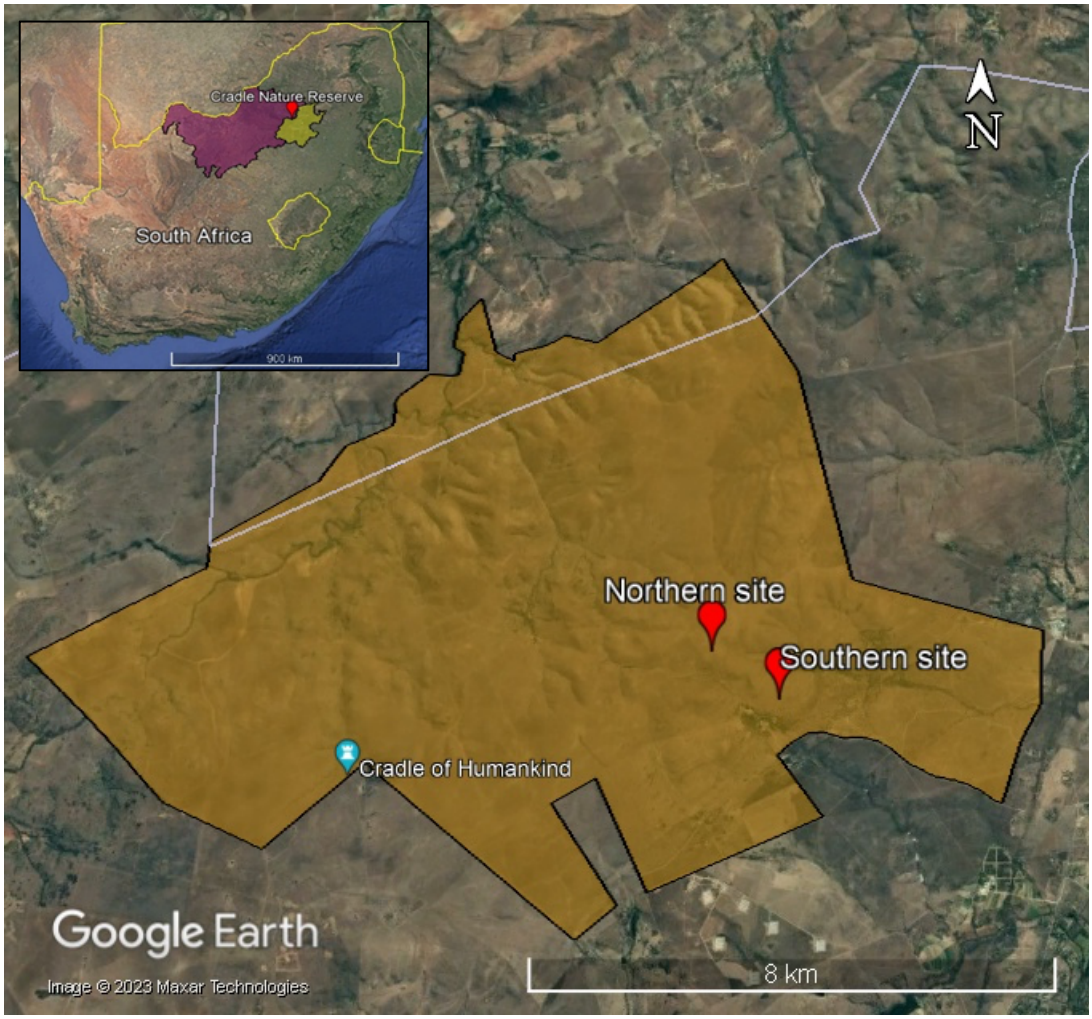


Figure 1. Map showing the locality of the two study sites within the Cradle Nature Reserve and South Africa. The orange polygon represents the area covered by the Cradle Nature Reserve, while the red pins represent the location of the study sites. The inset map of South Africa indicates the location of the Cradle Nature Reserve (blue pin) in relation to North West (purple area) and Gauteng (yellow area) provinces.



Figure 2. The landscape of the northern site. The picture was taken on the 11 October 2021 (Summer period) while facing the south-east direction.



Figure 3. The landscape of the southern site. The picture was taken on the 5 January 2022 (Summer period) toward the south-west direction.

SAMPLING PROCEDURE

At each site, I set up a permanent 140 m x 40 m grid marked in 10 m units with metal stakes hammered into the ground. This formed a five-by-fifteen grid configuration, labelled as A-E and 1-15 (e.g., A1-A15 to E1-E15). PVC live traps (7.5 cm x 6 cm x 29 cm) were set up in the permanent grid, with one trap at each stake. Each site had a total of 75 traps, with 15 traps per line. Each trap was marked with an identifying number indicating its position within its line configuration and its coordinates were recorded using a handheld GPS (GPSMAP 62, Garmin, Kansas, USA). Once correctly positioned, the surrounding vegetation was used to cover the traps for insulation of sampled animals and for camouflage.

Small mammal sampling was done over one year (October 2021 – September 2022), with sampling sessions taking place five days each month. The two grassland sites were sampled within the same sampling session. The traps were baited with a mixture of oats, granola, sunflower seeds, sunflower oil and salt. In winter, a generous amount of cotton wool was added to the traps to provide nesting material and to provide additional insulation (Hoffmann *et al.*, 2010). The quantity of bait in each trap was checked and replenished if necessary while traps were inspected.

Traps were checked only during the morning for potential small rodent captures. During the morning inspection, once the traps were checked, they were turned over to allow for small mammals to enter the live traps without being captured throughout the day. This was necessary as the study focussed on nocturnal rodents only. Leaving traps active during the day put potential diurnal rodents at risk of predation from diurnal animals, such as baboons which frequented my study sites.

If a successful capture occurred, the individual was carefully removed from the trap and marked with a numbered Monel metal ear tag (5 mm, 0.25 g; National Band and Tag, Newport, Kentucky (KY), USA; Figure 4) as suggested by Schoepf *et al.* (2017). This number served to identify individuals as a new capture or a recapture. Ear tags were used in this study over other marking methods since they are considered to be one of the most ethical, efficient and cost-effective marking methods for small mammals (Jung *et al.*, 2019). Along with the ear tag number, the trap number, time and date of the capture was recorded for every capture. Each individual was identified to species level, weighed (to the nearest g), their body, tail and hindfoot length measured (cm), categorized by age (adult or juvenile), sexed and their reproductive state recorded, see below. For the rodents that were identified as

recaptures within the same sampling session, re-measuring all measures was redundant as these would not change within the same sampling session and only their body weight was recorded. These measurements were all be done at the field sites, so that individuals were released at the site of capture. Data processing took an average of five minutes per individual.



Figure 4. Ear tagging a *Gerbilliscus leucogaster* ear with a numbered Monel metal ear tag.

Identifying the small mammals to species level was done on-site. Individuals were weighed inside a strong transparent plastic bag using a spring balance (the weight of the bag and the ear tag was subtracted from the total weight to give the actual weight of the sampled individual). A body mass index (BMI) was calculated for every capture using its body mass and nasal-to-anal length: (mass (g) / length (cm)^2 * 100; this was used as a proxy to determine body condition. The length of the animal was made up of two measures: body length (from the tip of the nose to the base of the tail) and tail length (from the base of the tail to the tip of the tail), this was done using digital callipers (body length) and 30 cm metal ruler (tail length, because tail length often exceeded the length of the calliper). Each individual was categorised either as a juvenile or adult by their size and weight; this was done separately per species. Rodents were categorised by age using the average weight guides in Monadjem *et al.* (2015) and Skinner and Chimimba (2005). Individuals were sexed according to the anogenital distance (larger in males than females). Reproductively active females were identified by a

perforate vagina or signs of lactation or pregnancy (palpated abdominal area) and non-reproductive females had a closed/non-perforate vagina. Reproductively actives males were identified by whether they were scrotal or non-scrotal (non-reproductive).

VEGETATION ASSESSMENT

General vegetation characteristics were recorded at both sites once per season (winter, August and summer, February). I recorded the percentage of plant cover, plant height and the dominant plant species within a 1 m² quadrat. Each site (5600 m² - 140 m x 40 m) was divided into 56 smaller plots measuring 100 m² (10 m x 10 m). These smaller plots were marked out using the existing animal trapping grid (described above). Each metal stake marked the corners of the vegetation assessment plot. I placed two quadrats randomly within each of these plots by tossing the quadrat over my shoulders to ensure random placement.

The plant cover was assessed visually using an altered version of the Walker's scale (Walker, 1976). The scale converted the proportion of vegetation within a quadrat into a scale of 0 – 5 where 1 = < 20% cover, 2 = 21% - 40%, 3 = 41% - 60%, 4 = 61% - 80% and 5 > 80% cover. The percentage of cover in the grid was assessed according to the cover from a rodent's perspective. For example, leaf litter that a rodent could not hide beneath was not considered cover. I also measured cover by calculating the light passing through the vegetation. I used an EXTECH instruments light meter (401025), at 100x lux, to calculate the amount of light in lux. I took three readings at the soil surface and directly above this at the median plant height per quadrat. The measurement of light readings within the quadrat were chosen at random. Each pair of light measurements (above and below the vegetation) was converted into a percentage (the amount of light measured at the soil surface divided by the light at the median plant height x 100). The three percentages were then averaged to generate a value for that entire quadrat.

Plant height was calculated as the average height of the vegetation found within the quadrat. The shortest, tallest and median height of the plants were measured in each quadrat. This was converted into an average per height measurement (i.e. average shortest, average median and average tallest plant height) per quadrat. The shortest plant was most often ground cover which was too short to offer cover for rodents; this was measured from the base of the plant to the tip of its stem. The median plant height was the height of the majority of the plant

canopy; this was a measure from the ground to the top of the vegetation canopy. The tallest plant height was measured from the base of the tallest plant to the tallest part of the plant in the quadrat, this was often the top of a single grass fluorescence.

I recorded the dominant plant species in each quadrat, defined by the species that had the highest proportion of cover in the quadrat. Dominant plant species per 100 m² grid was recorded as the dominant plant species per quadrat added together, so each 100 m² grid had up to two dominant plant species. Samples of species that could not be identified in the field were collected, pressed, frozen and identified later using field guides and herbarium specimens at the CE Moss Herbarium, University of the Witwatersrand, Johannesburg, South Africa.

DATA ANALYSIS

All statistical analyses were conducted in R Studio (version 4.2.0), using the Rbase package (R Core Team, 2022) and a variety of other packages detailed below. Statistical analyses were conducted by site and season. Season was divided into two periods, summer and winter. The summer season consisted of the spring – summer period, which was from October 2021 to February 2021 and included September 2022. Due to unforeseen circumstances, the commencement of the study was postponed and could only be started in October 2021 and therefore September of the following year was included in the summer sampling session to complete the summer data. The winter season consisted of the autumn-winter period between March 2021 to August 2021.

Rodent diversity measures

Rodent diversity was calculated using the total captures, the total individuals captured, species richness and the diversity indices. The total number of rodent captures was calculated as the count of every rodent capture per species in each site (northern and southern site) and for each season (summer and winter period). The total individuals captured was the count of every individual sampled (excluding recaptures). This was also calculated per species, site and season. Species richness was a count of the total number of species per site per season. A chi-square test was then used to analyse differences in the total captures, the total individuals

captured and the species richness between the sites and seasons. Simpson's and Shannon's diversity indices were used to assess the rodent diversities of each site per season. Both indices were considered since the Simpson's diversity index accounts for the more common species, while the Shannon's diversity index accounts for the rarer species. Diversity indices were calculated using the vegan package in R (Oksanen *et al.*, 2022). Using chi-square tests, the rodent diversities were tested for differences between sites and seasons.

Rodent demography

The demography of the rodent population was assessed using five variables: population size; sex; age; reproductive activity; and body condition. Only the three most common species were used, and each species was assessed independently. The most common species were determined by having either the highest total captures or number of individuals captured per site. Population size of each species at each site was estimated for each trapping session using a closed population design. The population was assumed to follow a closed population design during the five-day trapping session, as I assumed that no births, deaths, or migrations occurred during the five days trapping occurred (Lima *et al.*, 2003). Population size estimations were calculated using the FSA package (Ogle *et al.*, 2022) in R Studio. The models for sex ratios, reproductive activity and body condition excluded juveniles since they were difficult to sex because their bodies were still underdeveloped.

To assess the rodent demography, five linear mixed models were performed to determine variation in the variables mentioned above. Before running the mixed models, the vegetation characteristics were tested for autocorrelation using the Durbin-Watson test in the lmtest package (Zeileis and Hothorn, 2002) in R studio. Linear models were created for each demographic variable (response variable) with the vegetation height (minimum height, median height and maximum height) and vegetation cover (Walker scale and the percentage of light penetrating through the vegetation cover) as the predictor variables, which I ran as separate models. These models were then used to test for autocorrelation between the various vegetation height measures and the cover associated measures. Autocorrelation was found in the population size, age, reproductive activity and body condition models for both vegetation height and cover. Although, for the sex model, neither vegetation height or cover were autocorrelated.

For the demography, mixed models analyses were conducted using the lme4 (Bates *et al.*, 2015) and car packages (Fox and Weisberg, 2011) in R Studio. The demography variables (population size, sex, age, reproductive activity and body condition) were all tested for normality and generalised linear mixed models (GLMMs) were used on the variables that did not follow a normal distribution, while variables that did follow normal distributions were analysed using linear mixed models (LMMs).

In these models, season, minimum vegetation height, median vegetation height, maximum vegetation height, Walker's scale and the percentage of light penetrating through the vegetation cover were used as fixed factors, unless autocorrelation was detected. For models that were autocorrelated (population size, age, reproductive activity and body condition), only one variable was selected to represent that vegetation characteristic in the demography analyses. Therefore, in the models where the vegetation height variables were autocorrelated, median height was selected, as the median height was a better representative of the height of most of the sample quadrat, while the minimum and maximum height represented the extremes in each quadrat. When the vegetation cover measures were autocorrelated, the percentage of light penetrating through the vegetation cover was selected. This was a mean of three measurements, whereas the Walker scale was a single measure based on the researchers perspective which could lead to bias. Demography analysis of the sex of the rodents investigated all three of the vegetation height characteristics and both Walker's scale and the light penetration through the vegetation, as these were not autocorrelated.

The sex of the rodents was included as an additional fixed factor for the reproductive activity and body condition GLMM models. In addition, the interaction between sex and season was included in the body condition analysis to account for the changes in body condition of each sex due to seasonal reproduction. Field site and rodent identification (ear tag number) were used in the GLMM models as the random factors. Field site was included as a random factor because the two study sites were qualitatively different, while rodent identification was included as a random factor to avoid pseudo replication. Population size and body condition models used the family gamma and the inverse link function. Sex, age and reproductive activity models used the binomial family with the link function logit.

Vegetation characteristics

I used principal components analysis (PCA) to analyse vegetation characteristics between seasons and sites. PCAs were conducted using the FactoMineR (Le *et al.*, 2008), factoextra (Kassambara and Mundt, 2020) and corrplot R packages (Wei and Simko, 2021). Two PCAs were performed. The first PCA used site as a grouping variable while the second used season. Walker's scale, percentage of light penetration, minimum plant height, median plant height and maximum plant height were used for both the site and season PCAs. The number of principal components extracted was based on whether they accounted for more than 70% of the total variance in the data. Based on the correlation matrix, the highest positive correlation value and the lowest negative correlation value were used to describe each principal component axis. Following the analysis, corresponding biplots were created to visualise the data and identify patterns to describe the vegetation characteristics associated with each site. The vegetation characteristics (Walker's scale, percentage of light penetration, minimum plant height, median plant height and maximum plant height) means were calculated separately and compared between seasons and sites using students t-tests in R.

Relationship between density, demography and vegetation.

I also conducted two PCAs to visualise the relationships between rodent density, rodent demography and vegetation variables. The PCAs focused on the demography and their associated vegetation characteristics for the three most common species in the study (*Gerbilliscus leucogaster*, *Otomys angoniensis* and *Mastomys coucha*). The demography variables used in this PCA were the population size, sex ratio, age ratio (juvenile versus adult), reproductive activity and body condition of the three study species. Vegetation variables for the PCA were Walker's scale, the percentage of light penetrating through the vegetation, minimum plant height, median plant height and maximum plant height.

