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Population dynamics of *Rhabdomys bechuanae* (Rodentia, Muridae) in two localities of the Free State Province

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A dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg in fulfilment of the requirements for the degree of Master of Science.

Johannesburg, 2019

Declaration

I declare that this dissertation is my own unaided work. It is being submitted for the degree of Master of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other university.



Leon Kotze
13/03/2019

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Abstract

My study aimed at investigating the population dynamics of the African striped mouse *Rhabdomys bechuanae*, in two semi-arid localities, Tussen die Riviere (TDR) and Soetdoring (SO) Nature Reserves in the Free State Province, South Africa, and analyse the influence of extrinsic factors on population dynamics of these populations. Live trapping and habitat assessments were conducted at eight sessions from April 2015 to February 2017. For both study sites, regional temperature and precipitation data were obtained from the South African Weather Service and Florisbad Quaternary Research Station. The *R. bechuanae* habitat was highly seasonal with clear fluctuations in temperature, precipitation and plant cover. A total of 586 *R. bechuanae* were trapped at TDR compared to 120 individuals at SO. An equal number of female to male *R. bechuanae* were captured at TDR, indicating parity in the sex ratio of this species, at least where sample size is adequate. Contrary to *R. pumilio* of the Succulent Karoo, no sexual dimorphism was apparent in *R. bechuanae* body mass. Potentially reproductively active individuals were observed in seven out of eight trapping sessions. Peaks in breeding activity were expected in Summer 2015 (prior to the first trapping session) and Autumn 2016. I used simple capture-mark-recapture models in program MARK to estimate *R. bechuanae* population size (full-likelihood model) and survival rate (Cormack-Jolly-Seber). Population size and survival rates fluctuated seasonally for *R. bechuanae* at both reserves. Peak density was lower than compared to studies of other *Rhabdomys* species and may be attributed to methodological differences between studies and / or differences in species ecology, specifically life-history. I analysed associations between four population parameters, i.e. population size, survival rate, reproductive activity and body mass, and five extrinsic factors, i.e. mean monthly minimum- and maximum temperature; total rainfall for one month and three months preceding trapping sessions as well as median total plant cover. Different combinations of extrinsic factors were associated with variation in each population parameter. According to the literature, weather (temperature and rainfall) could act both directly and indirectly, although an indirect effect is more likely for *R. bechuanae*. Plant cover likely acted directly on population parameters and was associated, among other factors, with reproductive activity and body mass. I posit that the lack of correlations occurring between *R. bechuanae* population parameters and extrinsic environmental factors may point to non-linearity in the response of *R. bechuanae* to environmental variation. Additionally, the extrinsic factors could act additively on *R. bechuanae* dynamics most likely through determining the availability of resources. Future research on the population dynamics of *R. bechuanae* should aim to analyse density dependence in population dynamics; the effects of interaction between causal factors, both intrinsic and extrinsic as well as the effect of dispersal, through immigration and emigration, on population growth.

1. Introduction

The study of population dynamics seeks to describe the observed patterns of fluctuating abundance of populations across time and space and endeavours to explain these patterns through both mathematical and theoretical modelling (Gotelli 1995; Turchin 2003; Krebs 2013). Scientific research in this field of study has been conducted for little over a century (Turchin 2003). The first notable publications were concerned with recording periodic eruptions of small mammal populations and developing ecological theory to explain these events (Collett 1895; Elton 1924). Advances in the mathematical study of biological systems- and population dynamics were initiated around the same time (Lotka & Dublin 1925; Volterra 1926) but contributed little to early studies of population dynamics as the complementary importance of mathematical modelling and biological / ecological theory was not yet understood (Turchin 2003). Much progress has been made in the past 100 years towards estimating population parameters using modern mathematical techniques that incorporate ecological theory. Arguably the greatest contributions came from Cormack (1964), Jolly (1965) and Seber (1965). The work of these three scientists in estimating abundance and return rate, along with Maximum Likelihood theory developed by Sir Ronald A. Fisher (reviewed in Edwards 1972), form the backbone of present-day population modelling (Lebreton *et al.* 1992).

The incentive to study rodent dynamics has consistently been provided from their impacts on plant dynamics and human health. The most ambitious study to date, with 1000 study sites sampled over more than 30 years, was launched in order to study the impacts of seedling predation by the Gray-sided vole *Myotes rufocanus* in the coniferous forests of Hokkaido, Japan (Saitoh *et al.* 1998). Information developed in this field of research also informs wildlife management plans aimed at controlling or eradicating damage causing and / or invasive rodent species, e.g. House mice *Mus domesticus* in Australia (Singleton 1989; Singleton *et al.* 2001; Stenseth *et al.* 2003a). More recently, accompanying the advances of statistical modelling software, the dynamics of rodent-host populations have been analysed to predict the spread and prevalence of infectious diseases (Murúa *et al.* 2003; Kausrud *et al.* 2007; Luis *et al.* 2010; Wilschut *et al.* 2018). Additionally, studying rodent population dynamics will move us closer to predicting their response to rapid environmental change (Benton *et al.* 2006; McLean *et al.* 2016) and, even more urgently, anthropogenic disturbance in natural habitats (Andreo *et al.* 2009; Ehrlén & Morris 2015; Gasperini *et al.* 2016).

The research presented in this dissertation pertains to two populations of the African striped mouse *Rhabdomys bechuanae* (Thomas, 1893) located in semi-arid habitats within the Free State Province, South Africa. As the first study of the demography of this species, I set out to describe short-term population dynamics, in two years, in response to biologically relevant extrinsic factors. The genus

Rhabdomys comprises of several mitochondrial clades recently revealed to have experienced radiation associated with historic environmental changes and the establishment of the currently recognised southern African biomes (Rambau *et al.* 2003; du Toit *et al.* 2012). Species, within the genus, are broadly distinguished as arid (i.e. *R. pumilio*, *R. intermedius* and *R. bechuanae*) and mesic adapted (i.e. *R. dilectus dilectus* and *R. dilectus chakae*). The distribution range of each *Rhabdomys* taxon appears to be largely constrained by climatic tolerance and vegetation type, indicative of differentiation within the environmental niche (du Toit *et al.* 2012; Ganem *et al.* 2012; Meynard *et al.* 2012). Molecular dating indicated detached phases of differentiation: the first 4-5 million years ago (MYA), separating *R. bechuanae* from the rest of the group, and several events separating *R. pumilio*, *R. intermedius* and *R. dilectus*. Two subclades are recognised within *R. dilectus*, *R. d. dilectus* and *R. d. chakae*, having separated most recently, around 2 MYA (du Toit *et al.* 2012). Although further taxonomic revision is still required for the genus (Castiglia *et al.* 2012; du Toit *et al.* 2012), behavioural studies and interspecies breeding in captivity suggest divergence of mate recognition (Pillay *et al.* 2006), high levels of aggression as well as reduced interfertility between some arid- and mesic adapted lineages (Pillay 2000), supporting phylogenetic distinction between putative taxa.

Apart from only two published papers concerning *R. bechuanae* (Ganem *et al.* 2012; Dufour *et al.* 2015), relatively little is known about this species and I therefore make extensive reference to studies regarding the entire genus *Rhabdomys*. *R. bechuanae* is a small diurnal murid rodent (mean body mass of 33 – 44 g) predicted to occur throughout arid and semi-arid southern Africa (Figure 1) in habitats with open shrubland vegetation (du Toit *et al.* 2012; Dufour *et al.* 2015). Small mammals, such as *Rhabdomys*, are characterised by short life spans, low survival prospects, early age at sexual maturity and high reproductive rates (Krebs & Myers 1974; Oli & Dobson 2003; Duncan *et al.* 2007).

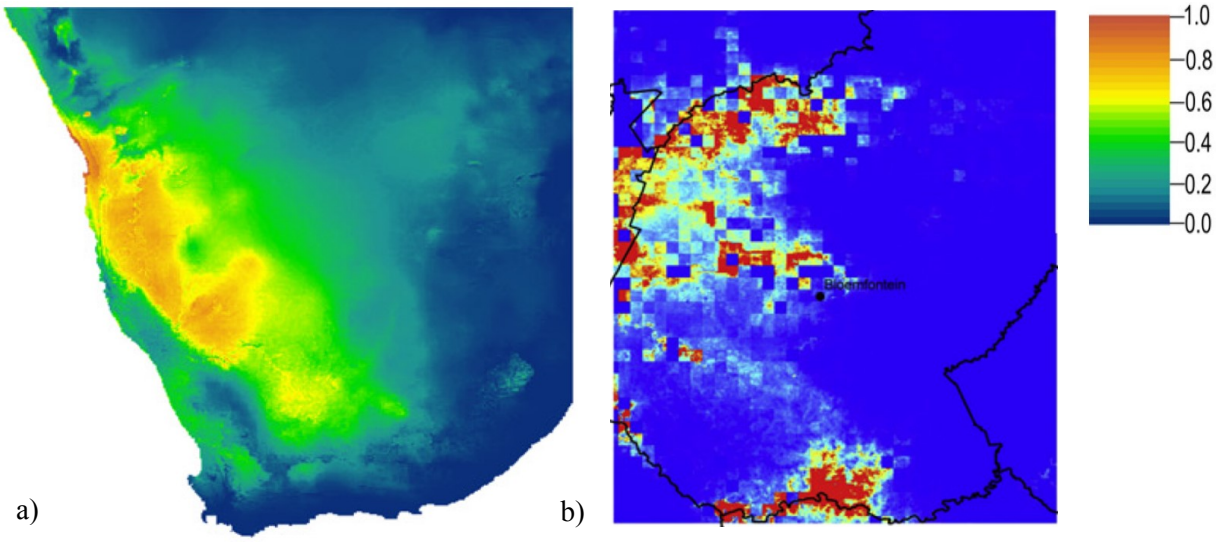


Figure 1. Predicted distribution range of *R. bechuanae* in a) southern Africa (note: though the map has been truncated, its distribution in the entire area of South Africa is included) (du Toit *et al.* 2012) and b) the Free State Province, South Africa (Ganem *et al.* 2012). Maps are shaded according to probability (see legend), where red indicates the highest probability of *R. bechuanae* occurrence and blue indicates the lowest probability of occurrence.

1.1. Understanding population dynamics through survival and reproductive rates

The key question in studying the population dynamics of any animal is what factors determine population growth rate (i.e. the apparent increase or decrease in population size) (Krebs 2013)? All changes in population size are the result of survival, reproduction and movement / dispersal into and out of the population (Krebs 2013). Survival rate is an estimate of the probability of an individual surviving from one time period to the next (White & Burnham 1999). In studies of *Rhabdomys*, it has also been expressed as the average period of time an individual is expected to remain alive (*R. pumilio* of the Cape flats; David & Jarvis 1985) or directly estimated from the difference in the number of individuals captured at the start compared to the end of an intensive trapping period (Schradin & Pillay 2005a). Survival probability can decrease according to multiple factors, both abiotic and biotic, including: extreme weather (i.e. droughts or flooding) (Brown & Ernest 2002), predation (Lima *et al.* 2002; Prevedello *et al.* 2013), disease and parasites (Krebs 2013). The study of wildlife demography considers current population size to be a function of past abundance and vital rates, i.e. survival and reproductive rates (Begon *et al.* 1990). Therefore, to understand the effects of survival on population dynamics one needs to consider reproductive rates in parallel.

Reproductive rates, as it is used here, refers simply to recruitment into the population through fecundity. Reproductive rates are related to the life-history strategy of a species and are altered by factors both

intrinsic and extrinsic to the population (Krebs 2013). *Rhabdomys* has a mean litter size of 5.3 ± 2 pups (Brooks 1982; David & Jarvis 1985; Willan & Meester 1989; Schradin & Pillay 2005a) and the gestation period is 23 days (Brooks 1974). For both xeric and mesic adapted species, the inter-litter interval is approximately 23 to 25 days (Pillay 2000). Seasonal reproductive activity has been illustrated in several ecologically distinct populations of *Rhabdomys* (David & Jarvis 1985; Schradin & Pillay 2005a). The length of this breeding season varies from 3 months in the Succulent Karoo (Schradin & Pillay 2005a); 7 months in mesic grasslands (Brooks 1974; Perrin 1980a) and 6 – 8 months in the Cape flats (David & Jarvis 1985). However, *Rhabdomys* is considered an opportunistic breeder- able to reproduce if an adequate supply of protein rich forage is available (Perrin 1980b), irrespective of ambient temperature (Nater *et al.* 2015; Willan & Meester 1989).

1.2. Types of dynamics in rodents

The dynamics of population size can be stable to cyclic. Stable populations show relatively little fluctuation between peak- and low densities. Data for such populations are scarce, but they are expected to occur in aseasonal, productive environments such as the tropics. On the other hand, populations that illustrate distinct periodic cycles of growth and decline are considered cyclic (Krebs 2013).

In populations where fluctuations are cyclic, a clear differentiation can be made between population growth and decline. The cyclic pattern of population dynamics may illustrate considerable variation (Lidicker 1988): population growth and decline as well as realised peak population size could vary both temporally and spatially for a single species (Reid *et al.* 1997; Saitoh *et al.* 1998). Additionally, for a single population the interval length between peaks in population size may vary along with considerable disparities in the amplitude of the fluctuations (Kokorev & Kuksov 2002; Saitoh *et al.* 1998). A multi-annual interval between periods of peak density (number of animals per unit area) is often a characteristic of cyclic population patterns (Framstad *et al.* 1993; Kokorev & Kuksov 2002). Given the interval length between periods of peak density as well as the fluctuation in amplitudes, cyclicity is not easily determined with short term datasets (Krebs 2013). Therefore, although I expected *R. bechuanae* to illustrate cyclic dynamics in population size, I did not focus on the characteristics of *R. bechuanae* population cycles in the short period of data gathered for this study.

1.3. The broader role of the environment

Climate (e.g. temperature and rainfall) and food availability are important extrinsic factors influencing the dynamics of animal populations. Environmental effects impact population dynamics by altering demographic rates (survival- and reproductive rates), which in turn determine population size (Benton *et al.* 2006). The majority of short-term studies (≤ 8 years) in semi-arid to arid regions support bottom-

up regulation of granivorous small mammal populations through fluctuations in rainfall directly determining plant cover and food availability (Ernest *et al.* 2000; Brown & Ernest 2002), as with similar correlations observed in *Rhabdomys* populations (Christian 1979; Schradin & Pillay 2005a). Temperature, food availability and population density jointly affect demography (i.e. survival, reproduction and maturation) across all life history stages of *R. pumilio* in the arid Succulent Karoo, although the impact of each factor on each specific demographic rate varied considerably (Nater *et al.* 2015).

Weather, considered here as temperature and rainfall, is a major determinant of individual fitness (Stenseth *et al.* 2002) and therefore dynamics at a population level (Stenseth *et al.* 2003). Similar to other *Rhabdomys* species, *R. bechuanae*, of the Namib desert, regulates its activity pattern according to ambient temperature, activity being concentrated to crepuscular periods (Krug 2004). During peak mid-day temperatures, *R. bechuanae* remain in shelters (most often under large shrubs) with suitable microclimates, reducing exposure to solar radiation and evaporative water loss (Krug 2004). Therefore, by regulating the timing and duration of activity bouts, temperature has an indirect effect on individual fitness. At the other extreme, low temperatures incur energetic costs through thermoregulation and can induce starvation if sufficient food is not available (Howard 1951).

1.4. The role of life-history in demography: social organisation in *Rhabdomys*

The environment determines a species' life history (i.e. species-specific intrinsic processes, e.g. social organisation, activity routines), which directly affects population size through temporal changes in demographic rates (i.e. survival and reproduction) (Benton *et al.* 2006). Different studies have assessed specific demographic indices of the *Rhabdomys* genus in different habitats and geographical locations. From the literature, clear differences in population density have been observed with the largest densities in arid to semi-arid regions (David & Jarvis 1985; Krug 2002; Schradin & Pillay 2005a) and the lowest densities in mesic grassland areas (Brooks 1974; Perrin *et al.* 2001; Schradin & Pillay 2005b) (Table 1).

It is important to note that these population densities were 1.) estimated during different years, with decades in between some and 2.) their sampling and statistical approaches were not identical to those performed in my study. All studies followed a capture-mark-recapture protocol. In the pro-Namib and Succulent Karoo populations, trapping was conducted directly at the nest and all *Rhabdomys* individuals were marked (Krug 2002; Schradin & Pillay 2005a). In grassland *Rhabdomys*, where nest-sites were not exposed, trapping was conducted on grids of set configurations with a constant trapping period (Perrin *et al.* 2001; Schradin & Pillay 2005b). Nevertheless, the compilation of results reported in these studies suggest significant variation in realised population density as well as survival that could be

explained by apparent ecological differences (e.g. rainfall period, plant community composition, food availability) as well as social organisation (Schradin 2005; Schradin & Pillay 2005b).

Table 1: The distribution, population density and survival rate of *Rhabdomys* species in six studies. Rainfall patterns (levels and timing) were obtained from Rutherford *et al.* (2006).

Species	Biome; bioregion	Population density	Survival rate	Mean annual rainfall; season
R. bechuanae (Krug 2002)	Desert; Namib desert	30 – 2000	13 %	30 mm; Summer
R. dilectus (Brooks 1974)	Grassland; mesic highveld	35 – 93	3 %	730 mm; Spring, Summer
R. dilectus (Perrin *et al.* 2001)	Grassland; sub-escarpment grassland	10 – 40	N/A	760 mm; Spring, Summer
R. dilectus (Schradin & Pillay 2005b)	Grassland; sub-escarpment grassland	10 – 40	N/A	760 mm; Spring, Summer
R. pumilio (Schradin & Pillay 2005a)	Succulent Karoo; Namaqualand hardeveld	50 – 200	27 %	150 mm; Winter
R. pumilio (Nater *et al.* 2016)	Succulent Karoo; Namaqualand hardeveld	N/A	80 %	150 mm; Winter

R. pumilio in the Succulent Karoo associates in social groups which forage and reproduce within the same home range (Schradin & Pillay 2004), whereas solitary *R. dilectus* of mesic grasslands maintain exclusive territories six to ten times larger than the Succulent Karoo sister species (Schradin & Pillay 2005b). In a social species, such as *R. pumilio*, the home range of 5 to 30 individuals overlap to a significant extent (Schradin & Pillay 2005b). Population density estimates of group living *R. bechuanae* (Table 1) result, in part, from exactly these life-history traits as up to 30 individuals occupy a single nara plant *Acanthosicyos horridus* (Krug 2004).

Clear differences in survival prospects exist among *Rhabdomys* populations of mesic versus xeric habitats (Table 1). In addition to ecology, social organisation could act on survival and, in this case, specifically juvenile survival. In *R. pumilio*, pups may remain in the natal group as philopatric adults, investing in somatic development till the next breeding season, whereas *R. dilectus* disperse post-weaning, investing in reproduction soon after leaving the nest (Schradin & Pillay 2005b). These differences are expected to contribute significantly to survival prospects (Schradin & Pillay 2005b). Although group living, the low survival rates of *R. bechuanae* in the Namib desert (13 %) compared to *R. pumilio* in the Succulent Karoo (27 – 80 %), could be due to the greater degree of aridity in the

Namib (total precipitation of ± 30 mm per annum; Table 1), limiting food availability and nesting opportunities (Brown & Ernest 2002).

Differences in social organisation may also imply interspecific differences in reproduction. Since *R. pumilio* females maintain the same home range as the breeder male, the probability of a female and male reproducing should be greater than in the grasslands where a male *R. dilectus* first has to locate a female in oestrus at or outside the periphery of his home range (Schradin & Pillay 2005b). The need for comparatively longer distance dispersal to reproduce should also increase the chance of *R. dilectus* males to be preyed upon. In small rodents, age at sexual maturity is considered an important life-history trait affecting reproductive rates (Oli & Dobson 2003). In studies of *Rhabdomys*, minimum mass is commonly used to determine the earliest age of reproduction. Marked differences in age at maturity have been recorded between *Rhabdomys* populations, with *R. dilectus* reaching sexual maturity at a body mass of 24 – 36 g (Brooks 1974; David & Jarvis 1985; Schradin & Pillay 2005b) compared to *R. pumilio* where breeding is only initiated at a body mass of 40 - 44 g (Schradin & Pillay 2004).

Though I did not aim to study the life-history of *R. bechuanae*, its importance with regards to demography is clear. Whether *R. bechuanae* is a social species maintaining a territory within its natal group or dispersing early in its life-history could have a significant impact on not only survival rates but also the probability of an individual successfully reproducing, ultimately determining population dynamics.

1.5. Methods used to measure population dynamics

Direct observation has been used to provide count-data for *R. pumilio* occupying a relatively open habitat (Schradin 2005b; Schradin & Pillay 2005a). Although this procedure provides accurate data, its applications are limited to animals occupying open habitats. Lethal snap-trapping, although ethically precarious, is often used in long term studies to estimate population abundance and record fluctuations in populations (Framstad *et al.* 1993; Kokorev & Kuksov 2002). Though the method is uncommon, snap-trapping has been used in conjunction with live trapping if invasive physiological / anatomical data are to be gathered for demographic purposes, e.g. determining birth rate in females or spermatogenesis in males (David & Jarvis 1985).

In this study I employed a capture-mark-recapture (CMR) protocol in recording live-captures (Pradel 1996). Capture-mark-recapture (CMR) is the most popular protocol utilised to acquire the data necessary for analysing population dynamics. With the appropriate marking method (e.g. ear tags in small rodents or ring tags in birds), one can distinguish among individuals, establishing their presence or absence for each monitoring (i.e. trapping) session. Capture histories are constructed from these data

for each individual observed and used in the estimation of population parameters, such as population growth- and survival rates (Pradel 1996; White & Burnham 1999). In the simplest terms, the frequencies of the different capture histories of individuals within this dataset determine the probability values derived for each population parameter. Additionally, CMR allows for the monitoring of physical changes of each individual (e.g. body mass, reproductive state) with time.

A simple model used to estimate survival is the Cormack-Jolly-Seber model (Cormack 1964; Jolly 1965; Seber 1965). The model specifies return rate (the number of marked individuals observed from first to subsequent captures) to be, simply, determined by two probabilities: the probability of an animal surviving from one trapping session to the next (survival probability or Φ) and the probability that, conditional on the animal being alive, it is recaptured (recapture probability or *p*). Differences in capture histories therefore indicate variation in survival- and /or recapture probabilities. The Cormack-Jolly-Seber model also allows for testing variation in both survival- and recapture rates between groups (i.e. females and males). The survival estimate assumes that each marked individual remains within the study site during the study period and therefore disregards the effect of dispersal (White & Burnham 1999). Dispersal through immigration and emigration has a definite role to play in population dynamics. However, given the time and effort required to study dispersal at an appropriate scale, attempts to quantify the impacts of dispersal are rare and I therefore refrain from discussing it here (Krebs 2013). I assumed that each respective population being studied was contained within the designated study site and therefore that dispersal played a minor role in affecting population growth (White 1982).

Compared to, for example, syntopic *Otomys irroratus* in the grasslands and *Otomys unisulcatus* in the Succulent Karoo, *Rhabdomys* is generally considered a trap happy species (Neville Pillay *pers. comm.*; *pers. obs.*), making it a suitable model organism to study population dynamics in a small murid rodent. Using a CMR protocol, I investigated the dynamics on *R. bechuanae* population size, survival rates, reproductive rates as well as body mass in two populations of *R. bechuanae* and the influence of temperature, rainfall and plant cover on these parameters. I further described their demography in terms of sex ratio and body size classes present at different times of the year. I discuss the basic morphology (body size, body mass and sexual dimorphism in mass) of the species and compared these to other *Rhabdomys* populations and species. I refrained from making *a priori* predictions as to the response of *R. bechuanae* to environmental conditions since, within the genus, only two other studies have comprehensively described striped mouse demography, both concerning the currently recognised *R. pumilio* species (David & Jarvis 1985; Schradin & Pillay 2005a), with environmental factors only recently included in the analysis of *R. pumilio* demography (Nater *et al.* 2015).

Although the genus *Rhabdomys* is commonly described as an opportunistic omnivore, with a diet consisting mainly of seeds, particular plant material (e.g. bark, wildflowers and young, nitrogen rich vegetative growth) and insects, seasonal and geographic variation exists in the composition of its diet (Curtis & Perrin 1979; Perrin 1980a; Taylor & Green 1976). Without specific knowledge of the diet of *R. bechuanae*, I instead recorded plant cover, a discrete factor incorporating multiple essential resources, including nesting opportunities, cover from predators, habitat complexity for social interactions and sources of food (both plant and animal prey) (Krebs 2013). Finally, the different direct and indirect impacts of weather imply that rodent population sizes may respond rapidly or with a delay of several months (Brown & Ernest 2002; Luis *et al.* 2010). Therefore, in my analyses I considered the delayed effect of both temperature and rainfall on population size.

1.6. Aims

I aimed to analyse and describe some predictors of the population dynamics of the African four striped mouse, *Rhabdomys bechuanae* (Thomas, 1893), in two semi-arid localities at the central part of the genus range, over a two-year period.

1.6.1. Objectives

1) Assess how seasonality impacts *Rhabdomys* population dynamics. I assessed:
   a. Population size, seasonally
   b. Survival rates, according to the population model that best describes the observed capture histories
   c. How the above traits varied with season and year
2) Assess how seasonality impacts the demography of *Rhabdomys bechuanae*, in terms of:
   a. Sex ratio
   b. Reproductive activity
   c. Relative age class structure
3) Assess seasonal and sexual variations in *Rhabdomys bechuanae* body size and mass and address differences between the sexes and reproductive states. In particular, I addressed potential links between body size / mass and reproductive versus non-reproductive states.
4) Disentangle potential causal effects of extrinsic factors related to seasonality on *Rhabdomys bechuanae* population size, survival rate, reproductive activity and body mass. Extrinsic factors refer to:
   a. Minimum temperature
   b. Maximum temperature
   c. Rainfall for the 30- and 90 days preceding each trapping occasion

2. Materials and methods

2.1. Study localities

Data collection was conducted at two localities, Tussen die Riviere (TDR) Nature Reserve and Soetdoring (SO) Nature Reserve (Figure 2), in the Free State Province, South Africa, where *R. bechuanae* has been studied, and genetically identified, in the recent past (Dufour *et al.* 2015; du Toit *et al.* 2012; Ganem *et al.* 2012). These two localities occur approximately 183km apart, at the eastern edge of the species distribution range (du Toit *et al.* 2012; Ganem *et al.* 2012), within the semi-arid Dry Highveld Grassland bioregion (Rutherford *et al.* 2006).

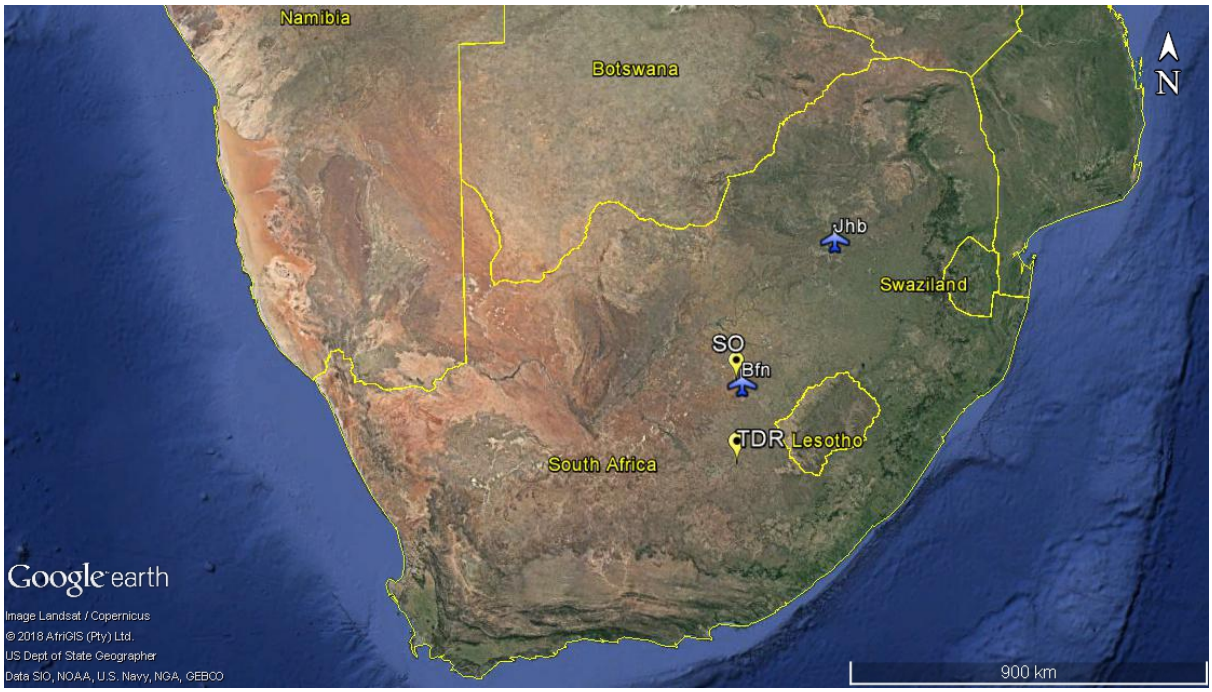


Figure 2. Satellite image of South Africa (earth.google.com), showing the position of Tussen die Riviere (TDR) and Soetdoring (SO) Nature Reserves at a national scale. The locations for Bloemfontein (Bfn) and Johannesburg (Jhb) were included for reference.