Diversity related variables used in this PCA were the total number of rodent captures, the total number of individuals captured, rodent species richness, Shannon's diversity index, Simpson's diversity index. The diversity variables included all the rodents sampled in my study to assess how the three focal species are influenced by the rodent community on the trapping sites.

The grouping variables for the first PCA were each of the three most common species in the study, (*Gerbilliscus leucogaster*, *Otomys angoniensis* and *Mastomys coucha*). While the second PCA was grouped by season. Much like with the vegetation characteristics PCA, the number of principal components extracted was based on whether they accounted for more than 70% of the total variance in the data. Based on the correlation matrix, the highest positive correlation value and the lowest negative correlation value were used to describe each principal component axis. Following the analysis, corresponding biplots were created to visualise the data. Using the biplots generated by the PCAs, patterns associated with the three study species and season were analysed.

RESULTS

Rodent trapping took place five days each month from October 2021 to September 2022, which is a total of 60 sampling days or 9000 trap-nights. Trap night success was calculated by site and month (Table S 1). A total of 223 rodents were captured during the study, of which 159 were recaptures. All captures belonged to the rodent family *Muridae*. Six different rodent species were captured during the study, namely *Gerbilliscus leucogaster* (sub-family: *Gerbillinae*), *Lemniscomys rosalia* (sub-family: *Murinae*), *Mastomys coucha* (sub-family: *Murinae*), *Micaelamys namaquensis* (sub-family: *Murinae*), *Mus minutoides* (sub-family: *Murinae*) and *Otomys angoniensis* (sub-family: Otomyinae) (Table S 2). The three most common species, which were *Gerbilliscus leucogaster* (n = 103), *Mastomys coucha* (n = 52) and *Otomys angoniensis* (n = 39), made up 87% (n = 194) of the total captures (n = 223).

RODENT DIVERSITY

Total number of rodent species captured.

The southern site had a significantly higher number (n = 175) of total rodent captures than the northern site ($\chi^2_1 = 72.33$; n = 48; $P < 0.001$). At both sites, *G. leucogaster* had the highest number of captures recorded and *M. namaquensis* was captured the least (

Figure 5). *Mastomys coucha*., *M. minutoides* and *L. rosalia* were only found at the southern site (

Figure 5). Overall, the summer period (n = 133) had a significantly higher number of total rodent captures than the winter period ($\chi^2_1 = 8.29$; n = 90; $P = 0.004$). *Gerbilliscus leucogaster* had the highest number of total captures in summer period but a decline in captures were seen in the winter period (

Figure 6). *Mus minutoides* was the only other rodent that had more captures in the summer period than the winter period and this species had the lowest number of captures in the winter period (

Figure 6). *Micaelamys namaquensis* had the lowest number of captures during the summer period but the number of captures increased slightly during winter period (

Figure 6). *Otomys angoniensis* and *Mastomys coucha* had the highest number of captures during the winter period (

Figure 6).

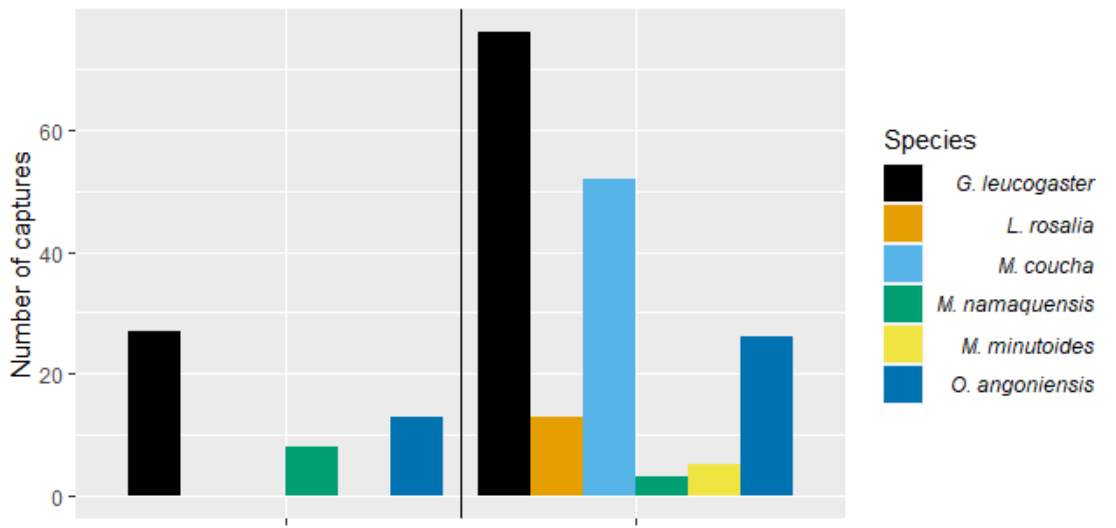


Figure 5. The total number of rodent captures by species and site at the Cradle Nature Reserve from October 2021 to September 2022. Rodent species captured include *Gerbilliscus leucogaster* (black), *Lemniscomys rosalia* (orange), *Mastomys coucha* (light blue), *Micaelamys namaquensis* (green), *Mus minutoides* (yellow) and *Otomys angoniensis* (dark blue).

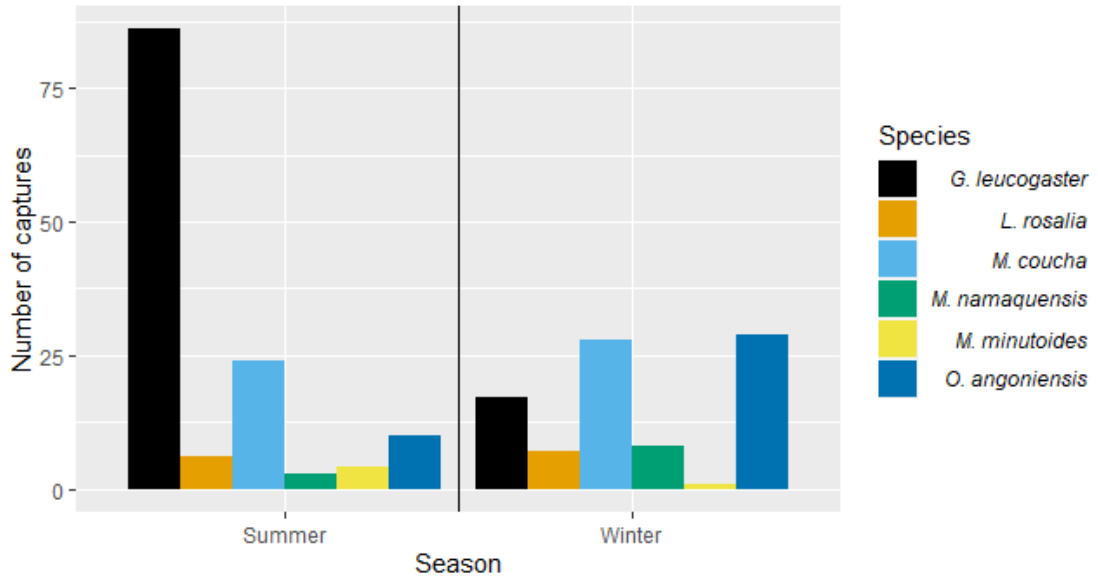


Figure 6. The total number of rodent captures by species and season at the Cradle Nature Reserve from October 2021 to September 2022. Rodent species captured include *Gerbilliscus leucogaster* (black), *Lemniscomys rosalia* (orange), *Mastomys coucha* (light blue), *Micaelamys namaquensis* (green), *Mus minutoides* (yellow) and *Otomys angoniensis* (dark blue).

Total number of individuals captured.

The total number of individuals captured significantly differed between the two sites (χ^2_1 = 24.14; $P < 0.001$), with 39 more individuals captured at the southern site (n = 51) than the northern site (n = 12). There were more *O. angoniensis* individuals captured at the northern

site, while more *M. coucha* individuals were captured at the southern site (Figure 7). *Micaelamys namaquensis* had the least number of individuals captured in both sites, although *M. coucha*, *M. minutoides* and *L. rosalia* were not captured on the northern site (Figure 7). The summer period (n = 38) had five more captured individuals than the winter period (n = 33) which was not significantly different ($\chi^2_1 = 0.35$; $P = 0.553$; Figure 8). *Mastomys coucha* had the highest number of individuals captured in both seasons, while *M. namaquensis* and *L. rosalia* had the least number of captured individuals during the summer period, and *M. minutoides* had the least number of captured individuals in the winter period (Figure 8). The number of individuals increased from summer to winter for *M. coucha*, *O. angoniensis* and *L. rosalia. Gerbilliscus leucogaster* and *M. minutoides* showed decreased in the number of individuals captured from summer to winter (Figure 8). *Micaelamys namaquensis* showed no difference in the number of individuals captured between summer and winter (Figure 8).

Figure 7. The number of individual rodents captured by species and site at the Cradle Nature Reserve from October 2021 to September 2022. Rodent species captured include *Gerbilliscus leucogaster* (black), *Lemniscomys rosalia* (orange), *Mastomys coucha* (light blue), *Micaelamys namaquensis* (green), *Mus minutoides* (yellow) and *Otomys angoniensis* (dark blue).

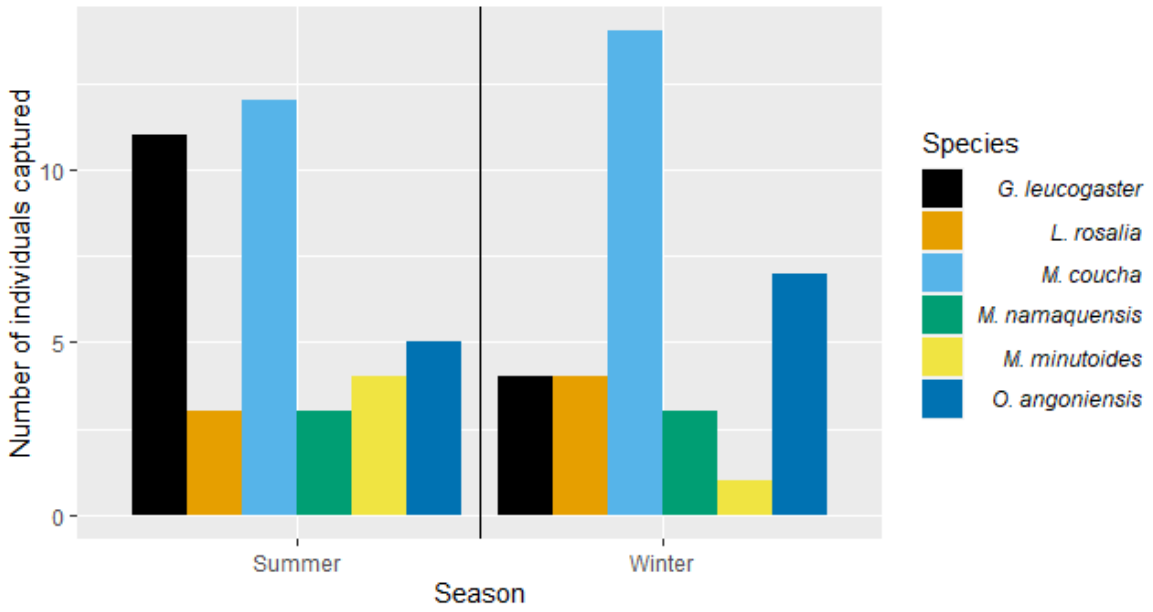


Figure 8. The number of individual rodents captured by species and season at the Cradle Nature Reserve from October 2021 to September 2022. Rodent species captured include *Gerbilliscus leucogaster* (black), *Lemniscomys rosalia* (orange), *Mastomys coucha* (light blue), *Micaelamys namaquensis* (green), *Mus minutoides* (yellow) and *Otomys angoniensis* (dark blue).

Species richness

The species richness was higher at the southern site (n = 6) than the northern site (n = 3) by three species, although this difference was not statistically significant ($\chi^2_1 = 1$; $P = 0.317$, Figure 9). The species richness at the southern site remained consistent between the seasons, while the species richness in the northern site was slightly less in the winter period compared to the summer period (Figure 9). Between seasons, the summer period and the winter period had the same species richness (n = 6) i.e. not statistically significantly different from one another; ($\chi^2_1 = 1$; $P = 1.000$).

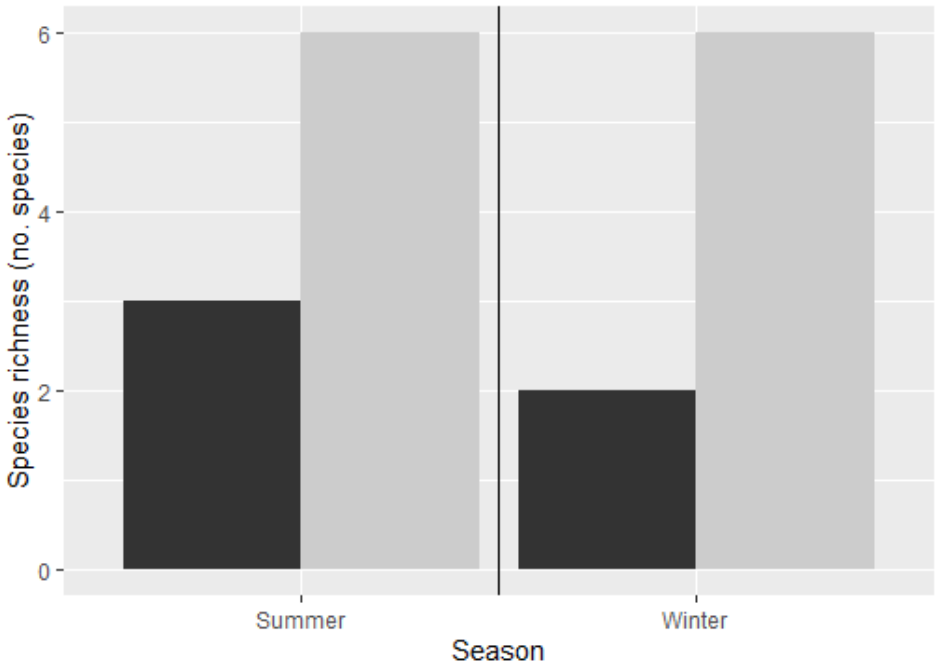


Figure 9. The species richness of rodent in the northern and southern sites by season at the Cradle Nature Reserve from October 2021 to September 2022. Northern site in dark grey, Southern site in light grey.

Species diversity indices

According to both Shannon and Simpson's diversity indices, the southern site had a higher diversity of species than the northern site (Table 1), although the difference between the two sites were not statistically significant for both the Shannon's diversity index ($\chi^2_1 = 0.084$; $P = 0.771$) and the Simpson's diversity index ($\chi^2_1 = 0.01$; $P = 0.943$). Similarly, there was a higher species diversity in the summer period than the winter period according to both the Shannon and Simpson's diversity indices (Table 1). The species diversity indices between the seasons did not differ significantly for either Shannon's ($\chi^2_1 < 0.01$; $P = 0.955$) or Simpson's ($\chi^2_1 < 0.01$; $P = 0.975$) diversity indices.

Table 1. The Shannon and Simpson's diversity indices of the rodents captured in each site and season at the Cradle Nature Reserve from October 2021 to September 2022.

Site	Shannon's diversity index	Simpson's diversity index
Northern site	1.08	0.65
Southern site	1.55	0.74
Summer	1.63	0.78
Winter	1.58	0.74

RODENT SPECIES

I focussed on the three most abundant species for more detailed analyses, namely *Gerbilliscus leucogaster*, *Mastomys coucha* and *Otomys angoniensis*. There were two possible species for both the *Otomys* and *Mastomys* species, namely *O. angoniensis*, *O. irroratus, M. coucha* and *M. natalensis,* which could have fitted the geographical distribution of the study, although, these species are not distinguishable by their external morphology (Skinner and Chimimba, 2005; D. Happold, 2013; Kneidinger *et al.*, 2014; Monadjem *et al.*, 2015). A concurrent study identified the species as *O. angoniensis* and *M. coucha* using ctyB genes. Samples were analysed by Dr C. Oosthuizen at the University of Pretoria.

Gerbilliscus leucogaster is a medium sized gerbil (60g – 99g), with a reddish-brown pelage and white underbelly. Some of its distinguishing features include large round eyes, a long hairy tail with a dark band running along its entire length, large hindfeet with a dark (almost purple) colouration on the feet pads (*pers. obs*). They are a relatively common species in their geographical distribution and are of least concern according to the IUCN Red List of Threatened Species (du Plessis *et al.*, 2016b). The presence of the species is known to be strongly linked to habitats with sandy soils, ranging from open grasslands to savanna woodlands (Skinner and Chimimba, 2005; Avenant, 2011). *Gerbilliscus leucogaster* is a nocturnal omnivore and can live in groups or pairs in interconnected burrows (De Graaff, 1981; Monadjem, 1997b; Dempster, 2013).

Otomys angoniensis are large (138g – 159g), stocky, shaggy murids, with a dark slate grey pelage and a dark to pale grey underbelly. The distinguishing features of *O. angoniensis* include their large stocky build; their short, finely scaled tail; their hairy round ears and their short muzzle (*pers. obs*). These species are common in their preferred habitat (wetlands, mesic grasslands and savannahs), and they are of least concern according to the IUCN Red List of Threatened species (Taylor *et al.*, 2016). *Otomys angoniensis* also occurs in drier habitats in the wet season (Bronner and Meester, 1988; Taylor, 2013). The species occurs in habitats with good vegetation cover, in which they make distinctive runways that are often used by other rodents such as *Mastomys* spp. and *Rhabdomys pumilio* (De Graaff, 1981; Bronner and Meester, 1988; Taylor, 2013). Skinner and Chimimba (2005) and Happold (2013) state that *O. angoniensis* is mostly diurnal, but have been found to be crepuscular and nocturnal. They are polyoestrous, breeding throughout the year, with a peak in the wet season (Bronner and Meester, 1988; Taylor and Green, 1976; Taylor, 2013). O*tomys angoniensis* are mostly found to be solitary and antisocial, but have been found in pairs or small groups (Bronner and Meester, 1988; Taylor, 2013).

Mastomys coucha is a small (25g – 44g) dark grey to rusty-brown murid, with a slightly lighter grey underbelly. Some of its distinguishing features are the 12 pairs of mammae, its long finely scaled tail with sparse bristly hair, the white ring or fur around the ankle and its very aggressive behaviour (*pers. obs*). It has large distributions across Africa (Avenant, 2011; Leirs, 2013; Monadjem *et al.*, 2015), and tends to be the most abundant rodent where they occur. As a result they are considered to be of least concern on the IUCN Red List of Threatened species (du Plessis *et al.*, 2016a). It has seasonal cyclic fluctuations in population sizes. *Mastomys coucha* is considered a generalist granivore-herbivore (Monadjem, 1997b; Kinahan and Pillay, 2008), and is used as an indicator of disturbance since it is a pioneer species, which often have population eruptions in uninhabited/disturbed habitats (De Graaff, 1981; Skinner and Chimimba, 2005; Avenant, 2011; Kneidinger *et al.*, 2014). *Mastomys coucha* is nocturnal and can live in large groups, but tend to become cannibalistic when the population density is high (De Graaff, 1981; Skinner and Chimimba, 2005).

RODENT DEMOGRAPHY

The three most common species (highest number of captures and individuals captured), used to assess the rodent demography were *G. leucogaster, M. coucha* and *Otomys angoniensis.*

Mastomys coucha was captured only on the southern site, so field site was excluded as a random factor in the *M. coucha* demography models. The body condition of *O. angoniensis* was the only demography variable that followed a normal distribution, so an LMM was used for analysis for this variable. All other variables did not follow a normal distribution and therefore GLMMs were used for analyses.

For the population size age, reproductive activity and body condition models, both the vegetation height (minimum height, median height and maximum height) and vegetation cover measures (Walker's scale and the percentage of light penetration) were positively autocorrelated (Durbin-Watson statistic < 1.5; Table 2). Therefore, median height and the percentage of light penetrating through the vegetation were used to represent the vegetation characteristics in the above-mentioned demography models. There was no autocorrelation detected (1.5 < Durbin-Watson statistic < 2.5) in the vegetation characteristics associated with the sex of rodents (Table 2).

Table 2. Durbin-Watson autocorrelation test results for the vegetation characteristics linked to the demography variables of *Gerbilliscus leucogaster, Mastomys coucha* and *Otomys angoniensis* at the Cradle Nature Reserve from October 2021 to September 2022. The plant height measures tested for autocorrelation were minimum, median and maximum height and the plant cover measures tested for autocorrelation were Walker's scale and the percentage of light penetrating through the vegetation.

Demography variable	Vegetation characteristic	Durbin-Watson statistic (DW) and *P*
Population size	Plant height measures	DW = 0.723, $P < 0.001$
	Plant cover measures	DW = 0.651, $P < 0.001$
Sex ratio	Plant height measures	DW = 1.588, $P = 0.002$
	Plant cover measures	DW = 1.621, $P = 0.004$
Age	Plant height measures	DW = 0.983, $P < 0.001$
	Plant cover measures	DW = 1.001, $P < 0.001$
Reproductive activity	Plant height measures	DW = 1.156, $P < 0.001$
	Plant cover measures	DW = 0.833, $P < 0.001$
Body condition	Plant height measures	DW = 0.902, $P < 0.001$
	Plant cover measures	DW = 0.881, $P < 0.001$

Population size

Population sizes were calculated monthly using a closed population design for *G. leucogaster, O. angoniensis and M. coucha* (

Table S *3*). The population sizes of *G. leucogaster* were significantly associated with season (χ^2_1= 6.53; P = 0.011), with a greater population size in the summer months (Figure 10). The median height of the vegetation had no statistically significant association with the population size of *G. leucogaster* (χ^2_1= 0.10; P = 0.752), while the percentage of light penetrating through the vegetation was statistically significantly associated with the population size of *G. leucogaster* (χ^2_1= 4.97; P = 0.026). The relationship between the percentage of light penetrating through the vegetation and the population size of *G. leucogaster* was significantly weakly negative (Spearman's correlation r = -0.30; P = 0.002). For every 10% increase in percentage of light penetrating through the vegetation there was a decrease in the estimated population size of *G. leucogaster* by 0.28 individuals ($F_{1,98}$ = 11.99; P < 0.001; Figure 11). However, the percentage of light penetrating through the vegetation accounted for only 10.9% of the variability of the estimated population size of *G. leucogaster*.

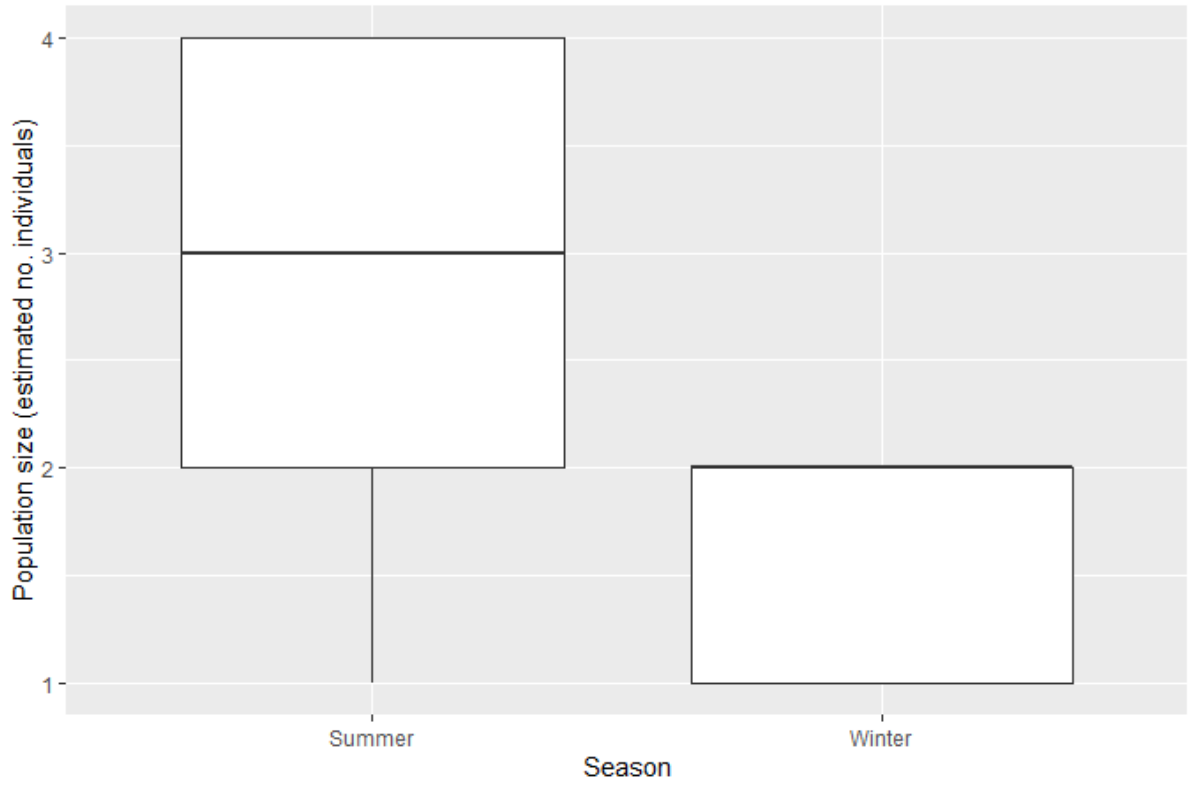


Figure 10. Box and whisker plot of the *Gerbilliscus leucogaster* population size between seasons at the Cradle Nature Reserve from October 2021 to September 2022. The box represents the upper and lower quartiles, while the centre line (darker line) represents the median population size and the whiskers represents the range of data from the minimum to maximum.

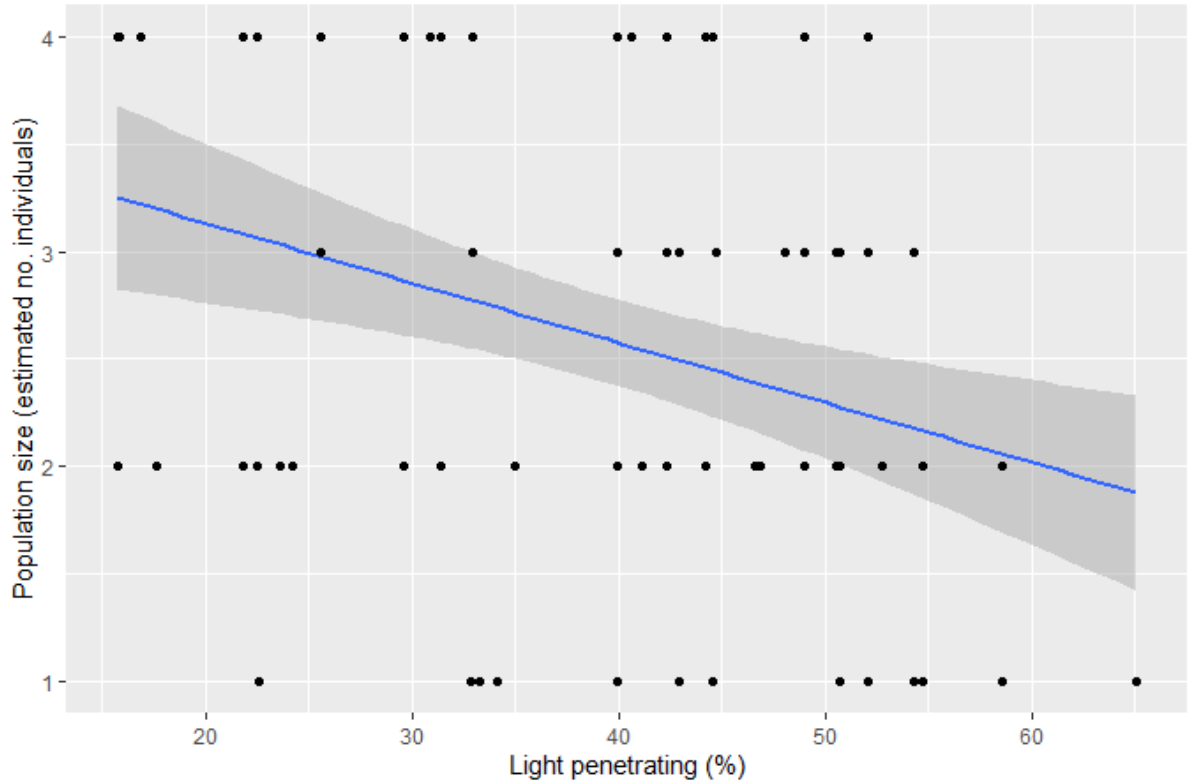


Figure 11. The relationship between the percentage of light penetrating through the vegetation and the population size of *Gerbilliscus leucogaster* at the Cradle Nature Reserve from October 2021 to September 2022. The trend line is significant, showing a negative weak relationship (Spearman's correlation r = -0.30; P = 0.002).

The population size of *O. angoniensis* had no statistically significant associations with season (χ^2_1 = 0.17; P = 0.680), median vegetation height (χ^2_1 = 0.31; P = 0.579), or the percentage of light penetrating through the vegetation (χ^2_1 = 0.21; P = 0.643). *Mastomys coucha* population size also had no statistically significant associations with season (χ^2_1 = 2.01; P = 0.156), median vegetation height (χ^2_1 = 0.05; P = 0.821), or the percentage of light penetrating through the vegetation (χ^2_1 = 0.03; P = 0.861).

Sex ratio

Sex ratios of *G. leucogaster, O. angoniensis* and *M. coucha* were calculated excluding juveniles (Table S 4). The sex ratio of *G. leucogaster* showed no statistically significant

associations with season ($\chi^2_1 = 0.14$; $P = 0.709$), minimum vegetation height ($\chi^2_1 = 0.07$; $P = 0.796$), median vegetation height ($\chi^2_1 = 0.01$; $P = 0.923$), maximum vegetation height ($\chi^2_1 = 0.03$; $P = 0.872$), Walker's scale ($\chi^2_1 = 0.03$; $P = 0.854$), or the percentage of light penetrating through the vegetation ($\chi^2_1 < 0.01$; $P = 0.953$). The sex ratio of *O. angoniensis* also showed no statistically significant associations with season ($\chi^2_1 = 0.01$; $P = 0.939$), minimum vegetation height ($\chi^2_1 = 0.07$; $P = 0.798$), median vegetation height ($\chi^2_1 = 0.08$; $P = 0.780$), maximum vegetation height ($\chi^2_1 < 0.01$; $P = 0.969$), Walker's scale ($\chi^2_1 = 0.06$; $P = 0.811$), or the percentage of light penetrating through the vegetation ($\chi^2_1 = 0.10$; $P = 0.757$). Likewise, there were no statistically significant associations for the sex ratio of *M. coucha* and season ($\chi^2_1 < 0.01$; $P = 0.959$), min vegetation height ($\chi^2_1 = 0.07$; $P = 0.795$), median vegetation height ($\chi^2_1 < 0.01$; $P = 0.995$), max vegetation height ($\chi^2_1 = 0.64$; $P = 0.424$), Walker's scale ($\chi^2_1 = 0.01$; $P = 0.905$), or the percentage of light penetrating through the vegetation ($\chi^2_1 = 0.07$; $P = 0.785$).

Age

The age of *G. leucogaster, O. angoniensis* and *M. coucha* was calculated as the ratio of juveniles to adult individuals (Table S 5). The ratio of juvenile to adult individuals of *G. leucogaster* had no statistically significant association with season ($\chi^2_1 < 0.01$; $P = 0.999$), median height ($\chi^2_1 < 0.01$; $P = 0.998$) or the percentage of light penetrating through the vegetation ($\chi^2_1 < 0.01$; $P = 0.998$). Likewise, the ratio of juvenile to adult individuals for *O. angoniensis* had no statistically significant association with season ($\chi^2_1 = 2.35$; $P = 0.126$), median vegetation height ($\chi^2_1 = 1.70$; $P = 0.193$) or the percentage of light penetrating through the vegetation ($\chi^2_1 = 1.21$; $P = 0.271$). Similarly, for *M. coucha* there were no statistically significant associations with the age and season ($\chi^2_1 = 0.08$; $P = 0.771$), median height ($\chi^2_1 = 2.48$; $P = 0.115$) or the percentage of light penetrating through the vegetation ($\chi^2_1 = 3.32$; $P = 0.069$).