2.2. Site descriptions

Sampling took place in a single site per locality. Study sites (Figures 3 & 4) were selected on the basis of *Rhabdomys* occurrence with reasonable abundance, as confirmed by prior trapping (2 weeks to 2 months annually, from 2009 to 2011) at each locality. The study site at Tussen die Riviere Nature Reserve (S30° 28' 02.7" E26° 09' 37.1"; Figure 3) was located 1270 m above mean sea-level and covered an area of approximately 17.53 ha. Bordering the site was the Caledon River to the north and a hill (koppie), with a steep slope and abundant boulders, to the south. Trees were common, regularly

dispersed (conspicuous black dots in Figure 3) and dominated the riparian zone. The site sloped downward from south to north. The study site at Soetdoring Nature Reserve (S28° 49' 05.9" E26° 05' 57.9"; Figure 4) was located 1260 m above mean sea-level and covered an area of approximately 10.97 ha. At the centre of the site was a seasonal wetland, surrounded, for the larger part, by dense woody vegetation and the site sloped downward towards the wetland area. At both sites, *Rhabdomys* was the only diurnal-crepuscular murid species (Appendix, Tables A1 & A2). Predators, both terrestrial and aerial, were observed on or in close proximity to each site. Predators most often spotted at TDR were Cape cobra *Naja nivea*, Slender mongoose *Galerella sanguinea* and Black-shouldered kite *Elanus caeruleus* and at Soetdoring Nature Reserve Puff adder *Bites arietans*, Yellow mongoose *Cynictis penicillata* and Southern pale chanting goshawk *Melierax canorus* were the most frequently observed.



Figure 3. The study site in Tussen die Riviere Nature Reserve. The study was conducted in the area indicated by the polygon in the centre of the image. The image was captured in February 2016.



Figure 4. The study site in Soetdoring Nature Reserve. The study was conducted in the area indicated by the polygon in the centre of the image. The image was captured in February 2017.

2.3. Regional weather

Compared to the mean annual precipitation expected for the Dry Highveld Grassland bioregion (± 496 mm; Rutherford *et al.* 2006), total annual rainfall at Tussen die Riviere was markedly lower during the first and second year of the study (342.15 mm and 347.8 mm, respectively) and at Soetdoring rainfall was lower during the first (375.88 mm) but not the second year (589.14 mm).

For Tussen die Riviere Nature Reserve, average minimum temperature in the two-year study period was 7.13 °C, average maximum temperature was 25.67 °C and annual average rainfall was 344.98 mm. The lowest mean monthly temperatures were experienced during June 2015 (-1.05 °C) and July 2016 (-1.46 °C) and the highest mean monthly temperatures during December 2015 (34.71 °C) and December 2016 (33.79 °C). A total of 128 frost days (days with a minimum temperature of less than 0 °C) were recorded in the two-year study period.

For Soetdoring Nature Reserve, average minimum temperature in the two-year study period was 8.56 °C, average maximum temperature was 27.73 °C and annual average rainfall was 482.51 mm. The lowest mean monthly temperatures were experienced during June 2015 (0.14 °C) and July 2016 (-0.65 °C) and the highest mean monthly temperatures during December 2015 (36.35 °C) and December 2016 (34.79 °C). A total of 91 frost days were recorded across the two-year study period.

2.4. Fieldwork

Fieldwork was done over two years (April 2015 - February 2017), sampling once every season. Summer comprised the period December to February, Autumn - March to May, Winter - June to August, and Spring - September to November. I completed 8 fieldwork sessions of 6 to 8 days per site, collecting data over a minimum of 60 days in two years at each site. The mean interval period between fieldwork was 86 days (SD = 11.12) at Tussen die Riviere and 87 days (SD = 7.81) at Soetdoring.

The biggest time and resource investment went into the live trapping of *R. bechuanae*. On average, 4 to 5 days of each sampling session was spent capturing, marking and recapturing the study species. Trapping ceased on the day that recaptured *R. bechuanae*, marked during the current trapping session, were ≥ 50 % of the *R. bechuanae* captured for that day. Plant cover was assessed continuously throughout the trapping period and completed 1 or 2 days after trapping ceased when necessary.

Within each study site, an average of 180 PVC box traps (length = 29 cm, height = 7.5 cm, width = 6 cm) were placed in a grid configuration. Traps were placed beneath plant cover, where available, approximately 15 m apart though traps were not equally spaced within or between trapping sessions. Transect lines of 10-20 trap stations were set parallel to each other and spaced approximately 30 m apart. The location of trap stations and distance between transects was not constant within or between trapping sessions. Total trapping effort varied across sessions mainly due to logistical complications (availability of traps, transport, assistance), though trapping was always conducted within the same area (illustrated by the polygon in Figures 3 & 4).

Each trap was numbered and its location coordinates recorded with a handheld GPS (Dakota 10, Garmin International, Kansas, USA). A numbered, plastic tag was used to indicate the position of a trap station within a transect (Dufour *et al.* 2015; Schradin & Pillay 2005b) and, by order of Reserve management, removed following each trapping session. Traps were baited with peanut butter, rolled oats, sunflower seed and coarse salt mixture (Dufour *et al.* 2015; Merritt *et al.* 2001). Cotton wool was added as an additional attractant, readily used by *Rhabdomys* as nesting material, and to provide thermal insulation to trapped individuals (Dufour *et al.* 2015; Perrin *et al.* 2001).

Traps were checked daily between 08:00 and 10:00 in the morning and again between 15:00 and 17:00 in the afternoon, during which all occupied traps were collected for captive *R. bechuanae* to be measured and assessed. These routine checks also served to ensure traps were baited and functioning optimally. A standardised procedure (Table 2) for handling the trapped animals was followed to minimise stress and increase efficiency. This handling process was repeated at each session. Small mammals, other than *R. bechuanae*, were identified to species level (where possible) and released at their respective trap stations.

Table 2. The handling procedure followed for *R. bechuanae* at first- and subsequent captures within a trapping session at two sites in the Free State Province, South Africa. Body mass and body size were recorded only once per trapping session on both marked and unmarked individuals.

Measurements	First capture	Recapture
Remove animal from trap into plastic 'handling' bag	1.	1.
Record trap number, time and date	2.	2.
Weigh	3.	N/A
Restrain animal by the skin over the scapulae	4.	3.
Record ear tag number, if already marked	N/A	4.
Apply ear tag and record number, if unmarked	5.	N/A
Record sex and inspect reproductive state	6.	5.
Measure body size	7.	N/A

Each *R. bechuanae* trapped during the study period was assigned a unique number, by marking it with a numbered metal tag on each ear (National Band & Tag Co., USA). At first and subsequent captures, the ear tag number, trap number as well as time and date of capture were recorded. Body mass (measured with a Pesola spring balance, to the nearest 0.5 gram) and body length (with a 30 cm inflexible, metal ruler, to the nearest millimetre) were only measured once per trapping session for each individual.

Sex and reproductive state were recorded at first and subsequent captures for each individual, using only the last recorded value (within season) in data analysis. Without dissection of the reproductive tracts I could not confirm whether individuals were indeed able to reproduce (i.e. if oogenesis or spermatogenesis took place; David & Jarvis 1985). I therefore referred to animals demonstrating particular reproductive traits as potentially reproductively active. Males were categorised as either non-scrotal (non-reproductive) or scrotal (potentially reproductively active), depending on whether the testes had descended. Female reproductive state was categorised as either non-reproductive (i.e. vagina closed) or potentially reproductively active if the female: 1) had a perforated vagina; 2) had a vaginal plug; and / or 3) showed obvious signs of lactation and / or pregnancy. Once all necessary data were gathered, the animal was released at the trap station of its capture, the trap re-baited and replaced.

Ethical clearance for this research was granted by the Animal Ethics Screening Committee of the University of the Witwatersrand (clearance certificate no. 2016/04/19/B). A research permit, allowing access to the study sites, was granted by the Free State Department of Economic Development, Tourism and Environmental Affairs (permit no. 01/26960).

2.5. Weather data

I obtained continuous long-term weather data (i.e. temperature and precipitation) from the South African Weather Service (www.weathersa.co.za) for the 2015 - 2017 sampling period from a weather station nearest to each locality. These weather stations were situated at Aliwal North Plaatkop (S30°48'07.20" E26° 52' 58.80", approximate altitude of 1350 m), 81 km from Tussen die Riviere Nature Reserve, and Glen College (S28° 56' 31.20" E26° 19' 30.00", approximate altitude of 1300 m), 27 km from Soetdoring Nature Reserve. Given the large distances between weather stations and my study sites, precipitation data were also collected for the nearest sources possible: Goedemoed Police Station (S30° 33' 30.48" E26° 24' 15.10", approximate altitude of 1300 m), 26 km from Tussen die Riviere, and Florisbad Quaternary Research Station (S28° 46' 07.46" E26° 04' 13.06", approximate altitude of 1250 m), 6.4 km from Soetdoring. The last-mentioned datasets were provided, respectively, by the South African Weather Services and Mr Jaco Smith of the National Museum, Bloemfontein. I did not assume that the conditions recorded at these sources were identical to those experienced at each study site but represent the conditions in the region directly surrounding each site.

The datasets contained numerous missing values (up to 35 of 365 recordings in 2017 for the Aliwal North Plaatkop weather station) and were used as obtained. To account for the missing data as well as possible variation caused by the difference in altitude and location between the weather stations and the study sites, rainfall records were averaged for the pair of stations associated with Tussen die Riviere (Aliwal North Plaatkop and Goedemoed Police Station) and the pair associated with Soetdoring (Glen College and Florisbad Quaternary Research Station). These average values were used in all analyses considering rainfall. Temperature data were only available for the Aliwal North Plaatkop- and Glen College weather stations and were used as obtained.

2.6. Vegetation assessment

Vegetation cover was assessed for each trap station from which at least one *R. bechuanae* was captured as well as for the same number of trap stations which did not catch *R. bechuanae*, chosen at random and sampled at varying distances from *R. bechuanae* habitat. I was unable to meet this goal in Autumn- and Winter 2015 at Tussen die Riviere and reported the relevant sample sizes in the Results section. The vegetation assessment was conducted continuously throughout each trapping session and completed up to two days after trapping ceased.

A 1x1m wire square was used to sample a 2x2m quadrat around each trap station, equalling 4 samples per station. For the first sample, the square was placed with one corner beneath / adjacent to the plastic

tag (indicating the position of a trap station) and, for each subsequent sample, moved clockwise around the tag with one side of the square bordering its previous position, the same corner of the square always remaining beneath / adjacent to the tag (Figure 5).

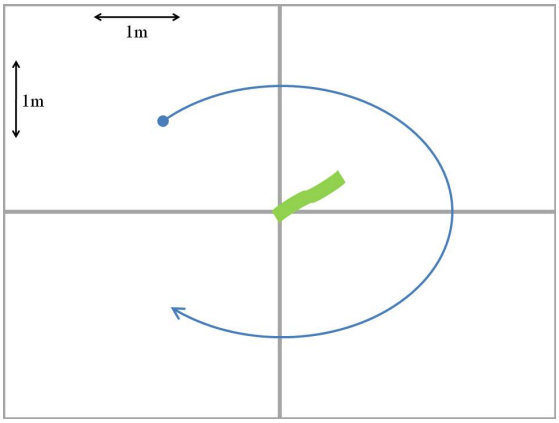


Figure 5. An illustration of the procedure used to record the cover in a 2x2m square around a trap station, using a single 1x1 m quadrat. The bright green strip at the centre illustrates the numbered tag used to mark each trap station.

Bare soil and total plant cover were first estimated and recorded as percentages of the 1x1 m quadrat area. The respective proportions of wood and grass cover were then obtained from the total amount of cover estimated and expressed as a percentage of the total area of the 1x1 m quadrat. For example, if the quadrat area consisted of 50 % bare soil, half of the quadrat would be completely devoid of vegetation. The remaining 50 % of the quadrat area would be assigned as 'total cover'. If this cover was a mix of grass and woody plants, the plant type providing most of the cover was first identified, and the approximate contribution of each plant type estimated. The sum of woody and grass cover was therefore always equal to the total cover initially estimated. For each sampling session, total-, grass- and woody cover were averaged across the four quadrats sampled at each station and these values used in data analyses.

2.7. Data analysis

Data for the two study populations were analysed separately throughout and I referred to trapping sessions by the season and year within which they were conducted, e.g. Autumn 2015 being the first trapping session. I used program MARK (version 8.2; www.phidot.org) to estimate the seasonal population size as well as survival rates for each study population, the details are further discussed below. The remainder of the analyses were conducted in program R (version 3.4.3; www.r-project.org)

with all tests being two-tailed and model alpha set at 0.05. Where relevant, chi-squared statistics were adjusted for multiple comparisons using a Bonferroni correction (p-values were reported as adjusted p or 'adj. p'). Using a Linear Mixed Effect Model (package *lme4*; Bates *et al.* 2014), or LMM, in program R, I assessed whether variation in five extrinsic factors determined seasonal variation in population size, survival rate, reproductive activity and body mass of *R. bechuanae* (Table 3). For each LMM I included mean minimum- and mean maximum temperature for the 30 days preceding each trapping session. As I expected *R. bechuanae* to breed opportunistically in reaction to new plant growth after sufficient rain, total rainfall was separately included in the LMM with a time-lag of 30- and 90 days before each trapping session to reflect both the short term and seasonal precipitation. The final predictor was median total plant cover for both trap stations that were successful and unsuccessful in capturing *R. bechuanae*. I included unsuccessful traps to account for the possible association of the surrounding area on the dynamics of the study species (Krebs 2013).

Table 3: The four Linear Mixed Effect Models computed in program R with the corresponding continuous predictors and random factors to assess the population dynamics of *R. bechuanae*.