Reproductive activity

The reproductive activity of *G. leucogaster, O. angoniensis* and *M. coucha* was assessed as either reproductively active or non-active in each season (Table S 6). The season had a

significant association with the proportion of reproductively active *G. leucogaster individuals* ($\chi^2_1 = 5.61$; $P = 0.018$). *Gerbilliscus leucogaster* was reproductively active in the summer period than in the winter period by 42.86% (Figure 12). However, there were no statistically significant associations with *G. leucogaster's* reproductive activity and sex ($\chi^2_1 = 3.15$; $P = 0.076$), median vegetation height ($\chi^2_1 = 0.07$; $P = 0.798$) or the percentage of light penetrating through the vegetation ($\chi^2_1 = 0.29$; $P = 0.592$).

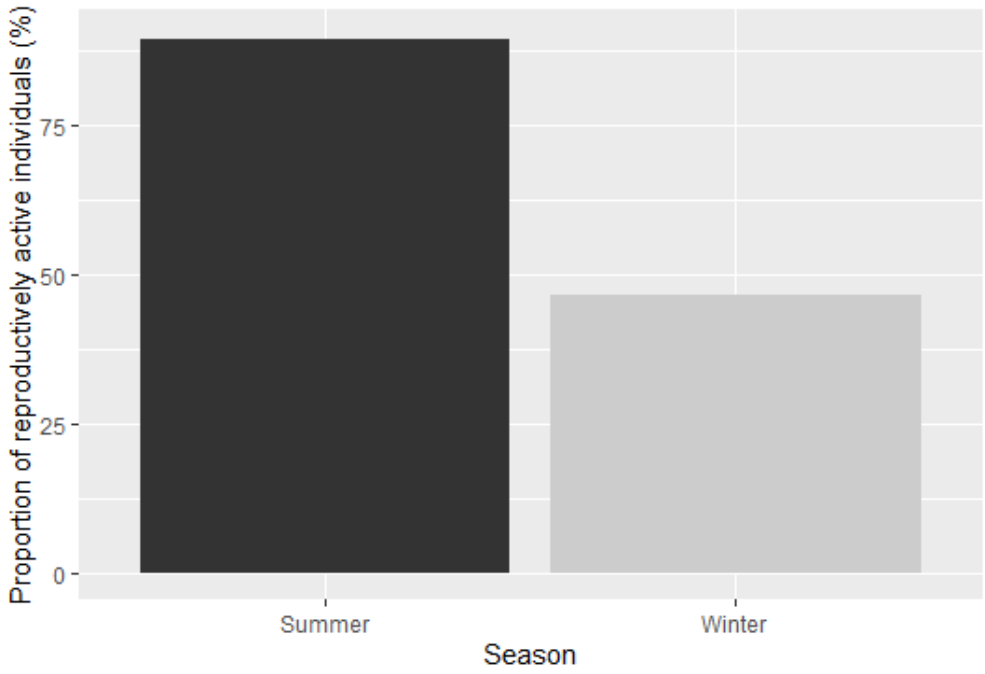


Figure 12. The proportion of reproductively active *Gerbilliscus leucogaster* individuals in summer and winter at the Cradle Nature Reserve from October 2021 to September 2022.

The reproductive activity of *O. angoniensis* was not significantly associated with season ($\chi^2_1 < 0.01$; $P = 0.998$), sex ($\chi^2_1 < 0.01$; $P = 0.997$), median vegetation height ($\chi^2_1 < 0.01$; $P = 0.997$) and the percentage of light penetrating through the vegetation ($\chi^2_1 < 0.01$; $P = 0.997$). Similarly, the reproductive activity of *M. coucha* showed no statistically significant associations with season ($\chi^2_1 < 0.01$; $P = 0.999$), sex ($\chi^2_1 < 0.01$; $P = 0.999$), median height ($\chi^2_1 = 0.12$; $P = 0.729$) and the percentage of light penetrating through the vegetation ($\chi^2_1 = 0.40$; $P = 0.529$).

Body condition

The body mass index (BMI) of *G. leucogaster, O. angoniensis* and *M. coucha* was calculated as a proxy of body condition and excluded juveniles (Table S 7). The body condition of *G. leucogaster* varied seasonally ($\chi^2_1 = 22.72$; $P < 0.001$), showing a significantly higher BMI value in the winter following the summer (Figure 13). However, sex ($\chi^2_1 = 0.40$; $P = 0.525$), median vegetation height ($\chi^2_1 < 0.01$; $P = 0.977$), the percentage of light penetrating through the vegetation ($\chi^2_1 < 0.01$; $P = 0.951$) and the interaction between season and sex ($\chi^2_1 = 3.52$; $P = 0.061$) was not statistically significantly associated with the body condition of *G. leucogaster*.

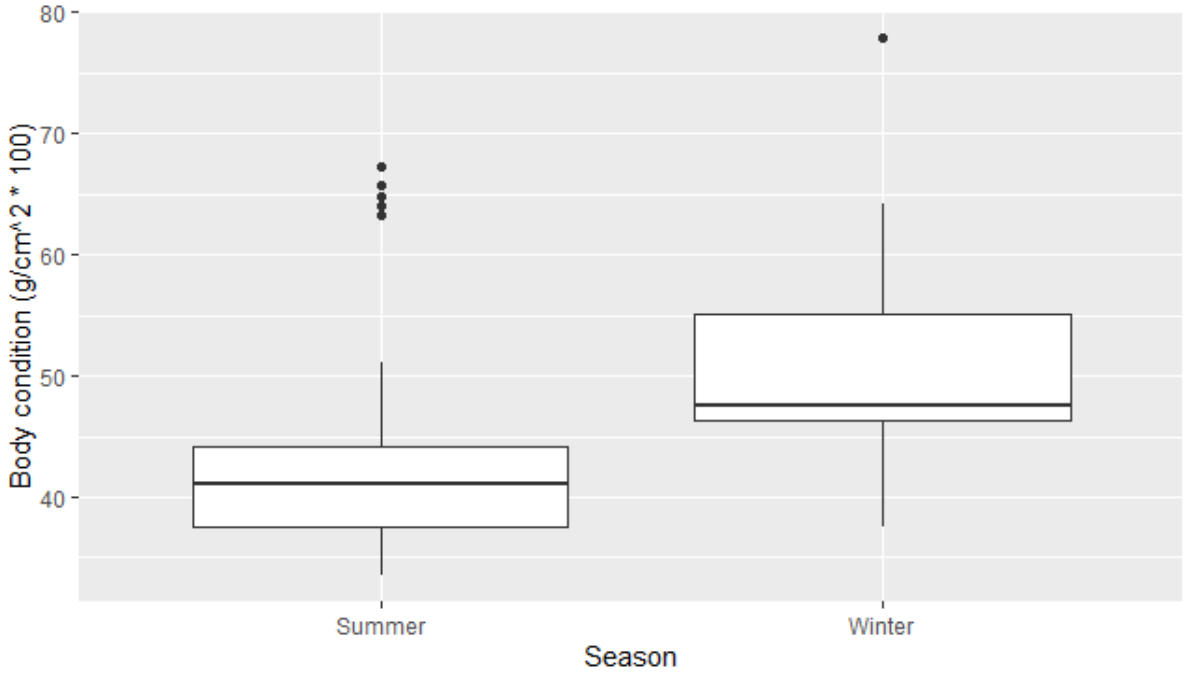


Figure 13. The body condition of *Gerbilliscus leucogaster* in summer and winter at the Cradle Nature Reserve from October 2021 to September 2022. The box represents the upper and lower quartiles and the centre line (darker line) represents the median body condition of *Gerbilliscus leucogaster* in the summer and winter periods and the dots are the outliers and the whiskers represents the range of data from the minimum to maximum.

There was no statistically significant seasonal association with the body condition for *O. angoniensis* ($\chi^2_1 = 0.12$; $P = 0.727$). However, the median vegetation height had a statistically significant association with the body condition of *O. angoniensis* ($\chi^2_1 = 5.43$; $P = 0.020$). A Spearman's correlation showed that the body condition of *O. angoniensis* and the median vegetation height had a weakly positive relationship, although it was not statistically significant ($r = 0.15$; $P = 0.422$). Likewise, regression analysis showed that median

vegetation height explained only 7.37% of the variance of the body condition of *O. angoniensis*, with a 1:0.63 relationship of median vegetation height to body condition, although this relationship was not statistically significant ($F_{1,27} = 2.15$; $P = 0.154$; Figure 14). The body condition of *O. angoniensis* was not significantly associated with sex ($\chi^2_1 = 3.40$; $P = 0.065$), the percentage of light penetrating through the vegetation ($\chi^2_1 = 0.32$; $P = 0.572$), or the interaction of season and sex ($\chi^2_1 = 0.07$; $P = 0.790$). The body condition of *M. coucha* individuals had no statistically significant associations with season ($\chi^2_1 = 0.73$; $P = 0.394$), sex ($\chi^2_1 = 1.41$; $P = 0.234$), median vegetation height ($\chi^2_1 = 0.22$; $P = 0.640$), the percentage of light penetrating through the vegetation ($\chi^2_1 = 0.05$; $P = 0.824$), or the interaction of season and sex ($\chi^2_1 = 1.04$; $P = 0.308$).

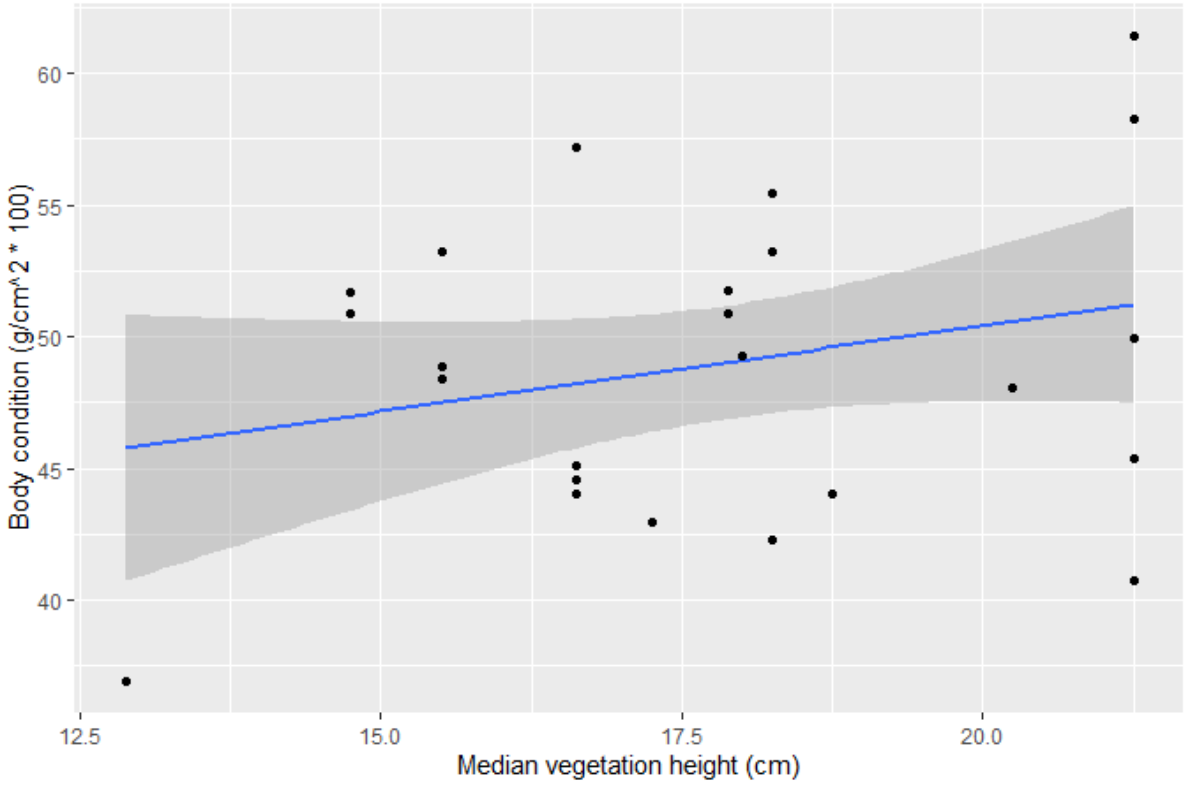


Figure 14. The relationship between the median plant height and the body condition of *Otomys angoniensis* at the Cradle Nature Reserve from October 2021 to September 2022. The trend line was not statistically significant (Spearman's correlation $r = 0.15$; $P = 0.422$).

VEGETATION CHARACTERISTICS

Three principal components were extracted from the PCA of the vegetation characteristics since they described 83.07% of all variance in the data (Table 3). From the correlation matrix, the highest positive and lowest negative values for each principle component (PC) were the median plant height and the percentage of light penetration, respectively, for principal component 1 (PC1), maximum plant height and Walker's scale for PC2 and the minimum and maximum plant height for PC3 (underlined in Table 4).

Table 3. Eigen values and variance percentages of the principal components analysis (PCA) of the vegetation characteristics in summer and winter at the Cradle Nature Reserve.

Principle component	Eigen value	Variance percentage (%)	Cumulative variance percentage (%)
PC 1	2.16	43.11	43.11
PC 2	1.21	24.28	67.39
PC 3	0.78	15.68	83.07
PC 4	0.48	9.70	92.76
PC 5	0.36	7.24	100.00

Table 4. The correlations between the principal components and the vegetation characteristics sampled by season and site at the Cradle Nature Reserve. Highest and lowest correlations between the principal components and the vegetation characteristics are in bold.

Vegetation characteristic	PC 1	PC 2	PC 3
Walker's scale	0.733	-0.521	-0.027
Percentage of light penetration	-0.783	0.271	0.310
Minimum plant height	0.530	0.514	0.604

Median plant height	0.807	0.142	0.115
Maximum plant height	0.270	0.765	-0.556

I used site as the grouping variable in the first PCA and found that the two sites overlapped with each other, indicating high similarity between the sites (Figure 15). Vegetation characteristics were spread widely across both sites in all PCs (Figure 15). In PC1 and PC2, the northern site showed a slightly higher association with taller median and maximum plant height, PC3 shows a high association between the northern site and taller minimum plant height, indicating in general that the northern site has taller vegetation (Figure 15). The southern site has a higher association with both the percentage of light penetration and the Walker's scale compared to the northern site (Figure 15B and Figure 15C). The southern site is spread relatively evenly and widely between the percentage of light penetration and Walker's scale, indication a large variation of cover within the site (Figure 15A). Whereas on the northern site the percentage of penetration and Walker's scale was not as widely distributed indicating less variation of vegetation cover (Figure 15A).

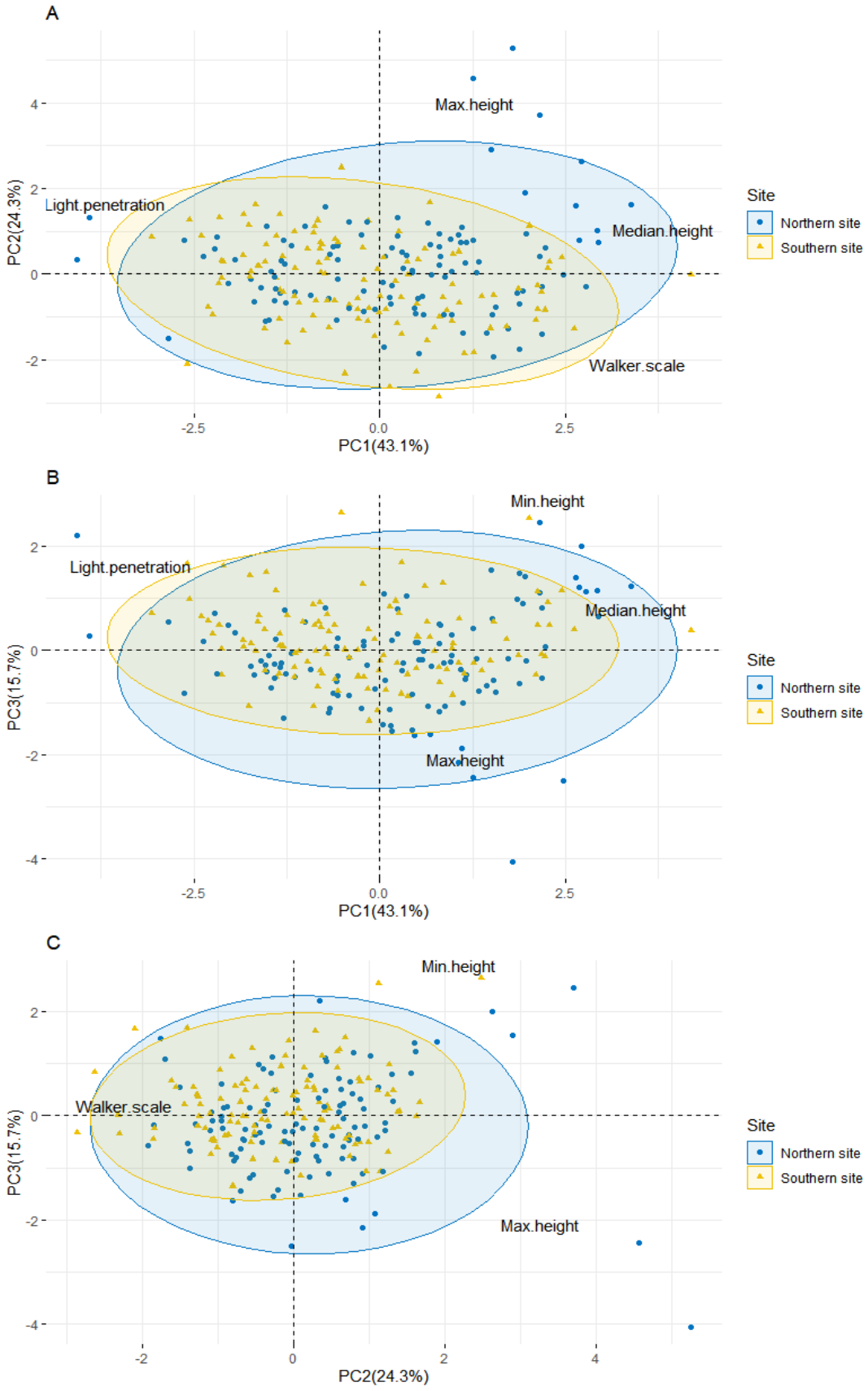


Figure 15. The principal components analysis (PCA) biplot showing the associations between the vegetation characteristics between northern and southern sites at the Cradle Nature

Reserve on the first vs second and first vs third and second vs third PC axes. A - PC1 and PC2 with the following vegetation characteristics: median plant height; maximum plant height; Walker's scale; and the light penetration. B - PC1 and PC3 with the following vegetation characteristics: minimum plant height; median plant height; maximum plant height; and Walker's scale. C - PC2 and PC3 with the following vegetation characteristics: minimum plant height; maximum plant height; and Walker's scale.

In the second PCA, I used season as the grouping variable. There was a high level of overlap between the seasons indicating similarity in vegetation between seasons (Figure 16). The summer vegetation showed a greater association with taller vegetation and higher Walker's scale than winter, while the winter vegetation is spread towards a higher percentage of light penetrating though the vegetation (Figure 16A and Figure 16B).



Figure 16. The principal components (PCA) analysis biplot showing the associations between the vegetation characteristics in summer and winter at the Cradle Nature Reserve on the first

vs second and first vs third and second vs third PC axes. A - PC1 and PC2 with the vegetation characteristics: median plant height; maximum plant height; Walker's scale and the light penetration. B - PC1 and PC3 with the vegetation characteristics: minimum plant height; median plant height; maximum plant height and Walker's scale. C - PC2 and PC3 with the vegetation characteristics: minimum plant height; maximum plant height and Walker's scale.

Both the median plant height and the maximum plant height were significantly taller at the northern site than the southern site (Table 5), whereas there were no statistically significant differences in means found between the two sites in the Walker's scale, the percentage of light penetration, or the minimum plant height (Table 5). However, between the seasons all the mean vegetation characteristics were significantly different. Compared to the winter period, the summer period had significantly higher Walker's scale, minimum plant height, median plant height and maximum plant height (Table 6). Similarly, the mean percentage of light penetrating through the vegetation in the winter period was higher than the summer period (Table 6).

Table 5. The mean (with standard deviation (SD) in parentheses) values for the vegetation characteristics and their statistical differences between the two sites at the Cradle Nature Reserve. Significant values are shown in bold.

Vegetation characteristics	Northern site	Southern site	*t*-value	df	*P*
Walker's scale	3.04 (0.80)	3.00 (0.83)	0.33	221.76	0.744
Percentage of light penetration	36.78 (19.86)	41.21 (18.68)	-1.72	221.18	0.086
Minimum height	2.46 (2.03)	2.32 (1.43)	0.61	199.55	0.543
Median height	18.67 (5.42)	16.93 (4.95)	2.52	220.15	**0.013**
Maximum height	92.45 (19.66)	81.92 (14.19)	4.60	201.96	**< 0.001**

Table 6. The mean (with standard deviation (SD) in parentheses) values for the vegetation characteristics and their statistical differences between summer and winter at the Cradle Nature Reserve. All comparisons were statistically significant.

Vegetation characteristics	Summer	Winter	*t*-value	df	*P*
Walker's scale	3.25 (0.80)	2.79 (0.77)	4.44	221.58	**< 0.001**
Percentage of light penetration	32.84 (15.09)	45.15 (21.19)	-5.01	200.57	**< 0.001**
Minimum height	3.20 (2.01)	1.58 (0.92)	7.76	155.55	**< 0.001**
Median height	19.95 (5.06)	15.65 (4.52)	6.70	219.19	**< 0.001**
Maximum height	90.68 (19.40)	83.69 (15.58)	2.97	212.12	**0.003**

RELATIONSHIP BETWEEN RODENT DENSITY, DEMOGRAPHY AND VEGETATION

From the PCA analysis of the total rodent density, rodent demography of the three most common species and the vegetation characteristics associated with the captures of the those species, four principal components were used since they accounted for 73.19% of all variance in the data (Table 7). The highest positive and lowest negative values from the correlation matrix for each principle component (PC) were the number of rodent individuals captured and the median plant height for PC1, rodent reproductive activity and rodent population size for PC2, minimum plant height and rodent body condition (BMI) PC3, and rodent age and sex ratios for PC4 (Table 8).

Table 7. Eigen values and variance percentages of the principal components analysis of the rodent density, rodent demography and vegetation characteristics variables at the Cradle Nature Reserve. The eigen values and variance percentages up to principal component (PC) 5 are shown.

Principle component	Eigen value	Variance percentage (%)	Cumulative variance percentage (%)
PC 1	5.74	38.24	38.24
PC 2	2.27	15.11	53.34
PC 3	1.66	11.06	64.41
PC 4	1.32	8.78	73.19
PC 5	1.08	7.18	80.37

Table 8. The correlation matrix between the principal components and the rodent density, rodent demography and vegetation characteristics variables. The highest and lowest correlations between the principal components and the other variable are in bold.

Variable	PC 1	PC 2	PC 3	PC 4
Total number of rodents captures	0.930	0.171	0.140	0.111
Number of rodent individuals captured	**0.978**	-0.019	-0.004	-0.013
Species richness	0.958	-0.068	-0.014	-0.067
Shannon's diversity index for rodents	0.970	0.093	0.117	0.030
Simpson's diversity index for rodents	0.954	0.141	0.153	0.061
Population size	0.220	**-0.525**	0.409	0.312
Sex ratios	-0.320	-0.084	-0.375	**-0.402**
Agee	-0.095	0.254	-0.198	**0.807**
Reproductively activity rodents	-0.092	**0.726**	-0.183	0.379
BMI (body condition)	-0.190	0.317	**-0.649**	0.108
Walker's scale	-0.312	-0.464	0.177	0.389
Light penetration through vegetation	0.531	0.526	-0.103	-0.238
Minimum plant height	-0.416	0.407	**0.570**	-0.114
Median plant height	**-0.576**	0.250	0.518	0.005
Maximum plant height	-0.237	0.712	0.407	-0.096

Relationship between density, demography and vegetaion between species

Overall, *G. leucogaster, O. angoniensis* and *M. coucha* tended to follow similar trends, and overlapped substantially with one another, especially *G. leucogaster* and *O. angoniensis*, which grouped closely together in almost all comparisons (Figure 17, Figure 18 and Figure 19). *Otomys angoniensis* had the widest spread across the variables in all the PCA biplots, while *M. coucha* had the smallest spread across the variables in all the PCA biplots (Figure 17, Figure 18 and Figure 19). In both *G. leucogaster* and *O. angoniensis*, the data points split into two distinct clusters across PC1 axis (Figure 17A, Figure 17B and Figure 19A). Since PC1 was associated with median plant height and total number of captures, *G. leucogaster* and *O. angoniensis* were either associated with taller median plant heights, or a higher number of individuals of all rodent species (Figure 17A, Figure 17B and Figure 19A). In comparison, *M. coucha* showed patterns of having a high association with a high number of captured rodent individuals of all species, large population sizes and low BMI scores (Figure 17A, Figure 17B and Figure 18A).

Population sizes of *G. leucogaster* were smaller than *M. coucha*, and the ratio of reproductively active rodents was higher for *G. leucogaster* than for *M. coucha* (Figure 17A, Figure 18A and Figure 18B). *Otomys angoniensis* had a smaller population size than *M. coucha* and was less reproductively active than *G. leucogaster* (Figure 17A, Figure 18A and Figure 18B). Reproductively active *G. leucogaster* individuals also tended to have higher BMI scores (Figure 18A). Overall, *O. angoniensis* had a higher BMI score compared to the other two rodent species (Figure 17B, Figure 18A and Figure 19B). All three rodent species favoured a male to female sex ratio according to the PCA (Figure 18B, Figure 19A and Figure 19B).

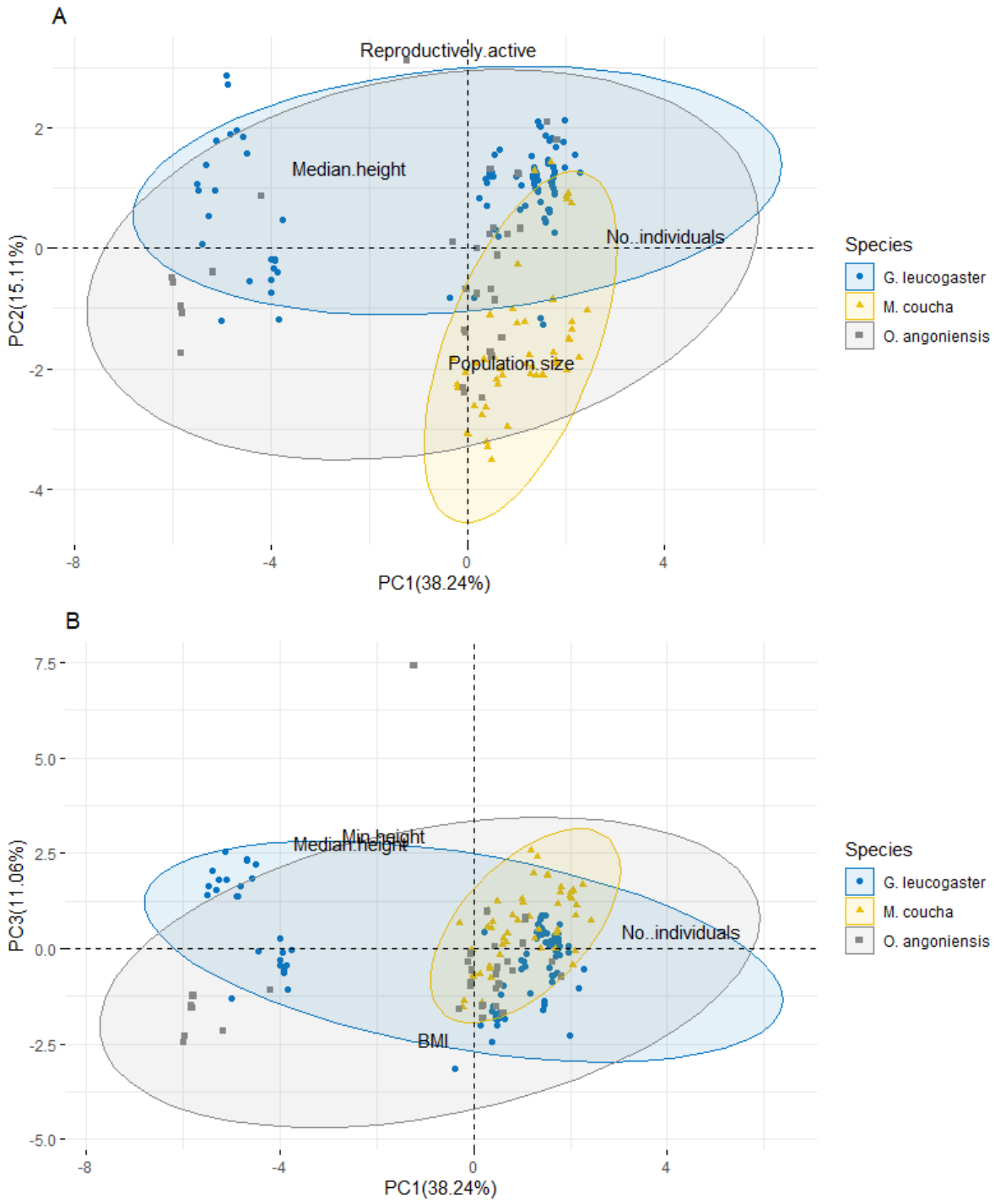


Figure 17. The principal components analysis (PCA) biplot, showing the relationship between rodent density, rodent demography and vegetation characteristics between *Gerbilliscus leucogaster, Mastomys coucha* and *Otomys angoniensis* on the first vs second and first vs third PC axes. A - PC1 and PC2 with the total number of rodent individuals captured (no. individuals); the median vegetation height (PC1, highest and lowest respectively); rodent reproductive activity (reproductively active) and rodent population size (PC2 highest and lowest respectively). B - PC1 and PC3 with the total number of rodent

individuals captured (no. individuals); the median vegetation height (PC1 highest and lowest respectively); minimum vegetation height and rodent body condition (BMI; PC3 highest and lowest respectively).