Dependent variables	Model 1: Population size Model 2: Survival rate Model 3: Reproductive activity Model 4: Body mass
Continuous predictors	Minimum temperature Maximum temperature Rainfall 30 days *a priori* Rainfall 90 days *a priori* Plant cover
Random factors	Year, included in all models Individual identity (ear tag number), Model 4

In the relevant LMM, I used the proportion of potentially reproductively active females as an index of reproductive activity (Krebs 2013). In the assessment of body mass, I only used data for males of body size 9 – 9.9 cm, accounting for the mass effect of body size and the mass bias caused by pregnancy in females. Dependent factors were tested *a priori* for heteroscedasticity using a Shapiro-Wilk test of residuals, applied to the fully parameterised LMM. Data were then power transformed according to a Box-cox transformation. Due to inadequate sample size for the Soetdoring population, I assessed variation in population size only and excluded plant cover from the continuous predictors for this population. To correct for pseudoreplication, I included study year (1 or 2) as a random factor in all four models, including individual identity (ear tag number) as an additional random factor for the body mass model. The most parsimonious linear models were built through step-by-step elimination of the

least significant continuous predictor until only significant variables remained. I analysed the direction and strength for significant continuous predictor effects *a posteriori* by means of simple regression analyses.

I estimated seasonal population sizes (N) of *R. bechuanae* at each site using a closed population, full likelihood capture-recapture model (Otis *et al.* 1978), in program MARK. I assumed that each *R. bechuanae* population represented a closed population during trapping sessions, i.e. no births, deaths, immigrations or emigrations took place for the 4 – 8 days that trapping was conducted. The capture histories used here varied in character length according to the number of days per trapping session and represented the daily presence or absence of each individual observed within a trapping session (Appendix, Tables A3 & A4). With regards to the models fit to the data, I assumed no difference in recapture probabilities between males and females and between first and subsequent within season captures (i.e. no variation between marked and unmarked individuals). The first model tested for variation in recapture probabilities with time (between days within the same season) and the second model was time invariant. The population size estimate was taken from the model with the lowest Akaike Information Criterion adjusted for small sample size (AIC_c). I estimated the approximate density (number of individuals per hectare) of each population seasonally by dividing the population size estimate with the surface area of the relevant study site. Using ArcGIS (version 10.5; www.esri.org), I calculated an approximate surface area of both study sites by creating a circular buffer with a 20 m radius around the GPS location of each trap station (for the first trapping session), merging the buffers to exclude overlap and using the cumulative area of the merged buffer zone. The 20 m buffer radius is a conservative value based on the average radius (30 m) of *Rhabdomys*' home range at the Tussen die Riviere- and Soetdoring localities (Dufour *et al.* 2015).

Survival (Φ) rates between seasons were estimated using the Cormack-Jolly-Seber live-capture (CJS) model for open populations, in program MARK (version 8.2; www.phidot.org). Adhering to the CJS model assumptions, only live captures were considered, excluding the complete history of animals that died accidently during sampling (extreme temperatures were the main cause of mortality). The capture histories used in this analysis consisted of a string of 8 characters reflecting the 8 trapping sessions per site. Each individual trapped within the first four days of each trapping session (the minimum amount of days trapped at each session, for both study sites) was represented in the dataset with its own history. The sex of each individual was included with the corresponding capture history and designated as a grouping factor in the CJS model. The dataset for the TDR population consisted of 402 capture histories and 87 for the SO population (Appendix, Table A5). Sixteen models were fit to the dataset, testing for the effects of variation in survival- and recapture rates due to season, sex and the interaction of these

factors. Due to small sample size, only 3 of the 16 models were estimable for the Soetdoring dataset. All model parameters were estimated using the sine link function. I continued to do model selection based on decreasing AIC_c. From the models carrying equal weight in the data (with $\Delta AIC_c < 2$), the most parsimonious model, i.e. with least parameters, was selected as the final model best describing survival rates (Brownie 1987; Nichols 1992). I calculated approximate longevity, for the female and male with the longest capture histories, as the period the individual was known to be alive plus age at first capture (according to the growth curve published by Henschel *et al.* 1982).

The Goodness of fit of the CJS model was assessed using a median ĉ test, a built-in feature of program MARK, with 1000 iterations. The test provides a variance inflation factor, 'ĉ', that reflects the over- or underdispersion of a general- or nested model to the data, perfect fit being indicated by an estimated ĉ of 1 (Burnham *et al.* 1987) and relative fit, i.e. negligible overdispersion, indicated by a $\hat{c} \leq 3$ (Lebreton *et al.* 1992). The model showed negligible overdispersion of the Tussen die Riviere dataset to the fully-parameterised (general) model ($\hat{c} = 1.17$). For the Soetdoring dataset, I tested goodness of fit on the final model selected and found negligible overdispersion ($\hat{c} = 1.77$).

I assessed demography of the population at each study site seasonally with regards to sex ratio and reproductive activity. By means of a chi-squared test, deviation from parity (1:1) in the sex ratio of *R. bechuanae* was assessed for the entire sample as well as seasonally by comparing the observed proportion to the expected (50 %) proportion of each sex. For reproductive activity, I examined the total proportion of potentially reproductively active individuals per trapping session, identifying periods of peak reproductive activity. To assess whether reproductive activity was synchronous between males and females I compared the proportion of female to male potentially reproductively active individuals within each season (chi-squared test).

I described the basic morphology of *R. bechuanae* in each of the two study sites according to body size and body mass. I reported the morphological state, i.e. minimum mass and body size, of mature / potentially reproductive *R. bechuanae* individuals (Hagen *et al.* 1980). Additionally, I reported the maximum size and mass observed for each sex. To minimise the effect of measuring error, I assigned body size classes to each individual *a priori* The dataset consisted of six size classes: 7 – 7.9 cm, 8 – 8.9 cm, 9 – 9.9 cm, 10 – 10.9 cm, 11 – 11.9 cm and 12 – 12.9 cm. I assessed the variation in the proportion of the population representing each size class seasonally (single-factor Anova) and compared the composition of each population according to body size between the same seasons of different years (Tukey HSD). Within season, I compared the proportion of small- (< 9 cm) to large individuals (> 10

cm) using a chi-squared test. This was done to substantiate which seasons were preceded by peaks in reproduction, i.e. seasons with a high proportion of large individuals have potential to produce a high proportion of small individuals in the subsequent season, discussed in parallel with environmental conditions. Variation in body size by sex and reproductive state was assessed by means of a two-way Anova. I included the interaction between sex and reproductive sate to account for the effect of sex on body size in individuals in reproductively active or non-reproductive states.

Variation in body mass was analysed according to season and reproductive state, including an interaction factor (two-way Anova). For this analysis, I used only records for males of size class 9 (the median and most frequently observed size class at each site; see Results), accounting for the biased effect of pregnancy on female mass and the mass effect of body size. To gauge whether the result of the two-way Anova was temporally consistent, I compared body mass of potentially reproductively active- to non-reproductive males between the same seasons of different years (*post hoc* Tukey HSD). Due to the small sample size at Soetdoring, I could not analyse the interaction of season and reproductive state on body mass and also could not compare body mass between reproductively active and non-reproductive males of similar seasons between different years. Finally, I assessed sexual dimorphism in body mass of *R. bechuanae* during non-breeding seasons, i.e. trapping sessions where no potentially reproductively active individuals were observed, separately for each size class with an adequate sample of females and males (single-factor Anova). Analysis during the non-breeding season was not biased by weight gain during pregnancy.

I finally provided a descriptive analysis of the continuous predictors (i.e. rainfall, temperature and plant cover) used in the LMM's. The environment occupied by my study species is highly seasonal in both temperature and rainfall, with mean temperature and total precipitation peaking during summer months and declining to a low during Winter months (Rutherford *et al.* 2006). To compare conditions in the two years of study, I compared temperature (Tukey HSD) and rainfall (chi-squared test) between the same seasons of different years. Plant cover was assessed according to the three indices recorded: total, wood and grass cover. Seasonal variation in median plant cover was analysed for all three indices separately (single-factor Anova). As wood cover, specifically shrubs, is expected to determine the niche of *R. bechuanae* (Dufour *et al.* 2015; Ganem *et al.* 2012), I compared median wood- and grass cover for each season (chi-squared test) to determine the dominant vegetation type.

3. Results

3.1. Tussen die Riviere (TDR) Nature Reserve

3.1.1. Trapping scheme and sample size

Data collection at TDR took place over 52 days or 9526 trap-nights. A total of 586 *R. bechuanae* individuals were tagged during this period, corresponding to 1268 captures (including first and subsequent recaptures). The approximate surface area of the study site was 17.53 ha. Nine other small mammal species were trapped at this study site (Appendix, Table A1). Below, I briefly discussed the sample size (number of *R. bechuanae* captured and assessed) for each trapping session as these relate directly to the analyses that follow. Trapping effort was discussed in parallel as it is the primary variable determining the probability of an animal being caught in a specified area.

Figure 6A illustrates the differences in trapping effort (mean = 1190.75, SD = 359.12) in the 8 sampling sessions. The variation was a consequence of differences in both the duration (days) of a trapping session as well as the number of traps set per day, the latter having been determined by the number of field assistants available for a given trapping session. The lowest sampling effort occurred during Summer 2016 (710 trap nights) and the greatest in Spring 2016 (1768 trap nights) (Figure 6A). The number of individuals trapped decreased from Autumn 2015 to Summer 2017 (Figure 6B). The only change in the downward trend was in Spring 2015 and Winter 2016, both of which had a slight increase in the number of individuals trapped compared to the preceding trapping session (Figure 6B). For Spring 2015, this could be a result of an increase in trap nights from Winter 2015; the slight increase seen in Winter 2016 was accompanied by a decrease in trap nights from Autumn 2016 (Figure 6A). The four largest sample sizes were recorded in the first year of the study (Autumn 2015 – Summer 2016) (Figure 6B).

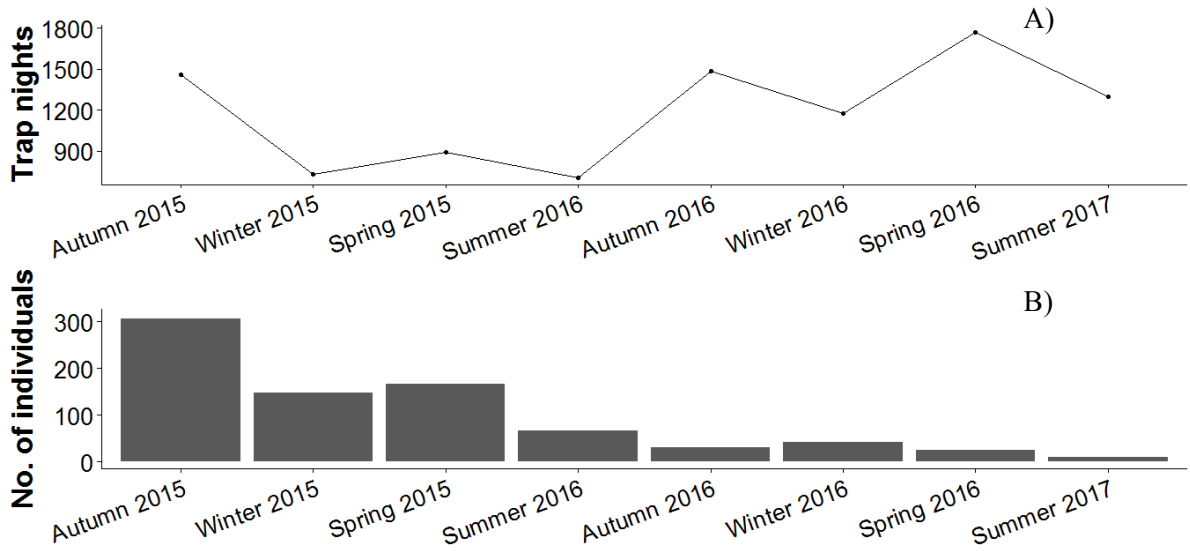


Figure 6. A) Total number of trap nights and B) the number of individual *R. bechuanae* per trapping session seasonally at TDR.

3.1.2. Population size

The best supported full-likelihood model for 5 of the 8 seasons indicated time dependence in the probability of capture. This suggests that for these trapping sessions there were daily differences in the probability of an individual *R. bechuanae* being captured. The most parsimonious model fit to the data sets of Summer 2016, Spring 2016 and Summer 2017 indicated no temporal, within season, variation in probability of capture (Table 4). For the first study year, the peak population size was observed in Autumn / May 2015 and for the second year in Winter / August 2016 (Table 4). The mean population size (N Estimate) in the two-year study period was 132.03 (SE = 50.02). Peak density of *R. bechuanae* at TDR was 24 individuals / ha (mean of 8 individuals / ha).

Table 4. The minimum number of animals alive (MNA), estimated seasonal population size (N Estimate), along with standard error, lower as well as upper Confidence Intervals (CI) for *R. bechuanae* at TDR. Estimates for seasons marked with '*' were computed with a model specifying time invariance in recapture probability.

Season	MNA	N Estimate	Standard Error	Lower CI	Upper CI
Autumn 2015	283	418.88	22.36	381.63	470.20
Winter 2015	139	201.81	15.21	178.34	239.29
Spring 2015	165	226.37	13.78	204.74	259.77
Summer 2016*	67	87.87	7.89	77.20	109.70
Autumn 2016	30	32.38	2.13	30.53	40.72
Winter 2016	39	50.29	5.70	43.43	67.74
Spring 2016*	24	26.74	2.38	24.63	35.91
Summer 2017*	9	11.93	3.31	9.49	26.36

Using a LMM, I analysed the effects of minimum and maximum temperature (30 days prior to each trapping session), rainfall (30 and 90 days prior to each trapping session) as well as median plant cover on estimated population size at TDR. The most parsimonious model indicated a significant effect of rainfall 30 days- and rainfall 90 days *a priori* on population size (Table 5). A strong negative correlation was observed between population size and rainfall 30 days *a priori* (r_s = -0.81, adj. p = 0.022).

Table 5. Continuous predictor estimates for the most parsimonious model with population size as dependent variable in *R. bechuanae* at TDR. Standard error, t- and p-values (Kenward-Roger approximation), corresponding with each estimate, have been included.

Predictor	Estimate	Standard error	t-value	p-value
Rain 30	-2.55	0.63	-4.07	0.007
Rain 90	1.22	0.24	5.05	0.002

3.1.3. Survival rates and capture histories

Of the 16 CJS models fit to the capture histories data set for *R. bechuanae* at TDR, the three best supported models accounted for 95.90 % of the AIC_c weight (Table 6). Given the small difference in AIC_c ($\Delta AIC_c < 2$), these models have approximately equal support in the analyses. All three models indicate variation in survival with season but not sex. The model with the least number of parameters (model 'Φ(season) p(.)') (Table 6) was taken to best describe the data set.