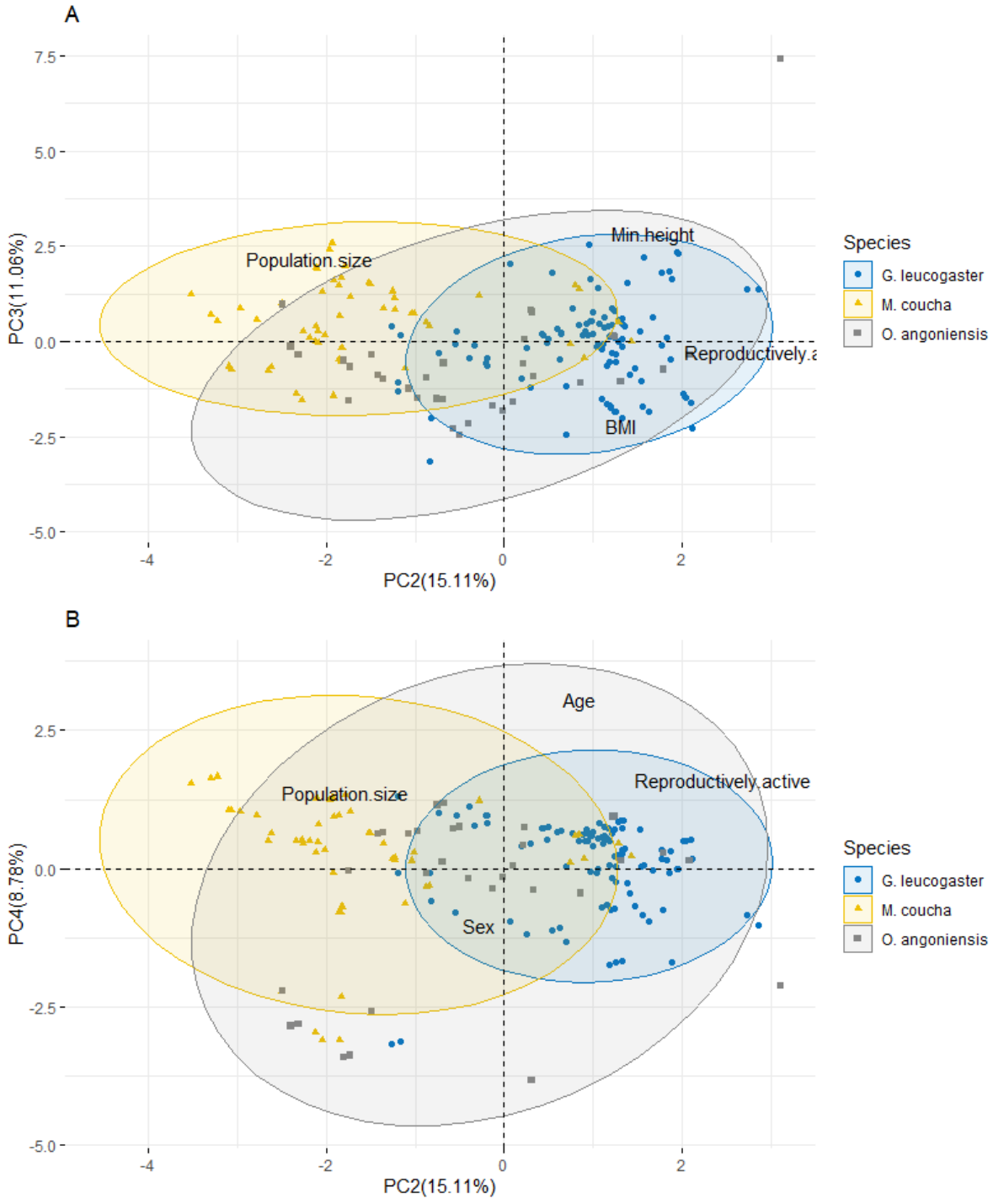


Figure 18. The principal components analysis (PCA) biplot, showing the relationship between rodent density, rodent demography and vegetation characteristics between

Gerbilliscus leucogaster, Mastomys coucha and *Otomys angoniensis* on the first vs second and first vs third PC axes. A - PC2 and PC3 with the rodent reproductive activity (reproductively active); population size (PC2 highest and lowest respectively); minimum vegetation height (min height); and rodent body condition (BMI; PC3 highest and lowest respectively). B - PC2 and PC4 with the rodent reproductive activity (reproductively active); population size (PC 2 highest and lowest respectively); age and sex ratios (PC4 highest and lowest respectively).

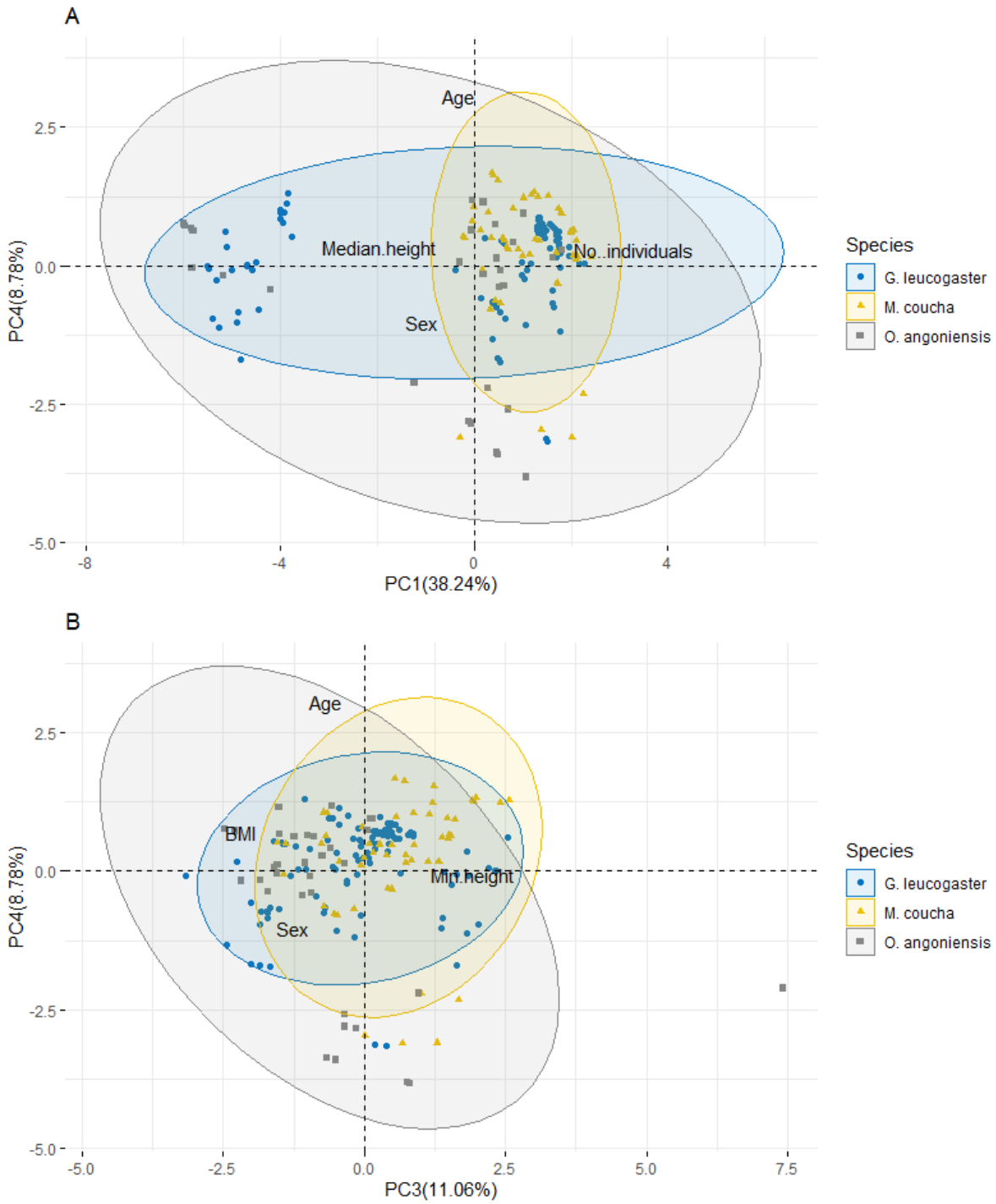


Figure 19. The principal components analysis (PCA) biplot, showing the relationship between rodent density, rodent demography and vegetation characteristics between *Gerbilliscus leucogaster, Mastomys coucha* and *Otomys angoniensis* on the first vs second and first vs third PC axes. A - PC1 and PC4 with the total number of rodent individuals captured (no. individuals); the median vegetation height (PC1 highest and lowest respectively); age and sex ratios (PC4 highest and lowest respectively). B - PC3 and PC4

with the minimum vegetation height (min height); rodent body condition (BMI; PC3 highest and lowest respectively); age and sex ratios (PC4 highest and lowest respectively).

Relationship between density, demography and vegetaion between seasons

Overall, the two seasons overlapped substantially with one another (Figure 20, Figure 21 and Figure 22) in terms of the total number of rodent individuals, population size, sex, age, reproductive activity, BMI, minimum vegetation height and median vegetation height. The general trends showed that summer was associated with taller minimum and median height plants (Figure 20B, Figure 21A, Figure 22A and Figure 22B) and a higher proportion of reproductively active rodents (Figure 20A, Figure 21A and Figure 21B). In contrast, winter was associated with larger rodent population sizes (Figure 20A, Figure 21A and Figure 22B) and high rodent BMI (Figure 20B, Figure 21A and Figure 21B). The age and sex ratios of rodents seasonally overlapped, with both seasons showing a high adult to juvenile ratio and a high male to female ratio (Figure 21B, Figure *22*A and Figure 22B). Summer had slightly more adults and males than winter (Figure 21B, Figure *22*A and Figure 22B). Winter had slightly more juveniles and more females than summer (Figure 21B, Figure *22*A and Figure 22B)



Figure 20. The principal components analysis (PCA) biplot, showing the relationship between rodent density, rodent demography and vegetation characteristics in summer and winter on the first vs second and first vs third PC axes. A - PC1 and PC2 with the total number of rodent individuals captured (no. individuals); the median vegetation height (PC1, highest and lowest respectively); rodent reproductive activity (reproductively active) and rodent population size (PC2 highest and lowest respectively). B - PC1 and PC3 with the total number of rodent individuals captured (no. individuals); the median vegetation height (PC1

highest and lowest respectively); minimum vegetation height and rodent body condition (BMI; PC3 highest and lowest respectively).

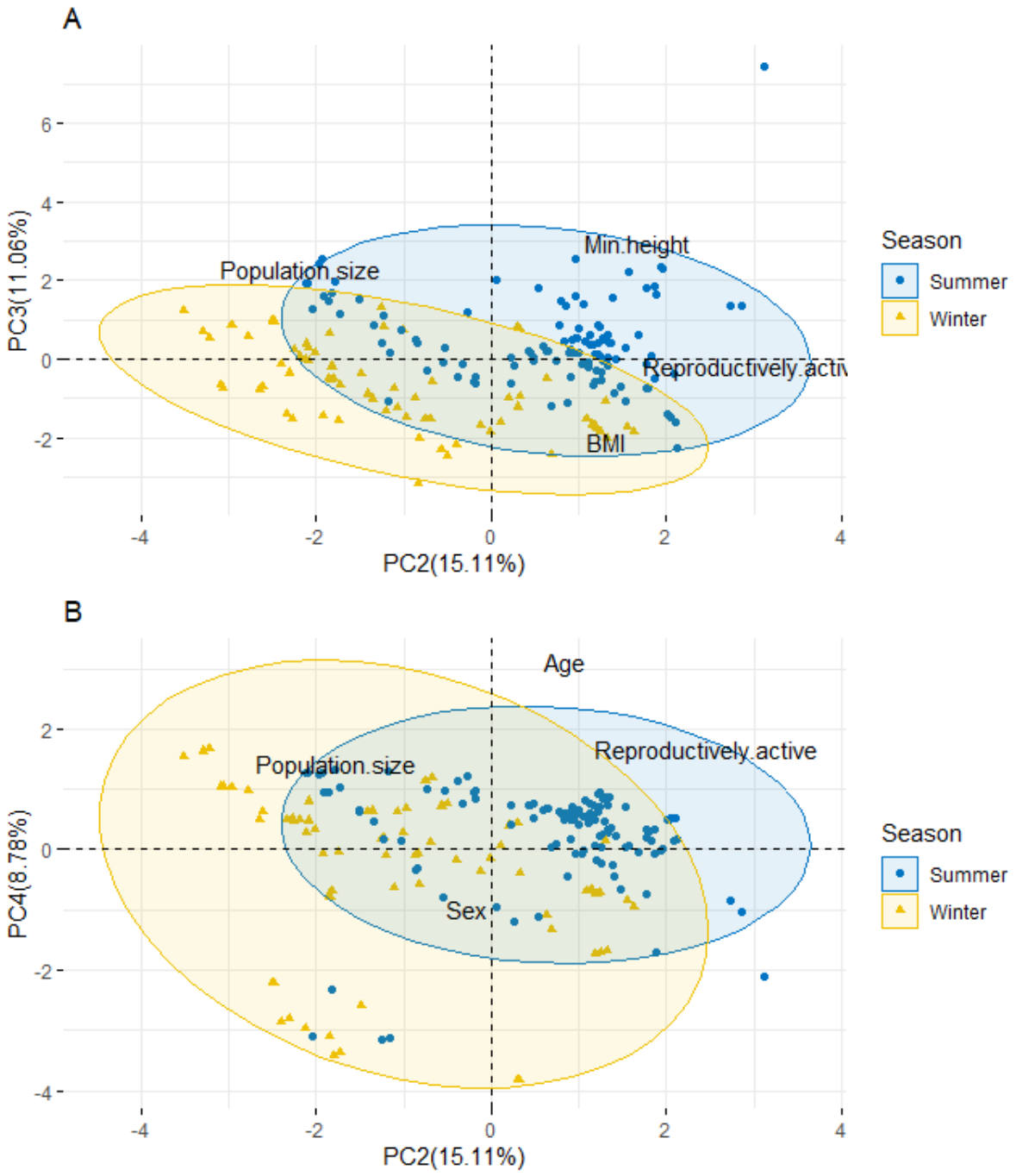


Figure 21. The principal components analysis (PCA) biplot, showing the relationship between rodent density, rodent demography and vegetation characteristics in summer and winter on the second vs third and second vs fourth PC axes. A - PC2 and PC3 with the rodent reproductive activity (reproductively active); population size (PC2 highest and lowest

respectively); minimum vegetation height (min height) and rodent body condition (BMI; PC3 highest and lowest respectively). B - PC2 and PC4 with the rodent reproductive activity (reproductively active); population size (PC 2 highest and lowest respectively); age and sex ratios (PC4 highest and lowest respectively).

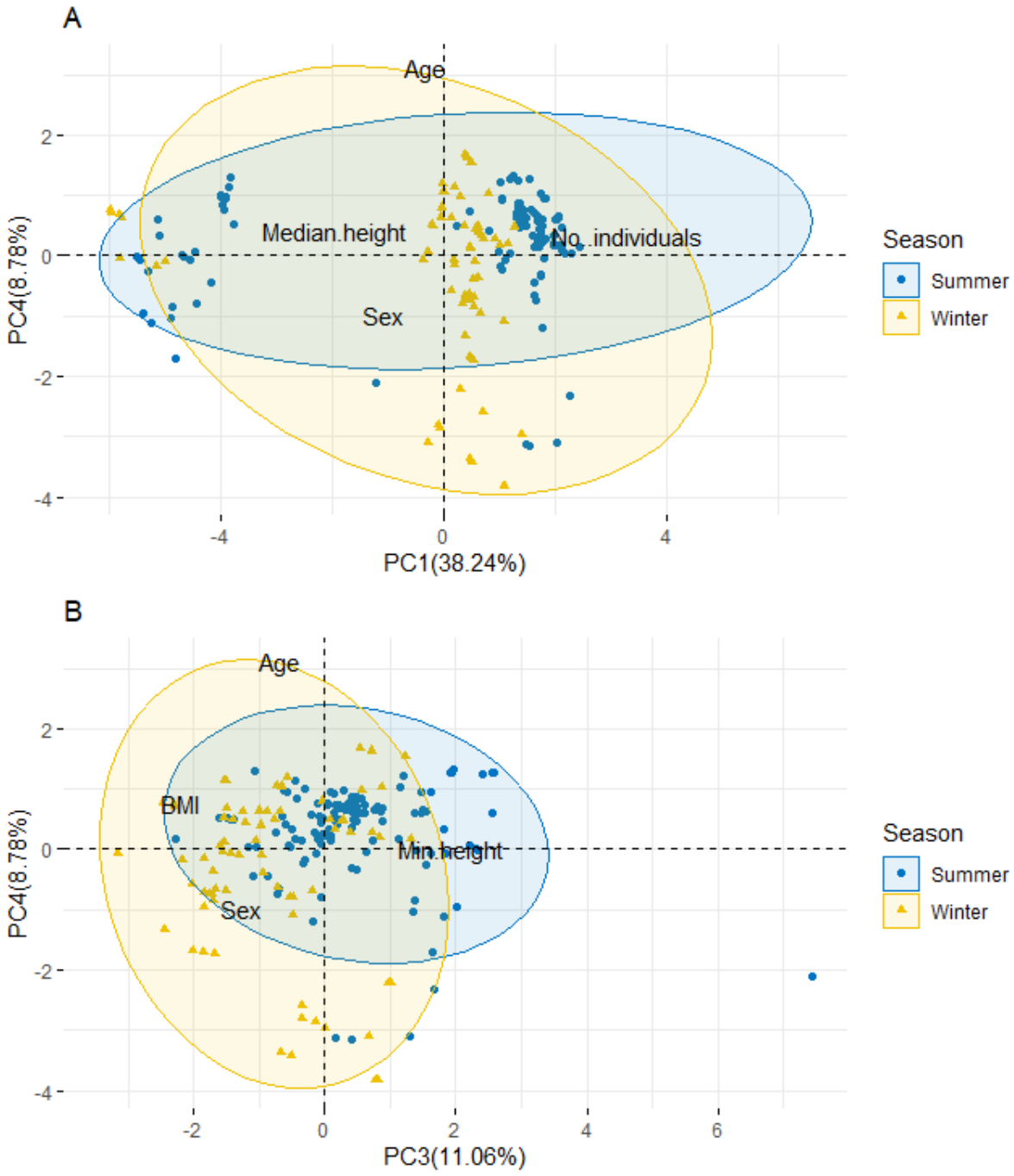


Figure 22. The principal components analysis (PCA) biplot, showing the relationship between rodent density, rodent demography and vegetation characteristics in summer and

winter on the on the first vs forth and third vs forth PC axes. A - PC1 and PC4 with the total number of rodent individuals captured (no. individuals); the median vegetation height (PC1 highest and lowest respectively); age and sex ratios (PC4 highest and lowest respectively). B - PC3 and PC4 with the minimum vegetation height (min height); rodent body condition (BMI; PC3 highest and lowest respectively); age and sex ratios (PC4 highest and lowest respectively).