Table 6. The 3 best supported models estimating survival and recapture probability for the *R. bechuanae* population at TDR.

Model structure	AIC_c	Delta AIC_c	AIC_c weight	Number of parameters
Φ(season) p(.)	713.79	0	0.44	8
Φ(season) p(season)	714.46	0.66	0.32	13
Φ(season) p(sex)	715.35	1.56	0.20	9

The most parsimonious model indicated variation in survival rate with season but not sex. The greatest probability of survival was observed between Winter and Spring 2015 (Φ = 0.54, SE = 0.07) and the second greatest between Autumn and Winter 2016 (Φ = 0.44, SE = 0.16) (Table 7). The lowest probability of survival was observed between Spring 2016 and Summer 2017 (Φ = 0.14, SE = 0.10) and the second lowest between Summer and Autumn 2016 (Φ = 0.15, SE = 0.05) (Table 7). Mean survival rate across the two-year study period was 0.33 (SE = 0.06). The model indicated season and sex invariance of recapture rate across the two-year study period (p = 0.61, SE = 0.06) (Table 7).

Table 7. The survival rate estimates for the *R. bechuanae* population at TDR between successive trapping sessions as well as the rate estimate in all sessions. Standard error as well as lower and upper Confidence Intervals (CI) are reported for each estimate.

Parameter	Estimate	Standard Error	Lower CI	Upper CI
Survival, Autumn 2015 to Winter 2015	0.38	0.05	0.29	0.48
Survival, Winter 2015 to Spring 2015	0.54	0.07	0.40	0.67
Survival, Spring 2015 to Summer 2016	0.30	0.05	0.21	0.42
Survival, Summer 2016 to Autumn 2016	0.15	0.05	0.08	0.27
Survival, Autumn 2016 to Winter 2016	0.44	0.16	0.18	0.74
Survival, Winter 2016 to Spring 2016	0.38	0.13	0.17	0.65
Survival, Spring 2016 to Summer 2017	0.14	0.10	0.03	0.45
Recapture	0.61	0.06	0.49	0.72

Of the 431 individuals collectively trapped in the first 4 days of the 8 trapping sessions, 75.17 % were trapped once and females (n = 171) and males (n = 153) were equally likely of being only recorded once during the two-year study period (χ^2 = 1, p = 0.317, df = 1). The mean number of sessions an individual was observed was 1.32 (SE = 0.03).

Only one individual was observed at 6 consecutive trapping sessions (the longest capture history): a female *R. bechuanae*, trapped for the first time in Autumn 2015 at 32g (body size class 8) and for the final time in Winter 2016 (at body size class 10). The second longest capture history was for a male recorded for the first time in Spring 2015 at 47g (body size class 11) and at 4 consecutive trapping sessions thereafter, being finally observed in Spring 2016 (at body size class 11). The longevity of this female was approximately 73 weeks and approximately 66 weeks for the male.

Using an LMM, I analysed the effects of minimum and maximum temperature (30 days prior to each trapping session), rainfall (30 and 90 days prior to each trapping session) as well as median plant cover on survival rate at TDR. The most parsimonious model indicated a significant effect of minimum temperature, maximum temperature and rainfall 90 days *a priori* on survival rate (Table 8). However, no significant correlation occurred between survival rate and any of the continuous predictors that tested significant in the LMM.

Table 8. Continuous predictor estimates for the most parsimonious model with survival rate as dependent variable for *R. bechuanae* at TDR. Standard error, t- and p-value (Kenward-Roger approximation), corresponding with each estimate, have been included.

Predictor	Estimate	Standard error	t-value	p-value
Min. temp. 30	-3.10	1.33	-2.33	0.037
Max. temp. 30	2.86	1.27	2.26	0.042
Rain 90	-0.19	0.05	-3.59	0.003

3.1.4. Sex ratio

Over the two-year study period, a total of 390 females and 398 males were recorded (χ^2 = 0.08, p = 0.776, df = 1), indicating parity in the two-year data set. Indeed, for the trapping sessions of Autumn 2015 to Summer 2016, the proportions of females and males remained relatively constant around a 1:1 ratio (Figure 7). Seasonal comparisons showed significant deviation from parity in Winter 2016 (χ^2 = 13.38, adj. p < 0.001, df = 1) and Summer 2017 (χ^2 = 11.11, adj. p < 0.001, df = 1). In Winter 2016 the sex ratio was skewed towards males (68.29 % male) and reversed to greater female ratio in Summer 2017 (66.67 % female) (Figure 7).

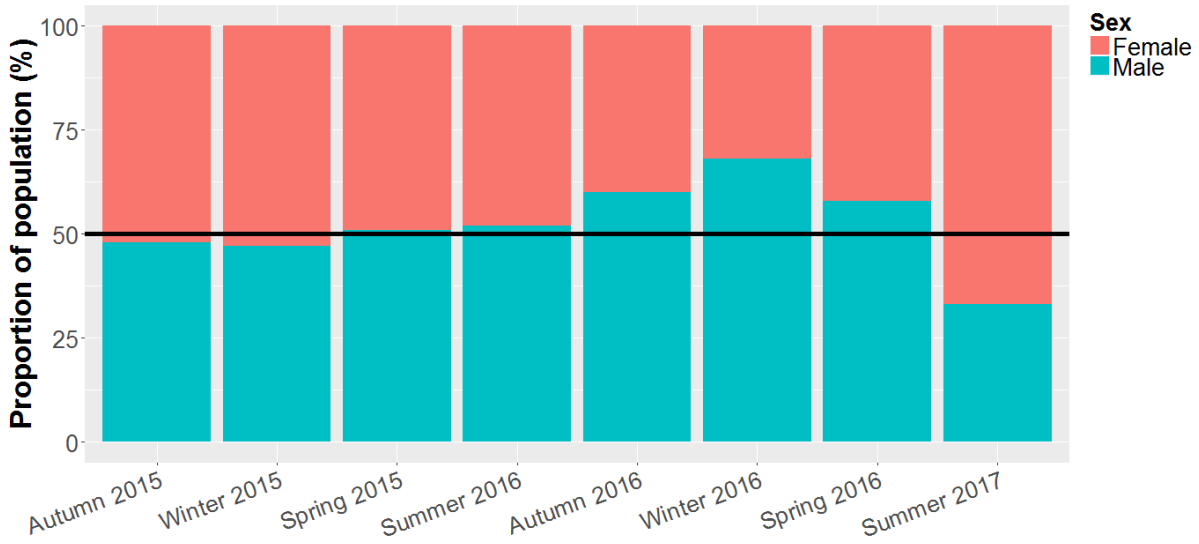


Figure 7. The seasonal female: male proportions of *R. bechuanae* at TDR. The horizontal black line indicates the position of parity (i.e. a sex ratio of 1:1).

3.1.5. Reproductive activity

Of the populations captured at each trapping session, Autumn 2016, Summer 2016, Summer 2017 and Autumn 2015 had the largest proportions of potentially reproductively active individuals (in descending order; Table 9). Reproductively active males would have been recorded as scrotal and females as pregnant, lactating and / or vagina perforated. No reproductively active individuals were recorded in Winter 2015 compared to Winter 2016 (Table 9).

Table 9. Proportion of potentially reproductively active individuals of the total number (n) of *R. bechuanae* captured at each trapping session at TDR. Data for females and males are pooled (see Figure 8 for differences between the sexes).

Trapping session	Autumn 2015	Winter 2015	Spring 2015	Summer 2016	Autumn 2016	Winter 2016	Spring 2016	Summer 2017
Proportion	44.19 %	0 %	28.31 %	58.21 %	80.00 %	27.50 %	41.67 %	44.44 %
n	301	147	167	67	30	41	24	9

Autumn- ($\chi^2 = 0.19$, adj. p = 0.662, df = 1) and Winter 2016 ($\chi^2 = 0.81$, adj. p = 0.367, df = 1) were the only two sessions when the proportions of female to male reproductively active individuals were near parity (Figure 8). No reproductively active individuals were trapped in Winter 2015 and no

reproductively active males were recorded in the small number of *R. bechuanae* captured in Summer 2017 (n = 9) (Figure 8).

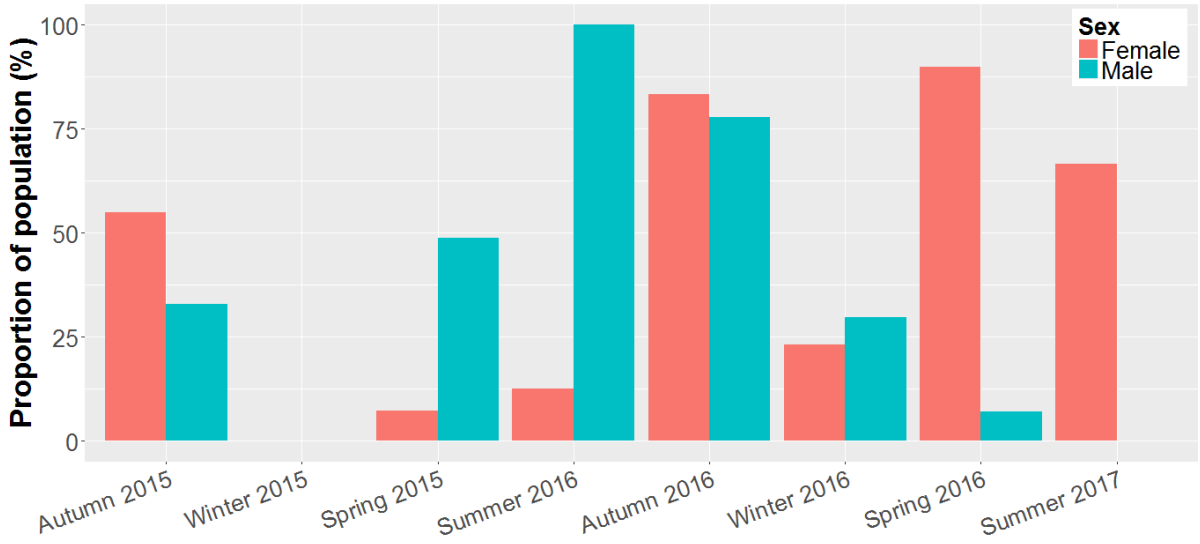


Figure 8. Proportion of potentially reproductively active female and male *R. bechuanae* in each trapping session at TDR.

Using an LMM, I analysed the effects of minimum and maximum temperature (30 days prior to each trapping session), rainfall (30 and 90 days prior to each trapping session) as well as median plant cover on the seasonal proportion of reproductively active *R. bechuanae* females at TDR. All the extrinsic factors, included as continuous predictors in the fully parameterised linear model, significantly affected the proportion of reproductively active females (Table 10). However, no significant correlation occurred between female reproductive activity and any of the continuous predictors tested in the LMM.

Table 10. Continuous predictor estimates for the fully parameterised model with reproductive rate as dependent variable for *r. bechuanae* at TDR. Standard error, t- and p-value (Kenward-Roger approximation), corresponding with each estimate, have been included.

Predictor	Estimate	Standard error	t-value	p-value
Min. temp. 30	6.51	0.03	204.33	< 0.001
Max. temp. 30	-2.40	0.03	-79.97	< 0.001
Rain 30	-0.59	2.20^{-3}	-269.49	< 0.001
Rain 90	0.11	4.98^{-4}	215.32	< 0.001
Plant cover	2.05	5.78^{-3}	353.65	< 0.001

3.1.6. Body size

The smallest body size among reproductively active individuals was observed for age class 8 (8 – 8.9 cm), for both females and males. The largest size class observed for females was 11 – 11.9 cm (n = 5) and 12 – 12.9 cm for males (n = 1), all were recorded as reproductively active. Individuals in size classes 8, 9 and 10 were the most frequently recorded during the two-year study period, comprising 94.43 % of all the individuals trapped (Table 11). Size class 9 was the most common class during the two-year study period (Table 11).

Table 11. Frequency of female and male *R. bechuanae* at TDR observed during the entire study period for each size class as well as the proportion of the captured population represented by each size class.

Size class	Class breadth	Frequency females	Frequency males	Proportion of total sample (n = 718)
7	7 – 7.9 cm	6	2	1.11 %
8	8 – 8.9 cm	112	49	22.42 %
9	9 – 9.9 cm	181	169	48.75 %
10	10 – 10.9 cm	50	117	23.26 %
11	11 – 11.9 cm	5	26	4.32 %
12	12 – 12.9 cm	0	1	0.14 %

The number of individuals representing each body size class varied seasonally ($F = 11.48$, $p < 0.001$, df = 7, 710). A Tukey HSD test showed that *R. bechuanae* were significantly larger in Autumn 2016 compared to Autumn 2015 ($p < 0.001$) and Winter 2016 compared to Winter 2015 ($p < 0.001$). However, body size did not vary between Spring or Summer of the different study years ($p > 0.05$, Tukey HSD test). Using the median size class (size class 9), I compared the proportion of the population that was smaller- (size classes 7 and 8) with that larger (size classes 10 and 11) than the median seasonally (Figure 9). Winter 2015 had the most smaller individuals during the study ($\chi^2 = 29.88$, adj. $p < 0.001$, df = 1), with 48.15 % of the captured individuals falling within and below the 8 – 8.9 cm size class. In Autumn 2016 63.33 % of the captured individuals were within and above the 10 – 10.9 cm size class and was the trapping session where the most larger- compared to smaller individuals were recorded ($\chi^2 = 41.88$, adj. $p < 0.001$, df = 1) (Figure 9). From Summer 2016 to Summer 2017, the population consisted of significantly more large than small individuals (adj. $p < 0.05$, chi-squared test) (Figure 9).