DISCUSSION

I investigated the population demography and habitat selection of nocturnal rodents in two grassland sites in the Cradle of Humankind, South Africa. I sampled six species of rodents, all of which occurred within their known distributions on savannah grasslands (Happold, 2013; Monadjem et al., 2015). The most abundant species captured was *Mastomys* coucha, followed by *Gerbilliscus leucogaster*, which are commonly found together in high abundances within their overlapping distributions (Makundi *et al.*, 2005; Odhiambo *et al.*, 2005; Avenant *et al.*, 2008; Massawe *et al.*, 2011); in the discussion which follows I provide information on *Mastomys coucha* if such information is available for this species in the literature, otherwise I provide information for the genus *Mastomys*. The remaining four species, *Otomys angoniensis, Lemniscomys rosalia, Micaelamys namaquensis* and *Mus minutoides* all had relatively low abundances. Low abundances for *O. angoniensis* are relatively common in other parts of their distribution (Schwan, 1986; Bronner and Meester, 1988; Njunwa *et al.*, 1989; Monadjem and Perrin, 2003; Avenant, 2011), whereas the abundance of *L. rosalia, M. namaquensis* and *M. minutoides* are more variable in other parts of their distribution (Monadjem and Perrin, 2003; Avenant *et al.*, 2008; Avenant, 2011; Delcros *et al.*, 2013; Fagir *et al.*, 2014).

The rodent species richness and diversity indices did not differ between the two sampling sites. This could potentially suggest that the two habitats were somewhat similar in complexity. August (1983) defines habitat complexity as a measure of vertical vegetational strata, where highly complex habitats have dense and tall vegetation strata and simple habitats have very reduced vegetational strata. Grasslands are suggested to be comparatively simple in complexity (August, 1983; Adler, 1995; Ribeiro *et al.*, 2019). Mammal diversity is positively correlated with habitat complexity, as more complex habitats are able to support more species and individuals (August, 1983; Horváth *et al.*, 2001; Ortiz-Burgos, 2015), although August (1983) found that small mammals, such as rodents, showed little association with habitat complexity. Adler (1995) found that higher rodent densities were better associated with dense grass cover than vertical development of vegetation above the grass cover (i.e. trees and shrubs) in grasslands. Consequently, grassland habitats with similar richness or diversity indices are likely to have similar vertical vegetation characteristics (complexity).

However, the composition of rodent species at the two sites and the presence of specific species suggest differences in integrity between the sites (Avenant, 2011). Integrity is defined as the quality or condition of something in relation to its original or pristine condition (Karr, 1996); ecological integrity is the support and maintenance of the integrity of all interacting biotic and abiotic factors within a habitat (Karr and Dudley, 1981; Karr, 1996; Dorren *et al.*, 2004). An indicator of good ecological integrity is the presence of specialist species, which are habitat specific, such as *Otomys angoniensis, Micaelamys namaquensis* and *Mus minutoides* (Avenant, 2011). *Otomys angoniensis* and *Micaelamys namaquensis* were found at both sites, but *O. angoniensis* dominated in the northern site, with the highest number of captured individuals in that site. In contrast, the specialist, *M. minutoides*, was sampled only at the southern site, which may indicate that the southern site had better ecological integrity than the northern site as it had more specialist species (Avenant, 2011). However, the southern site was also the site where *M. coucha* was present. The presence of *M. coucha* here suggests that the site has a low ecological integrity since this species is an indicator of disturbance (or low ecological integrity) (Skinner and Chimimba, 2005; Avenant and Cavallini, 2007; Avenant *et al.*, 2008; Avenant, 2011). Even though the southern site has a higher number of specialists, these specialists were found in small numbers, whereas the generalist species, *M. coucha*, was found to numerically dominate the site, and the higher the proportion of *M. coucha* the lower the ecological integrity (Avenant and Cavallini, 2007; Avenant *et al.*, 2008). The absence of *Mastomys* spp. in southern Africa is also considered an indicator of good ecological integrity within a habitat (Avenant, 2011). Therefore, the northern site could be considered to have a better ecological integrity even though it had a lower abundance of rodents (Avenant and Kuyler, 2002; Monadjem and Perrin, 2003).

The southern site had a larger range, lower minimum and higher maximum measures, of vegetation height and cover, which suggests a more complex habitat in comparison to the northern site (Ortiz-Burgos, 2015). The larger range of vegetation cover provides a variety of cover that is able to support a greater number of species since it can support species that are highly dependent on dense cover, such as *O. angoniensis* (Green and Taylor, 1975; Bronner and Meester, 1988) and species which are less dependent on cover such as *Mastomys* spp. (Green and Taylor, 1975; Monadjem and Perrin, 1998). The southern site had significantly taller vegetation that could support a greater number of individuals because taller vegetation can provide a greater abundance of food for grassland rodents (Delcros *et al.*, 2013).

The rodent richness and diversity indices did not differ significantly between the designated seasons (summer and winter), which was unexpected since most rodent survey studies report significant diversity increases in winter, after the wet season. Avenant and Kuyler (2002) and Monadjem and Perrin (2003) found rodent diversity and richness reached its peak in late winter in the subtropical grasslands of Eswatini (formally Swaziland). In southwestern Tanzania, rodent densities are highest in winter, with a peak in the late winter in cultivated land (Makundi *et al.*, 2005; Odhiambo *et al.*, 2005, 2008), grasslands and woodlands (Makundi *et al.*, 2005). In a cross-country comparative study between Tanzania, Namibia and Swaziland, Massawe *et al.* (2011) found the highest abundance of rodent species after the wet season in fallowed land near rural communities. Avenant and Cavallini (2007), Avenant *et al.* (2008) and Avenant (2011) found that rodent species abundance and densities in grasslands in the Free State Province, South Africa were at their highest after the breeding season in late autumn and early winter. In KwaZulu-Natal Province, Delcros *et al.* (2013) found that rodent diversity in the savannah was at its highest in winter. Abundance increases in the dry season are usually a consequence of increased population sizes following the breeding season (wet season) (Makundi *et al.*, 2005; Odhiambo *et al.*, 2005, 2008; Massawe *et al.*, 2011), a delayed response to the abundance of food availability in the wet season (Massawe *et al.*, 2011; Delcros *et al.*, 2013), or the decrease in food availability in the dry season resulting in a higher attraction to the bait in traps (Avenant and Cavallini, 2007; Avenant, 2011; Delcros *et al.*, 2013).

Vegetation varied seasonally, with summer having taller vegetation and more cover. Northwest and Gauteng Provinces are characterised by summer rainfall. The onset of the rainy season triggers vegetation growth, which provides murids with a source of food and cover (Taylor and Green, 1976). Delcros *et al.* (2013) found a significant positive correlation between rodent composition and vegetation characteristics such as grass height and cover in the KwaZulu-Natal savannah. Taller grasses are linked to an abundance of food for rodents (Jacob, 2008).

Summer was associated with a high reproductive activity and taller vegetation. Gonadal development of seasonal breeders is linked to the abundance of food brought on by the wet season (Muteka *et al.*, 2006; Dooley and Prendergast, 2012; Muteka *et al.*, 2019). Seasonal gonadal development begins in early spring for seasonal breeders such as *G. leucogaster* (Muteka *et al.*, 2019) and *M. namaquensis* (Muteka *et al.*, 2006). Dooley and Prendergast

(2012) found that rationing food of Siberian hamsters (*Phodopus sungorus*) in their reproductive season suspended the onset of gonadal development and once food became abundant, gonadal development initiated as normal. A higher abundance of food extends the breeding season of rodents (Taylor and Green, 1976). The onset of the breeding season in the wet summer period results in increases of rodent abundances in the dry winter season due to juvenile recruitment (Perrin, 1980).

Two of the species sampled in this study, *M. coucha* and *L. rosalia,* were the only seasonal breeders that showed an expected abundance increase in winter (Monadjem and Perrin, 1997, 2003; Avenant *et al.*, 2008; Delcros *et al.*, 2013). *Micaleamys namaquensis* is a seasonal breeder (Muteka *et al.*, 2006) and although the number of individuals remained consistent between seasons, the total captures for the species increased in winter. This suggests that individuals were recaptured more frequently in winter. This potentially could be due to the reduced availability of resources in the dry period, as food becomes scarce in winter but energy requirements increase with decreasing temperatures and traps had an abundance of nutrient rich food (Avenant, 2011; Delcros *et al.*, 2013).

Otomys angoniensis did not restrict its breeding to the wet season and is known to breed throughout the year (Taylor and Green, 1976; Bronner and Meester, 1988). Although breeding occurs year-round, the proportion of breeding varies seasonally, where breeding peaks in the wet summer period and decreases in early winter (Bronner and Meester, 1988). The breeding strategies of Otomyinae show a low reproductive effort, with small litter sizes and long gestation periods (Perrin, 1980; Willan and Meester, 1989; Phillips *et al.*, 1997). Although, compared to its sister species, *O. irroratus* and *O. sloggetti robertsi, O. angoniensis* has a higher reproductive effort, larger litter size and shorter gestation period (Phillips *et al.*, 1997). The difference in breeding is suggested to be a result of habitat selection, since *O. angoniensis* occurs in comparatively harsher habitats due to greater seasonal variability in resources (Phillips *et al.*, 1997). A higher level of seasonal variability results in the cyclic abundance of food sources and predation that affect mortality (Andreassen *et al.*, 2021). Therefore, to overcome the effects of seasonal variability, *O. angoniensis* has a breeding strategy favouring increased reproductive activity, with seasonal peaks of slight declines in the winter (Bronner and Meester, 1988; Phillips *et al.*, 1997). Although the reproductive activity of *O. angoniensis* is higher than its sister species, it is considerably lower than *G. leucogaster* (Odhiambo *et al.*, 2008) and *M. coucha* (Jackson and

Van Aarde, 2004), the other common species sampled in my study. Due to the small litter sizes and long gestation period of *O. angoniensis*, population sizes remained low throughout the year (Perrin, 1980).

The number of *O. angoniensis* captures increased in winter in my study. This could be due to the increase in population size following the peak in the breeding season, or the reduction of resources in the dry winter. *Otomys angoniensis* is reported to be trap shy (Taylor and Green, 1976; Happold and Happold, 1986; Schwan, 1986; Bronner and Meester, 1988; Monadjem, 1997a) and therefore its increase in winter is most likely due to the species entering the traps in response to the decreased resource availability in the dry season (Avenant, 2011; Delcros *et al.*, 2013).

The numbers of *M. minutoides and G. leucogaster* decreased during the dry winter season, which is uncharacteristic of these species. *Mus minutoides* in the subtropical grasslands of Swaziland occurred in high numbers in winter, but the species disappeared in the summer (Monadjem, 1999). Delcros *et al.* (2013) found that both *M. minutoides* and *G. leucogaster* in the KwaZulu-Natal Province savannah had the highest abundance in winter. Similarly, *G. leucogaster* reached its peak abundance in fallowed land in Namibia (Massawe *et al.*, 2011) and Tanzania (Odhiambo *et al.*, 2008) after the wet season. The increase in rodent abundance in winter, following breeding, results from juvenile recruitment (Shilereyo *et al.*, 2020). Therefore, the decrease in *M. minutoides* abundance in winter may be due to the lightness in body mass of the juveniles, since juveniles of this species weigh less than 5 g which may have been too light to set off the traps. Alternatively, Monadjem and Perrin (2003) found that the abundance of *M. minutoides* was negatively correlated with rainfall. The *La Niña* event in 2022, which resulted in significantly higher rainfall (Jones, 2022), could have impacted this species by reducing its population. Similarly the decline in *G. leucogaster* numbers could be a response to the increased rainfall experienced in the wet season during the *La Niña* event in 2022. Reed *et al.* (2007) found that increased rainfall reduced the survival of *Peromyscus maniculatus* pups and juveniles in the mixed-grass prairies of Kansas in North America. Therefore, a reduction in the juvenile cohort will result in a decline in the overall abundance of the species.

The population size of *G. leucogaster* typically declines with increased overhead cover (Blaum *et al.*, 2007), but I found the opposite relationship. This negative correlation with cover is usually linked to perceived predation risk (Wywialowski, 1987; Brown *et al.*, 1988;

Vibe-Petersen *et al.*, 2006; Loggins *et al.*, 2019). Laboratory studies have shown that increased predation risk results in decreased foraging in *G. leucogaster* (Rymer *et al.*, 2021). Since the vegetation cover was reduced in winter in my study, perceived predation risk is likely to have increased (Wywialowski, 1987; Loggins *et al.*, 2019). Therefore, to avoid predation, *G. leucogaster* may have spent more time under denser vegetation cover. As a generalist species, *G. leucogaster* is able to shift its behaviour to forage on less favourable food sources under vegetation cover, thereby avoiding open areas with a higher perceived predation risk (Wywialowski, 1987). This shift in behaviour may have resulted in *G. leucogaster* avoiding traps set in open areas.

Otomys angoniensis showed a more stable population size between the seasons, although population sizes were small overall. This is characteristic of the genus *Otomys,* as seen by Perrin (1980) in the Eastern Cape Province, and Willan and Meester (1989) in many areas in southern Africa. The stable populations of some *Otomys* spp. are owed to their year–round breeding pattern (Taylor and Green, 1976; Bronner and Meester, 1988; Phillips *et al.*, 1997). This might explain why there was no seasonal associations in the population size, age and reproductive activity of *O. angoniensis* in my study. Due to the year-round breeding of *O. angoniensis,* the ratio of juveniles to adults was relatively consistent throughout the year in my study, as reported by Perrin (1980). The body condition of *O. angoniensis* did not differ by season. This pattern is predictable for *Otomys* spp. since they have a stable herbaceous diet, facilitated by caecal fermentation, which enables them to live a low energy lifestyle with prolonged breeding and longevity (Perrin, 1980, 1981). The body condition of *O. angoniensis* in this study was associated by plant height, with higher BMI measures associated with taller grass heights. Tall grasses and dense cover are associated with an abundance of food (Delcros *et al.*, 2013). In addition, a regular food supply results in less seasonal variability in the body condition of *Otomys* spp. (Perrin, 1981). *Otomys* spp. is known to be highly dependent on dense vegetation cover (Green and Taylor, 1975; Monadjem, 1997a; Bronner and Meester, 1988). Dense cover reduces predations risk (Wywialowski, 1987; Loggins *et al.*, 2019). Specialists are limited in their habitat choices since they are unable to adjust to unfavourable habitats where predation is high (Wywialowski, 1987). Predator avoidance mechanisms are especially important for *O. angoniensis* since it is prey for avian predators, such as owls, making up a large proportion of the biomass found in owl pellets (Happold and Happold, 1986).

A common feature in *O. angoniensis* and *G. leucogaster* was their negative association between reproductive activity and population sizes, although the reason for this association differs between the species. The population size of *G. leucogaster* decreased after the breeding season and *O. angoniensis* had a low reproductive effort (as discussed above). High BMI was associated with reproductively active *O. leucogaster* and *G. leucogaster*. This was expected because body weight fluctuates with the onset of breeding (Korn, 1989), as gonadal mass and pregnancies in females add to the overall body weight of the rodents (Korn, 1989; Muteka *et al.*, 2019). For seasonal breeders, such as *G. leucogaster,* gonadal development is triggered by the availability of food during the wet season (Dooley and Prendergast, 2012; Muteka *et al.*, 2019), whereas for year-round breeders, such as *O. angoniensis,* there are only slight fluctuations in gonadal mass, which is facilitated by the availability of vegetation (Bronner and Meester, 1988).

Mastomys coucha did not show any significant associations linked with seasonal vegetation height or cover for population size, sex ratios, age, reproductive activity or body condition. Its population sizes were high, in both seasons, which is uncharacteristic of the genus. *Mastomys* spp. is known for seasonal population fluctuations, where their population declines in the wet summer and steeply increases in the dry winter, as occurs in the savannah in KwaZulu-Natal Province (Delcros *et al.*, 2013), the grasslands in Eswatini (Monadjem and Perrin, 2003), in the maize fields of Tanzania (Vibe-Petersen *et al.*, 2006), and the fallow lands in Tanzania, Namibia and Eswatini (Massawe *et al.*, 2011). This is due to their breeding season being triggered by abundance of food stimulated by rainfall (Makundi *et al.*, 2005; Odhiambo *et al.*, 2005; Massawe *et al.*, 2011). In my study, the rainfall was higher than usual due to the *La Niña* event in 2022. This high rainfall could have extended the breeding season and increased the abundance of food which would have supported a larger number of *M. coucha* individuals (Taylor and Green, 1976). Therefore, the increase in food abundance could have triggered an increase in *M. coucha* since the genus prioritises reproduction over survival in some parts of its distributional range (Lima *et al.*, 2003). Although the population sizes of *M. coucha* were large, reproductive activity was relatively low in the sampled individuals. This could be due to most of the captures taking place in winter, after the breeding season, or early summer before breeding began.

Winter was associated with larger population sizes, but it was also associated with high BMI. Perrin (1980) found that the body fat of the seasonal breeder *Rhabdomys pumilio* was higher

in winter, associated with a negative correlation between body fat and male breeding. The sex ratio favoured males in both seasons for *M. coucha* and *G. leucogaster.* This could explain the increase in BMI in winter, the non-breeding season, as body fat is increased in non-breeding males, and males made up the larger proportion of the population. In contrast, more females than male *O. angoniensis* were sampled in winter, and Perrin (1980) stated that female *Otomys irroratus,* a sister species of *O. angoniensis,* had higher body fat compared to males. Therefore, the higher proportion of females (the sex with a higher body fat) influences the higher BMI seen in winter. However, the BMI of both *M. coucha* and *O. angoniensis* was not influenced by sex or season. Similarly, season and vegetation characteristics did not influence the age or sex ratios of *G. leucogaster, O. angoniensis* and *M. coucha.*

The population increase in *M. coucha* could have contributed to the population decrease in *G. leucogaster,* since *M. coucha* dominated the habitat and may have led to *G. leucogaster* shifting its home range to avoid density dependent competition (Brown, 1989b). *Mastomys* spp. and *G. leucogaster* are often captured in the same habitats, but *Mastomys* spp. tend to dominate. Makundi *et al.* (2005) and Odhiambo *et al.* (2005) captured *Mastomys natalensis* and *G. leucogaster* in the same habitats, in southwestern Tanzania, where *M. natalensis* had high seasonal population fluctuations and *G. leucogaster* had a relatively small population with minimal fluctuations. In the grasslands of the Free State Province, *G. leucogaster* and *M. coucha* are often captured in the same habitats, but at different abundances (Avenant and Cavallini, 2007; Avenant *et al.*, 2008; Avenant, 2011). Avenant *et al.* (2008) found that *G. leucogaster* occurred more often in habitats with high ecological integrity, and *M. coucha* had the opposite relationship, occurring most often in habitats with the lowest ecological integrity.

Gerbilliscus leucogaster and *Mastomys coucha* are more likely to coexist than compete due to their body size difference (Adler, 1995). Rodent species of different body sizes are unlikely to compete more intensely than those of similar body sizes, allowing rodents of different body sizes to coexist (Bowers and Brown, 1982; Adler, 1995). This could explain the coexistence of the small sized *M. coucha,* the medium sized *G. leucogaster* and the large sized *O. angoniensis* in my study. Body size difference may also facilitate temporal coexistence through foraging efficiency, where larger sized rodents are more efficient at foraging at low resource densities and smaller sizes species are more efficient at times of high resource densities (Brown, 1989a; Perrin and Kotler, 2005). Similarly, species with a higher

reproductive effort are more efficient at foraging at high resource density, while those with low reproductive effort are more efficient at foraging at low resource density (Perrin and Kotler, 2005). Therefore, the small sized, high effort reproducer, *M. coucha,* can temporally coexist with the large sized, low effort reproducer, *O. angoniensis*. This leaves *G. leucogaster,* whose body size and reproductive effort lie between *M. coucha* and *O. angoniensis.*

Differences in diet preference can also facilitate coexistence between rodents (Perrin and Kotler, 2005; Kinahan and Pillay, 2008). *Otomys angoniensis* is a strict herbivore (Monadjem, 1997a), whereas both *G. leucogaster* and *Mastomys* spp. are omnivores, and therefore their diets consist of different proportions of seeds, foliage and arthropods, based on preference and gut morphology (Monadjem, 1997a; Kinahan and Pillay, 2008). *Mastomys* spp. has a gut morphology and preference favouring the consumption of more seed than foliage and very little arthropods, and is classified as a granivore-herbivore (Monadjem, 1997a; Kinahan and Pillay, 2008). In contrast, *G. leucogaster* has a gut morphology that allows for a higher consumption of foliage but still allows for a large proportion of seeds, as well as arthropods (Monadjem, 1997a; Kinahan and Pillay, 2008). Therefore, the herbivorous *O. angoniensis*, granivore-herbivorous *Mastomys* spp. and omnivorous *G. leucogaster* are able to coexist as a consequence of dietary partitioning.

Coexistence can occur between habitat specialist species and generalist species, but this is density dependent (Morris, 1996; Büchi *et al.*, 2014). Generalists are able to occupy parts of a habitat that have not been inhabited by specialists and several specialists can coexist if they do not have overlapping niches (Adler, 1995; Morris, 1996; Büchi *et al.*, 2014). *Otomys angoniensis* is a known specialist (Avenant, 2011; Perrin, 1980) and *G. leucogaster* can be considered a habitat specialist as it occurs in areas with sandy soils (Skinner and Chimimba, 2005; Avenant, 2011) while *M. coucha* is a generalist (Skinner and Chimimba, 2005; Avenant, 2011). Therefore, all three of the species should be able to coexist.

Overall, the species sampled in this study had different associations with their habitat, which resulted in different habitat selection decisions. Although they did show a high proportion of overlap in their habitat associations, which is to be expected because they occupied the same habitat, the species could have influenced the habitat selection decisions of other species because of density-dependent factors or being ecosystem engineers. Ecosystem engineers are species that physically create or maintain certain aspects of a habitat that benefit other species

(Davidson *et al.*, 2012). In my study, *O. angoniensis* created runway systems in dense vegetation, which likely provided travel routes for many other species when moving between resource patches (Bronner and Meester, 1988). *Gerbilliscus leucogaster* is a burrowing species whose burrows are often used by other species as nest sites and shelter from predation (Davidson *et al.*, 2012). Therefore, studying these species and understanding the factors influencing habitat selection will allow for further studies into other fields such as population or species conservation, as these species play important roles in the ecosystem (Montgomery and Roloff, 2017).

CONCLUSIONS AND RECOMMENDATIONS

In summary, rodent richness and diversity indices did not differ significantly between sites or seasons which is contrary to my predictions. For population demography, *G. leucogaster* had a larger population size and higher reproductive activity in summer in support of my prediction, while *M. coucha* and *O. angoniensis* showed no statistically significant differences between seasons for either population size or reproductive activity, which did not support my prediction. The predictions for sex ratios (predicted no significant differences between seasons) and age ratios (predicted to favour adults in both seasons) were supported for all three study species. Although predictions for body condition to be greater in summer were not supported in *M. coucha* and *O. angoniensis*. *Gerbilliscus leucogaster* displayed a better body condition during the winter than the summer which too contradicts my predictions. Vegetation characteristics did differ by season, as predicted: summer vegetation was taller and summer density of cover was greater than in winter. Predictions for differences in vegetation cover between sites were supported: the southern site had a higher density of cover than the rockier northern site. While predictions of differences in vegetation heights between sites were not supported, since the northern site had taller vegetation than the southern site. In general, considering all the tested parameters together there is evidence to support the prediction that parameter measures (density, demography or vegetation characteristics) are directly proportional to one another, such as the relationship between plant height and rodent reproductive activity; taller vegetation heights are associated with higher rodent reproductive activity in summer. Although this prediction has varying support and opposition when looking at the study species individually. *Gerbilliscus leucogaster* and *M. coucha* showed an inverse relationship between population size and reproductive activity. However, in *O. angoniensis*, this relationship was directly proportional, supporting the prediction.

In conclusion, population demography and habitat selection for the three most common rodent species captured at the Cradle Nature Reserve, Krugersdorp, was species specific. Each of the species selected the same habitat for different reasons, although the three species have different biologies that allow them to coexist within the same habitat. The demography of the generalist species, *M. coucha,* was not influenced by any external factors (e.g., season, vegetation height, vegetation cover), although it was the dominant species in the study. This highlights its opportunistic habits. The demography of *G. leucogaster,* was mostly associated with the season, since seasonal fluctuations were seen in population size, reproductive activity and body condition. The habitat specialist, *O. angoniensis,* only showed a significant positive relationship with vegetation height and body condition, and showed no seasonal fluctuations due to its breeding strategy and low energy lifestyle. The sites differed significantly only by vegetation height and rodent abundance, but rodent diversities and richness were not different. However, season had an overall effect on vegetation and demography. The summer season was associated with taller vegetation heights and greater reproductive activity, while winter was associated with a higher BMI and larger population sizes. My study showed the relationships between demography and habitat selection in grassland rodent community.

Limitations of the study could include the exclusion of diurnal species when sampling in the afternoon became challenging due to chacma baboon (*Papio ursinus*) disturbance. PVC live traps used in the study were not very sensitive, which may have led to small rodent species and juveniles not being able to set off the trap. Another limiting factor was the short sampling sessions per month, and the restriction of sampling to only one year which did not allow for replication of sampling through multiple seasons per site.

Future studies could focus on *G. leucogaster* and its behavioural and demographic response to high rainfall and predation risk. Long term studies could be conducted to assess the effect of different climatic conditions and monitor *G. leucogaster* population sizes after the *La Niña* event. Improvements to the current study could include using small mammal live traps that are more weight sensitive in order to get accurate abundance data for the smaller species such as *M, minutoides*. Dividing seasonal data into smaller units to include spring and autumn may have emphasised seasonal fluctuations that are not seen in the current study.

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SUPPLEMENTARY DATA

Table S 1. Trap night success rate (no. captures/ no. traps x no. trap nights) by month and site of rodents at the Cradle Nature Reserve from October 2021 to September 2022.

	Total trap night success (%)		
Sampling period	Overall	Northern site	Southern site
October	3.20	1.33	5.07
November	3.60	3.74	3.47
December	3.47	2.67	4.27
January	2.00	0.00	4.00
February	1.20	0.00	2.40
March	2.27	1.07	3.47
April	3.20	1.60	4.80
May	1.07	1.07	1.07
June	2.53	1.07	4.00
July	1.73	0.00	3.47
August	1.20	0.27	2.13
September	4.27	0.00	8.53
Summer	2.96	1.29	4.62
Winter	2.00	0.84	3.16
Overall	**2.48**	**1.07**	**3.89**

Table S 2. The number of individuals captured and the number of total captures (including recaptures) of each species (in brackets) per season and site at the Cradle Nature Reserve from October 2021 to September 2022.

Species	Summer		Winter	
	Northern site	Southern site	Northern site	Southern site
Gerbilliscus leucogaster	4 (26)	7 (60)	1 (1)	4 (16)
Lemniscomys rosalia	-	3 (6)	-	4 (7)
Mastomys coucha	-	12 (24)	-	14 (28)
Micaelamys namaquensis	1 (1)	2 (2)	2 (7)	1 (1)
Mus minutoides	-	4 (4)	-	1 (1)
Otomys angoniensis	2 (2)	3 (8)	3 (11)	4 (18)
Total	**7 (29)**	**31 (104)**	**6 (19)**	**28 (71)**

Table S 3. Population sizes, calculated using a closed population design per month, for *Gerbilliscus leucogaster, Mastomys coucha* and *Otomys angoniensis* at the Cradle Nature Reserve from October 2021 to September 2022.

	Gerbilliscus leucogaster		*Mastomys coucha*	*Otomys angoniensis*	
Month	Northern site	Southern site	Southern site	Northern site	Southern site
October	2	4	1	-	-
November	4	2	1	1	-
December	2	3	1	-	-
January	-	3	-	-	-
February	-	1	-	-	1
March	-	2	-	2	1
April	-	1	-	1	1
May	1	-	1	-	1
June	-	1	12	-	2
July	-	-	5	-	1
August	-	-	1	-	2
September	-	1	10	-	2
Total	**4**	**9**	**26**	**4**	**4**

Table S 4. The sex ratios of *Gerbilliscus leucogaster, Mastomys coucha* and *Otomys angoniensis* per season at the Cradle Nature Reserve from October 2021 to September 2022. Excluding juveniles

Species	Summer		Winter	
	Females	Males	Females	Males
Gerbilliscus leucogaster	3	8	2	3
Mastomys coucha	2	9	3	8
Otomys angoniensis	2	2	4	2
Total	**7**	**19**	**9**	**13**

Table S 5. Age ratios of *Gerbilliscus leucogaster, Mastomys coucha* and *Otomys angoniensis* per season at the Cradle Nature Reserve from October 2021 to September 2022.

Species	Summer		Winter	
	Adult	Juvenile	Adult	Juvenile
Gerbilliscus leucogaster	10	1	5	0
Mastomys coucha	10	2	11	3
Otomys angoniensis	4	1	4	3
Total	**24**	**4**	**20**	**6**

Table S 6. Ratio of reproductive active and non-active *Gerbilliscus leucogaster, Mastomys coucha* and *Otomys angoniensis* per season, at the Cradle Nature Reserve from October 2021 to September 2022. Excluding juveniles

Species	Summer	Winter
Gerbilliscus leucogaster	9:1	2:3
Mastomys coucha	2:8	0:11
Otomys angoniensis	4:0	5:1
Total	**15:9**	**7:15**

Table S 7. Mean body mass index (BMI %) of *Gerbilliscus leucogaster, Mastomys coucha* and *Otomys angoniensis* per season at the Cradle Nature Reserve from October 2021 to September 2022.

Species	Summer	Winter
Gerbilliscus leucogaster	42.32%	51.51%
Mastomys coucha	32.15%	38.16%
Otomys angoniensis	48.55%	49.31%

Table S 8. Proportion of the dominant grass species per season at the Cradle Nature Reserve from October 2021 to September 2022.

Summer Vegetation		Winter vegetation	
Plant species	Percentage contribution (%)	Plant species	Percentage contribution (%)
Eragrostis heteromera	39.29	*Eragrostis heteromera*	29.46
Digitaria tricholaenoides	8.04	*Eragrostis chloromelas*	13.39
Eragrostis gummiflua	7.14	*Eragrostis echinochloidea*	8.48
Andropogan chinensis	6.70	*Eragrostis gummiflua*	7.14
Eragrostis chloromelas	6.70	*Melinis nerviglumis*	5.80
Setaria sphacelata	5.80	*Pogonarthria squarrosa*	4.91
Sorghum bicolour	4.02	*Sorghum bicolour*	4.91
Digitaria brazzae	3.13	*Hyperrhenia filipendula*	4.02
Aristida diffusa	2.68	*Loudetia simplex*	4.02
Urelytrum agropyroides	2.68	*Panicum coloratum*	4.02
Hyparrhenia filipendula	2.23	*Schizachyrium sanguineum*	3.13
Melinis nerviglumis	2.23	*Setaria sphacelata*	3.13
Pogonarthria squarrosa	2.23	*Urelytrum agropyroides*	2.23
Eragrostis plana	1.79	*Digitaria brazzae*	1.79
Eragrostis racemosa	1.79	*Aristida diffusa*	1.34
Loudetia simplex	1.34	*Panicum natalense*	1.34
Panicum coloratum	0.89	*Eragrostis plana*	0.45
Panicum natalense	0.89	*Monocymbium ceresiiforme*	0.45
Eragrostis trichophora	0.45		