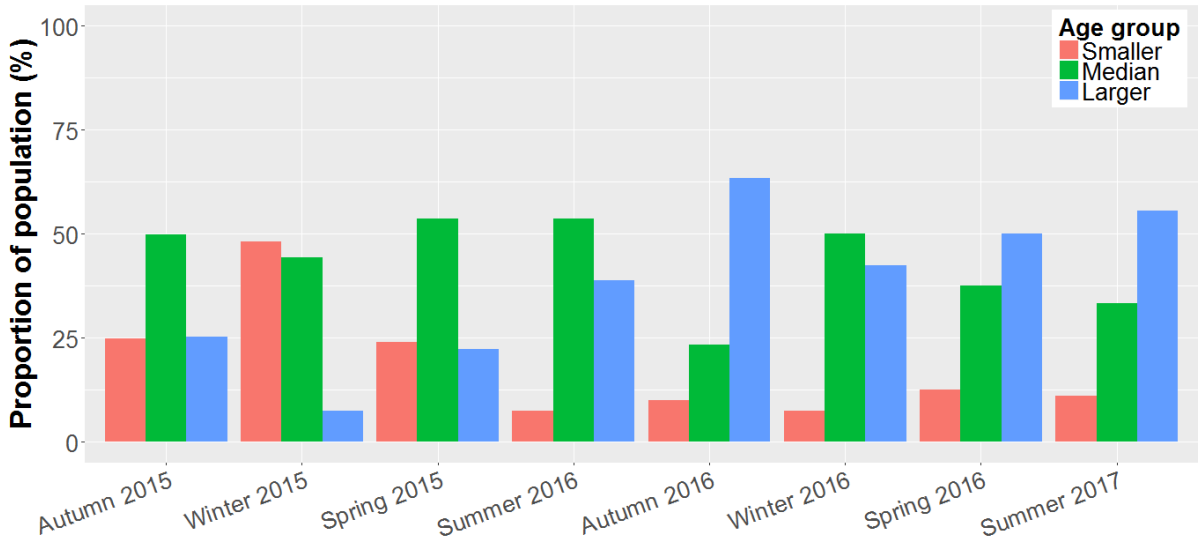


Figure 9. Proportion of *R. bechuanae* recorded in the smaller- (size classes 7 and 8; red columns) median- (size class 9; green columns) and larger (size classes 10 and 11; blue columns) body size classes seasonally at TDR. Data have been pooled for females and males

Considering the entire data set, body size varied significantly with sex ($F = 93.59$, $p < 0.001$, $df = 1, 714$), males being larger than females (Figure 10) and reproductively active individuals of both sexes being larger than non-reproductive individuals ($F = 179.48$, $p < 0.001$, $df = 1, 714$; Figure 11). There was no significant interaction between sex and reproductive state in affecting differences in body size *(*$F = 1.82$, $p = 0.178$, $df = 1, 714$*)*.

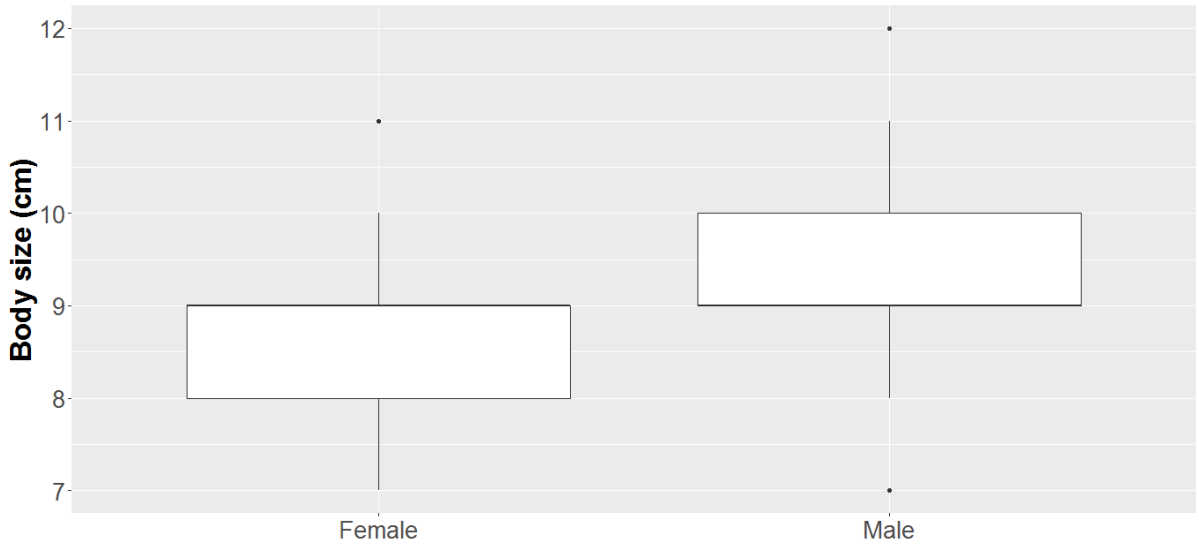


Figure 10. Body size variation of female and male *R. bechuanae* for 2015 to 2017 at TDR. Data for non-reproductive and reproductive individuals are pooled. The boxes indicate the first and third interquartiles, the darker horizontal lines along the box edges indicate median values, the whiskers indicate minimum and maximum values, and the black dots represent outliers.

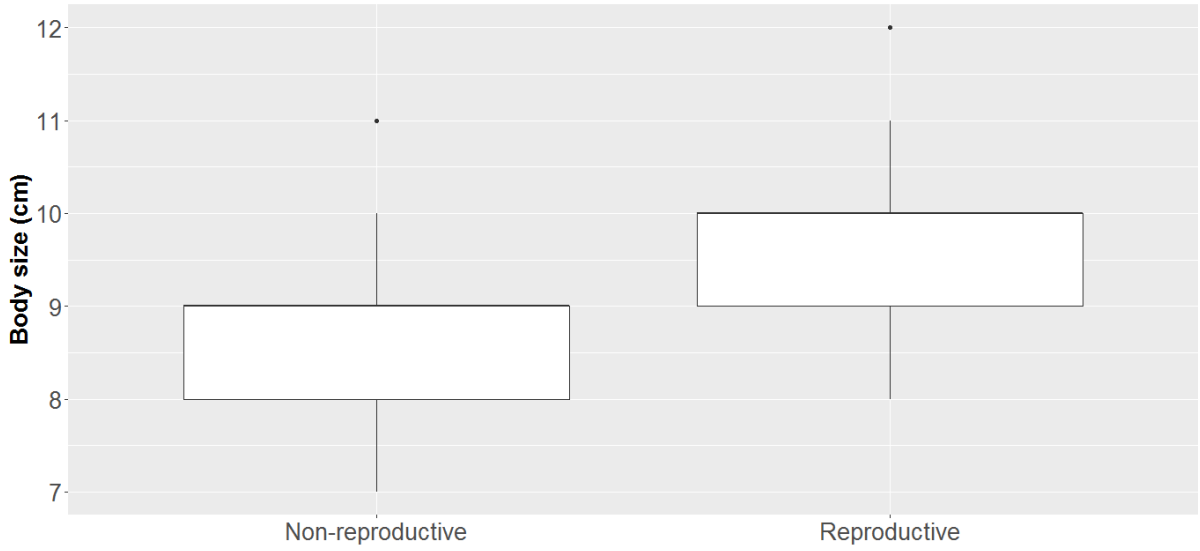


Figure 11. Body size variation of non-reproductive and reproductive *R. bechuanae* for 2015 to 2017 at TDR. Data for both sexes are pooled. The boxes indicate the first and third interquartiles, the darker horizontal lines along the box edges indicate median values, the whiskers indicate minimum and maximum values, and the black dots represent outliers.

3.1.7. Body mass

The minimum mass of a female *R. bechuanae* showing reproductive signs was 18.5 g (vagina perforate; Summer 2017) and that of a male *R. bechuanae* was 28 g (scrotal testes; Spring 2015). The maximum mass was 70.5 g in a female and 65 g in a male, both were reproductively active (the female was pregnant) and trapped in Autumn 2016. Male *R. bechuanae* in the two-year study period had a mean mass of 39.12 g (SE = 0.43). Peaks in mean mass were observed in Summer 2016 and Autumn 2016 and the lowest mass in Summer 2017 (Table 12).

Table 12. Mean ± SE mass recorded for male *R. bechuanae* at TDR for all age classes, in each trapping session. Sample size (n) is included.

Trapping session	Autumn 2015	Winter 2015	Spring 2015	Summer 2016	Autumn 2016	Winter 2016	Spring 2016	Summer 2017
Mass (g)	38.34 ± 0.78	38.09 ± 0.91	38.99 ± 0.80	43.03 ± 1.04	43.78 ± 2.68	38.85 ± 1.62	39.39 ± 1.70	33.23 ± 1.27
N	145	69	83	34	18	27	14	3

I analysed the effect of season and reproductive state on mass in male *R. bechuanae* of size class 9 (n = 167), accounting for the mass effect of body size. A two-way Anova with interaction (including season and reproductive state as fixed effects) showed significant differences in body mass according to reproductive state ($F = 17.07$, $p < 0.001$, df = 1, 155) and the interaction of reproductive state and season ($F = 2.46$, $p = 0.015$, df = 3, 155), though body mass did not vary significantly seasonally ($F = 1.10$, $p = 0.404$, df = 7, 155). Reproductively active males were significantly heavier than non-reproductive males (Figure 12). Of the 8 trapping sessions, the body mass of reproductively active to non-reproductive males was significantly different only in Autumn 2015 ($p < 0.001$, Tukey HSD test).

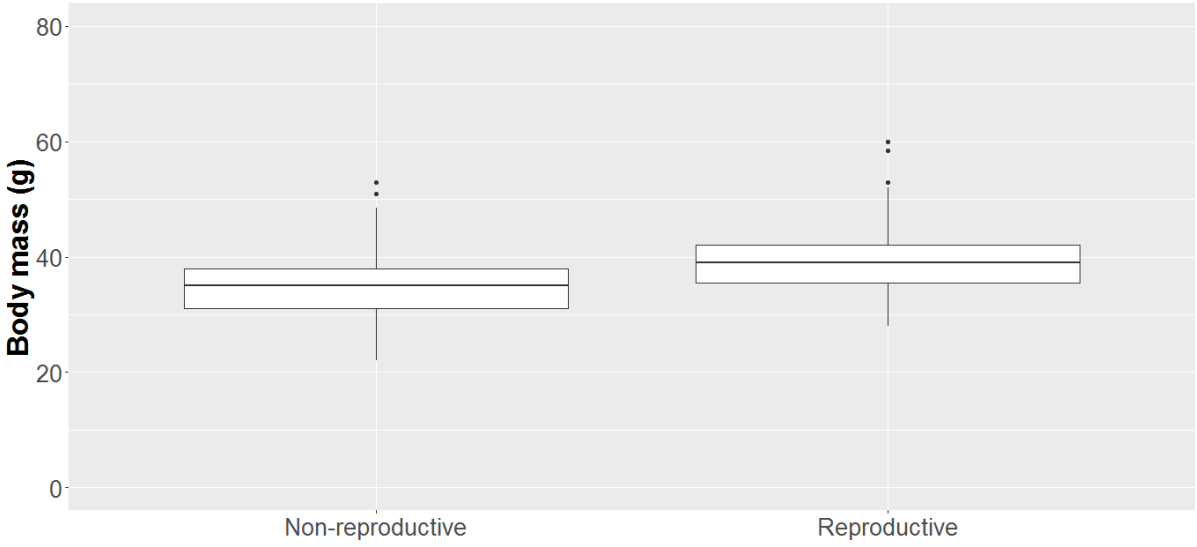


Figure 12. Comparison of body mass between non-reproductive (NR) and reproductive (R) males of size class 9 for 2015 to 2017 at TDR. The boxes indicate the first and third interquartiles, the darker horizontal lines inside the box edges indicate median values, the whiskers indicate minimum and maximum values, and the black dots represent outliers.

Using an LMM, I analysed the effects of minimum and maximum temperature (30 days prior to each trapping session), rainfall (30 and 90 days prior to each trapping session) as well as median plant cover on body mass of males of size class 9 at TDR. Variation in body mass was not affected by minimum temperature, maximum temperature, rainfall 30 days *a priori*, rainfall 90 days *a priori* or plant cover.

3.1.8. Sexual dimorphism in mass

Based on the reproductive characteristics of the individuals trapped, Winter 2015 was identified as the only non-breeding season (i.e. no reproductively active individuals trapped). Body mass records for individuals captured in this trapping session were used to investigate sexual dimorphism of *R. bechuanae* at TDR. No females of size class 10 (10 – 10.9cm) were recorded in this season, and therefore, comparisons were made between females and males of size classes 8 and 9. There was no difference in body mass between females and males of size class 8 ($F = 3.41$, $p = 0.073$, $df = 1, 37$) or 9 ($F = 0.14$, $p = 0.711$, $df = 1, 33$).

3.1.9. Regional temperature and rainfall

3.1.9.1. Regional temperature for the 30 days preceding each trapping session:

Significantly lower minimum temperatures were recorded 30 days prior to the Spring 2015 trapping session compared to Spring 2016 ($p = 0.001$, Tukey HSD test). Maximum temperature was higher in the 30 days prior to the trapping sessions of Summer 2016 compared to Summer 2017 ($p < 0.001$, Tukey HSD test). The lowest average temperatures were recorded 30 days prior to Winter 2015 and Winter 2016 (Table 13). The highest average regional temperatures were recorded 30 days prior to the Summer 2016 and Spring 2016 trapping sessions (Table 13).

Table 13: Mean ± SD regional temperature recorded during the 30 days preceding each trapping session, including counts of lower- (< 0 °C) and upper extremes (> 35 °C) at TDR.

Trapping session	Mean ± SD	Lower extremes	Upper extremes
Autumn 2015	Min.: 5.68 ± 4.39 Max.: 23.98 ± 3.62	3	0
Winter 2015	Min.: -0.46 ± 3.03 Max.: 17.34 ± 3.74	16	0
Spring 2015	Min.: 7.68 ± 3.52 Max.: 29.42 ± 4.17	0	0
Summer 2016	Min.: 14.80 ± 2.23 Max.: 34.08 ± 3.63	0	11
Autumn 2016	Min.: 5.91 ± 4.49 Max.: 24.08 ± 4.87	5	0
Winter 2016	Min.: -1.38 ± 2.23 Max.: 17.74 ± 3.39	22	0
Spring 2016	Min.: 11.21 ± 2.76 Max.: 29.67 ± 3.99	0	2
Summer 2017	Min.: 14.02 ± 2.50 Max.: 29.41 ± 3.39	0	0

3.1.9.2. Regional rainfall for the 30 and 90 days preceding each trapping session:

No correlation was observed between total rainfall 30- and 90 days preceding each trapping session ($r_s = 0.24$, $p = 0.582$). Total annual rainfall, i.e. cumulative rainfall for the 90 days preceding the first four- and the last four seasons respectively, did not vary ($\chi^2 = 0.16$, $p = 0.689$, $df = 1$) between the first- (314.95 mm) and second year (325.15 mm) of the study. Total rainfall for the 30 days preceding each trapping session differed significantly between Autumn ($\chi^2 = 16.36$, adj. $p < 0.001$, $df = 1$), Spring ($\chi^2 = 9.55$, adj. $p = 0.002$, $df = 1$) and Summer ($\chi^2 = 20.82$, adj. $p < 0.001$, $df = 1$) of the different study years (Figure 13). Total rainfall for the 90 days preceding each trapping session differed significantly between Autumn ($\chi^2 = 18.13$, adj. $p < 0.001$, $df = 1$) and Summer ($\chi^2 = 42.65$, adj. $p < 0.001$, $df = 1$) of

the different study years (Figure 13). The smallest differences in rainfall between the 30 and 90 days preceding a trapping session was recorded for Summer 2016 (4.80 mm) and Winter 2016 (7.90 mm) and the greatest differences were recorded for Autumn 2015 (191.15 mm) and Autumn 2016 (84 mm) (Figure 13).

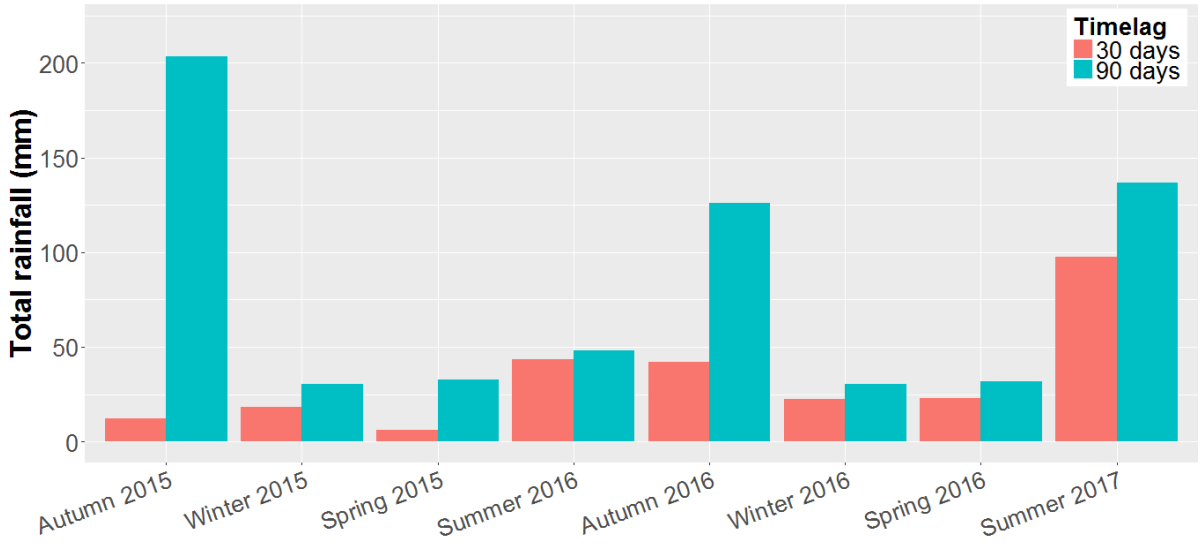


Figure 13. Total rainfall for the 30 and 90 days respectively preceding each trapping session at TDR.

3.1.10. Plant cover

A strong positive correlation occurred between median plant cover associated with *R. bechuanae* trap stations and the entire sample (Table 14) at this study site for total- (r_s = 0.83, p = 0.015), wood- (r_s = 0.93, p = 0.001) and grass cover (r_s = 0.98, p < 0.001). Due to this correlation, I only discuss here the median plant cover, for all three indices, recorded at trap stations that successfully captured *R. bechuanae*, even though the LMM analyses considered the entire sample (successful trap stations as well as randomly sampled trap stations of a similar number) at the TDR study site.

Table 14. Number of successful trap stations associated with *R. bechuanae* for which plant cover was sampled during each season and year of the study. Estimates concerning plant cover for the study site were calculated with the reported sample sizes.

Season	Number of successful trap stations	Sample size for study site
Autumn 2015	89	120
Winter 2015	57	82
Spring 2015	79	158
Summer 2016	62	124
Autumn 2016	25	50
Winter 2016	26	52
Spring 2016	18	36
Summer 2017	10	20
Total	366	642

Plant cover associated with R. bechuanae *trap stations*:

The median plant cover at trap stations with *R. bechuanae* varied significantly seasonally for total- ($F = 9.09$, $p < 0.001$, df = 7, 358), wood- ($F = 7.03$, $p < 0.001$, df = 7, 358) and grass cover ($F = 12.06$, $p < 0.001$, df = 7, 358). For the first and second study year, median total cover was greatest in Autumn 2015 (73.75 %) and Autumn 2016 (63.75 %) and lowest in Summer 2016 (51.25 %) and Summer 2017 (47.50 %). Grass cover was more abundant than wood cover at trap stations associated with *R. bechuanae* in Autumn 2015 ($\chi^2 = 14.08$, adj. $p < 0.001$, df = 1), Winter 2015 ($\chi^2 = 20.78$, adj. $p < 0.001$, df = 1), Spring 2015 ($\chi^2 = 12.08$, adj. $p < 0.001$, df = 1) and Summer 2017 ($\chi^2 = 15.02$, adj. $p < 0.001$, df = 1), median grass cover having been 35.50 % to 53.75 %. Wood cover was more abundant than grass cover but not significantly so in Summer-, Autumn-, Winter - and Spring 2016 ($p > 0.05$, chi-squared test).

3.2. Soetdoring (SO) Nature Reserve

3.2.1. Trapping scheme and sample size

Data collection at SO took place over 51 days or 9060 trap-nights. A total of 120 *R. bechuanae* individuals were tagged during this period, corresponding to 241 captures (including first and subsequent recaptures). The approximate surface area of the trapping grid was 10.97 ha. Five other small mammal species were trapped at this study site (Appendix, Table A2).

Figure 14A illustrates the differences in trapping effort (mean =1132.50, SD = 189.38) across the 8 sampling sessions. The variation was the result of differences in both the duration of a trapping session

(in days) as well as the number of traps set per day, the latter having been determined by the number of field assistants available for a given trapping session. The lowest sampling effort occurred during Summer 2017 (875 trap nights) and the greatest during Autumn 2016 (1434 trap nights) (Figure 14A). The number of individuals trapped decreased consistently from Autumn 2015 to Autumn 2016 and Winter 2016 to Summer 2017. Winter 2016, although sampling effort was comparatively low (Figure 14A), saw an increase in the number of animals trapped compared to Autumn 2016 (Figure 14B). The three largest sample sizes were recorded in the first year of the study (Autumn 2015 – Spring 2015) (Figure 14B). The sample sizes for trapping sessions from Summer 2016 onward were comparatively small ($n \leq 7$).

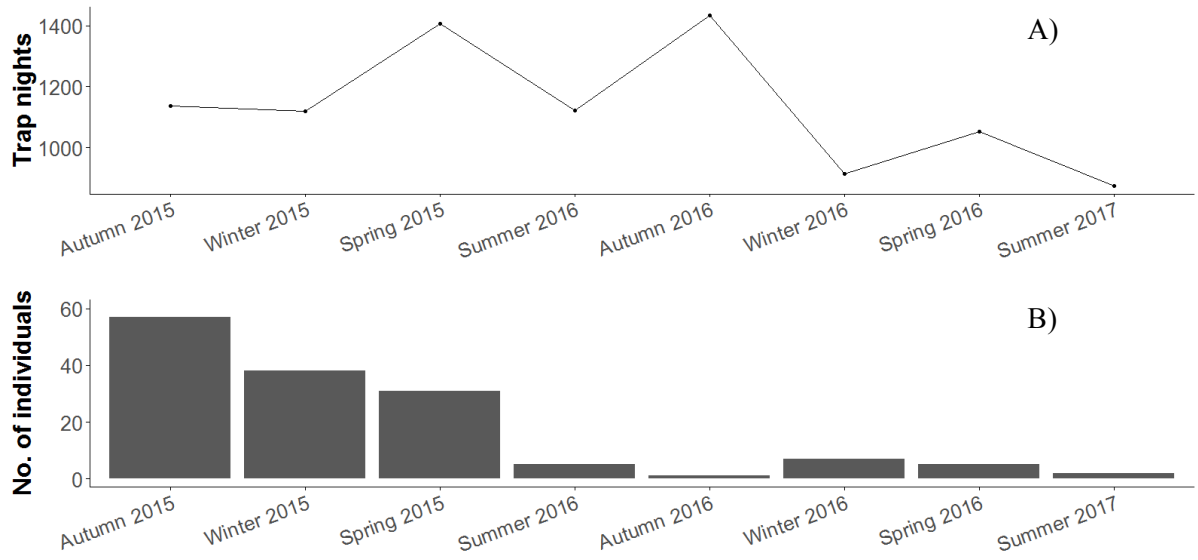


Figure 14. A.) Total number of trap nights and B.) the number of individual *R. bechuanae* per trapping session seasonally at SO.

3.2.2. Population size

The best supported full-likelihood model for 4 of the 5 estimable seasons indicated no time dependence in the probability of capture. This suggested that for these trapping sessions there were no difference in the daily probability of an individual *R. bechuanae* being captured. Due to the small sample size, population size could not be estimated for Summer 2016, Autumn 2016 and Summer 2017 and the values reported are equal to the number of *R. bechuanae* captured within the first four days of each respective trapping session (Table 15). For the first study year, the peak population size was observed in Autumn / April 2015 and for the second year in Winter / August 2016 (Table 15). The mean

population size (N Estimate) in the two-year study period was 21.70 (SE = 9.33). Peak density of *R. bechuanae* at SO was 11 individuals / ha (mean of 2 individuals / ha).

Table 15. The minimum number of animals alive (MNA), estimated seasonal population size (N Estimate), along with standard error, lower as well as upper Confidence Intervals (CI) for *R. bechuanae* at SO. Estimates for seasons marked with '*' were computed with a model specifying time invariance in recapture probability.

Season	MNA	N Estimate	Standard Error	Lower CI	Upper CI
Autumn 2015*	57	74.18	6.87	65.08	93.55
Winter 2015	29	37.31	4.85	31.87	53.03
Spring 2015*	30	40.09	5.52	33.70	57.52
Summer 2016	4	(3)	NA	NA	NA
Autumn 2016	1	(1)	NA	NA	NA
Winter 2016*	7	8.83	4.13	6.35	28.98
Spring 2016*	5	7.15	3.47	5.23	24.78
Summer 2017	3	(2)	NA	NA	NA

Using a LMM I analysed the effects of minimum and maximum temperature (30 days prior to each trapping session) as well as rainfall (30 and 90 days prior to each trapping session) on population size at SO. All the extrinsic factors included as continuous predictors in the linear model significantly affected variation in population size (Table 16). However, no significant correlation was observed between population size and any of the continuous predictors that tested significant in the LMM.

Table 16. Continuous predictor estimates for the fully parameterised model with population size as dependent variable for *R. bechuanae* at SO. Standard error, t- and p-value (Kenward-Roger approximation), corresponding with each estimate, have been included.

Predictor	Estimate	Standard error	t-value	p-value
Min. temperature	-8.06	1.21	-6.63	< 0.001
Max. temperature	8.04	1.24	6.48	< 0.001
Rain 30	-0.44	0.06	-7.82	< 0.001
Rain 90	0.46	0.04	11.83	< 0.001

3.2.3. Survival rates and capture histories

Of the 16 CJS models fit to the capture histories dataset for *R. bechuanae* in SO, the three best supported models accounted for 83.00 % of the AIC_c weight (Table 17). These were also the only three models

where all the parameters were estimable according to '2nd part' variance-covariance matrix estimation. Given the small difference in AIC_c ($\Delta AIC_c < 2$), these models have approximately equal support in the data set. The model with the least number of parameters (model 'Φ(.) p(.)') (Table 17) was taken to best describe the dataset. The most parsimonious model indicated both season and sex invariance of survival- and recapture rates (Table 18). No LMM was performed, given that survival remained constant across seasons.

Table 17. The 3 best supported models estimating survival and recapture probability for the *R. bechuanae* population at SO.

Model structure	AIC_c	Delta AIC_c	AIC_c weight	Number of parameters
Φ(sex) *p*(.)	77.20	0	0.39	3
Φ(.) *p*(sex)	77.91	0.71	0.28	3
Φ(.) *p*(.)	79.00	1.80	0.16	2

Table 18. The survival- and recapture rate estimates for the *R. bechuanae* population at SO. Standard error as well as lower and upper Confidence Intervals (CI) are reported for each estimate.

Parameter	Estimate	Standard Error	Lower CI	Upper CI
Survival	0.19	0.08	0.08	0.40
Recapture	0.54	0.27	0.13	0.91

Of the 87 individuals collectively trapped in the first 4 days of the 8 trapping sessions, 89.66 % were trapped once and females (n = 44) and males (n = 43) were equally likely of being only observed once during the two-year study period (χ^2 = 1.40, p = 0.237, df = 1). The mean number of sessions an individual was observed was 1.13 (SE = 0.04).

A single female and male were observed for 3 consecutive trapping sessions (the longest capture history), both trapped for the first time in Autumn 2015. At all three captures the female was observed at size class 9 with an initial body mass of 30.5g and the male at size class 10 with an initial mass of 46g. The longevity of this female was approximately 32 weeks and approximately 35 weeks for the male.

3.2.4. Sex ratio

Over the two-year study period a total of 85 females and 61 males were recorded ($\chi^2 = 3.94$, p = 0.047, df = 1), indicating a significant disparity in the overall sex ratio. Autumn 2015 was the only trapping session where the proportion of females to males captured was near parity ($\chi^2 = 0.77$, adj. p = 0.380, df = 1). From Winter 2015 to Autumn 2016 females were captured consistently more than males ($p < 0.05$, chi-squared test) and Winter 2016 to Summer 2017 saw significantly more males than females being captured ($p < 0.05$, chi-squared test) (Figure 15). Sample size was very small from Summer 2016 onward ($n \leq 7$) and the sex ratios for these trapping sessions were therefore not assumed to be representative of the population existing at that time.

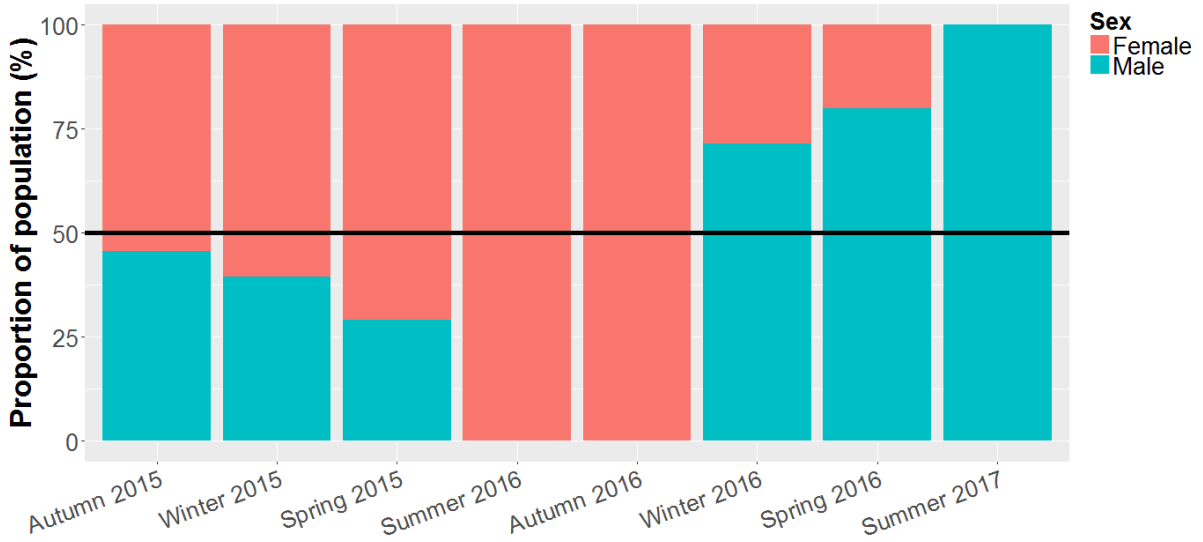


Figure 15. The seasonal female: male proportions of *R. bechuanae* at SO. The horizontal black line indicates the position of parity (i.e. a sex ratio of 1:1).

3.2.5. Reproductive activity

Reproductively active individuals were observed in all trapping sessions except Winter 2015. Of the trapping sessions with sample size > 7 *R. bechuanae* individuals, Autumn 2015 had the largest proportion of potentially reproductively active individuals (Table 19). Reproductively active males would have been recorded as scrotal and females as pregnant, lactating and / or vagina perforated. No reproductively active individuals were recorded in Winter 2015 compared to Winter 2016 (Table 19). Winter 2016 ($\chi^2 = 0$, adj. p = 1.00, df = 1) was the only trapping session where the proportions of female to male reproductively active individuals was equal (i.e. 2 females and 2 males; Figure 16).

Table 19. Proportion of potentially reproductively active individuals of the total number (n) of *R. bechuanae* captured at each trapping session at SO. Data for females and males are pooled.

Trapping session	Autumn 2015	Winter 2015	Spring 2015	Summer 2016	Autumn 2016	Winter 2016	Spring 2016	Summer 2017
Proportion	70.18 %	0 %	29.03 %	20.00 %	100 %	57.14 %	20.00 %	66.67 %
n	57	38	31	5	1	7	5	3

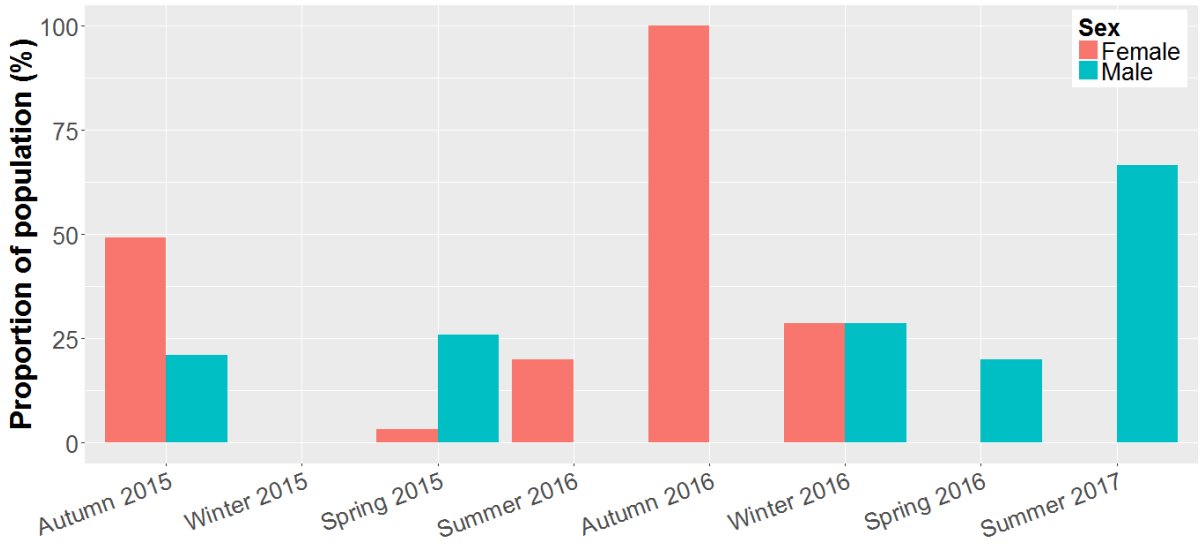


Figure 16. Proportion of potentially reproductively active female and male *R. bechuanae* in each trapping session at SO.

3.2.6. Body size

The smallest body size in reproductively active individuals was 8 – 8.9 cm for females and 9 – 9.9 cm for males. The largest size class observed for females was 11 – 11.9 cm (n = 2) and 12 – 12.9 cm for males (n = 1), all recorded as reproductively active. Individuals from size classes 8, 9 and 10 were the most frequently observed during the two-year study period comprising 92.31 % of all the individuals trapped (Table 20). Size class 9 was the most common class during the two-year study period (Table 20).

Table 20. Frequency of female and male *R. bechuanae* at SO observed during the entire study period for each size class as well as the proportion of the captured population represented by each size class.

Size class	Class breadth	Frequency females	Frequency males	Proportion of total sample (n = 143)
7	7 – 7.9 cm	2	1	2.10 %
8	8 – 8.9 cm	15	8	16.08 %
9	9 – 9.9 cm	44	22	46.15 %
10	10 – 10.9 cm	18	25	30.07 %
11	11 – 11.9 cm	2	5	4.90 %
12	12 – 12.9 cm	0	1	0.70 %

The number of individuals representing each body size class varied seasonally ($F = 2.83$, $p = 0.009$, df = 7, 135). Using median size class (size class 9), I compared the proportion of the population that was smaller- (size classes 7 and 8) with that larger (size classes 10 and 11) than the median seasonally (Figure 17), paying specific attention to trapping sessions with sample size > 7 (i.e. Autumn-, Winter- and Spring 2015) In Autumn 2015 46.43 % of the captured individuals were within and above the 10 – 10.9 cm size class (Figure 17) and was the trapping session where the most larger- versus smaller individuals were observed ($\chi^2 = 28.81$, adj. $p < 0.001$, df = 1). In Winter 2015, significantly more smaller individuals were recorded compared to larger individuals ($\chi^2 = 6.79$, adj. $p = 0.006$, df = 1). No individuals smaller than the median size class were observed during the Summer 2016, Autumn 2016 or Summer 2017 trapping sessions (Figure 17).

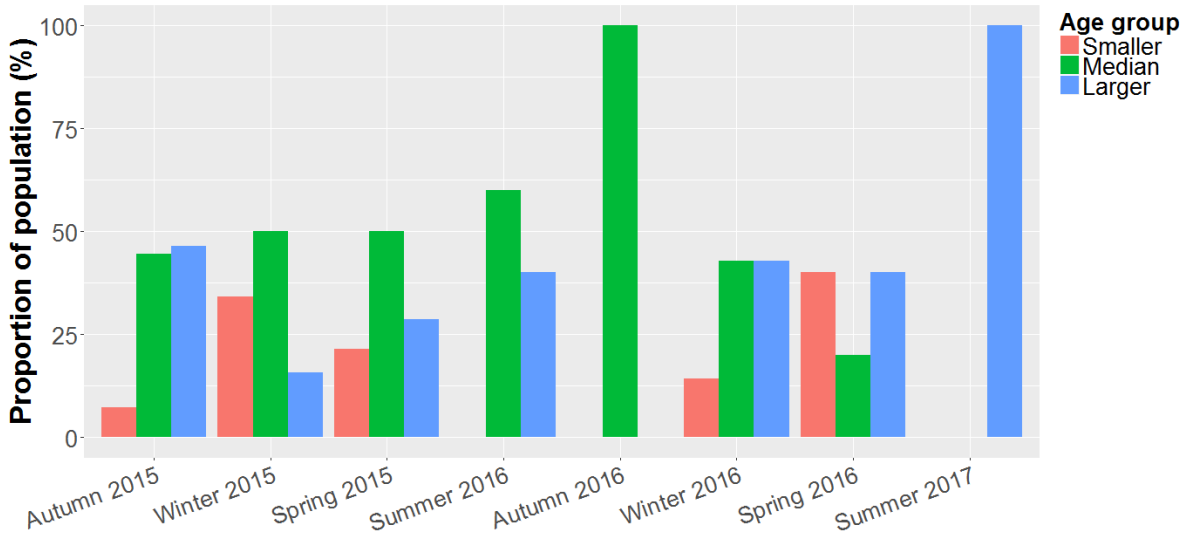


Figure 17. Proportion of *R. bechuanae* recorded in the smaller (size classes 7 and 8; blue columns) median- (size class 9; red columns) and larger- (size classes 10 and 11; green columns) body size classes seasonally at SO. Data have been pooled for females and males.

Considering the entire dataset, body size varied significantly with sex ($F = 8.32$, $p = 0.005$, $df = 1, 141$), with males being larger than females (Figure 18) and reproductively active individuals of both sexes were larger than non-reproductive individuals ($F = 46.50$, $p < 0.001$, $df = 1, 141$; Figure 19). There was no significant interaction between sex and reproductive state in affecting variation in body size *(*$F = 1.39$, $p = 0.240$, $df = 1, 139$*)*.

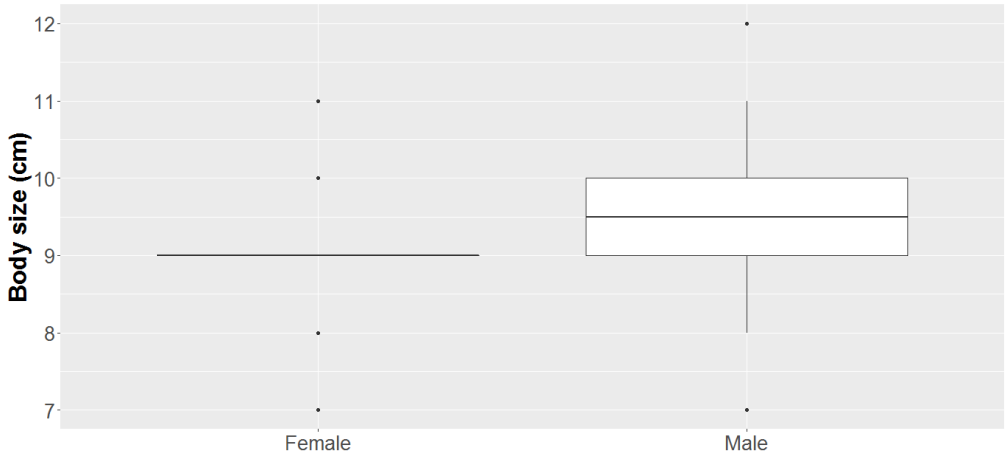


Figure 18. Body size variation for female and male *R. bechuanae* for 2015 to 2017 at SO. Data for non-reproductive and reproductive individuals are pooled. The boxes indicate the first and third interquartiles, the darker horizontal lines along the box edges indicate median values, the whiskers indicate minimum and maximum values, and the black dots represent outliers.

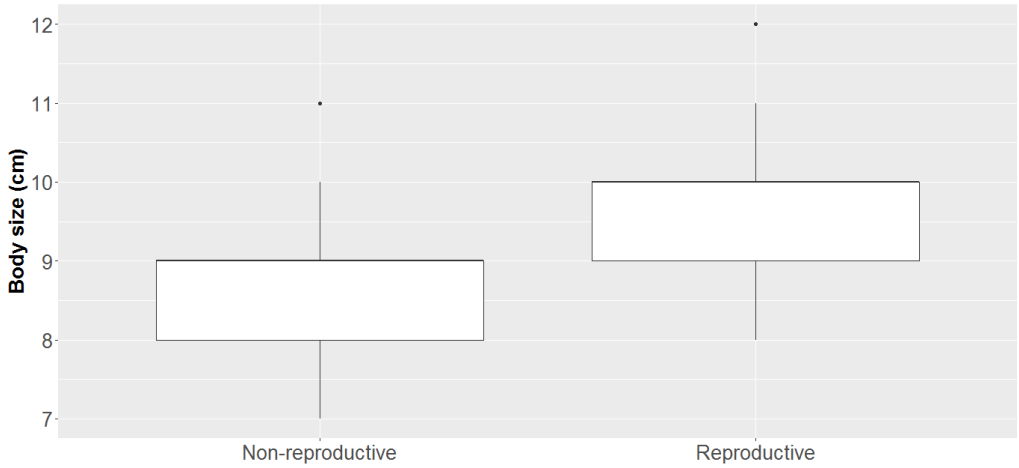


Figure 19. Body size variation for non-reproductive and reproductive *R. bechuanae* for 2015 to 2017 at SO. Data for both sexes are pooled. The boxes indicate the first and third interquartiles, the darker horizontal lines along the box edges indicate median values, the whiskers indicate minimum and maximum values, and the black dots represent outliers.

3.2.7. Body mass

The minimum mass of a female *R. bechuanae* showing reproductive signs was 28.50 g (Autumn 2015) and that of a male *R. bechuanae* was 33.00 g (Autumn 2015). The maximum mass was 50.50 g in a female and 65.00 g in a male, both were reproductively active (the female was pregnant) and trapped

in Autumn 2015. Male *R. bechuanae* in the two-year study period had a mean mass of 38.73 g (SE = 1.25). Peaks in mean mass were observed in Autumn 2015 and Spring 2015 and the lowest mass in Winter 2016 (Table 21).

Table 21. Mean ± SE mass recorded for male *R. bechuanae* at SO for all age classes, in each trapping session. Sample size (n) is included.

Trapping session	Autumn 2015	Winter 2015	Spring 2015	Summer 2016	Autumn 2016	Winter 2016	Spring 2016	Summer 2017
Mass (g)	39.79 ± 2.47	37.09 ± 1.82	40.38 ± 1.89			35.00 ± 4.90	38.88 ± 3.39	38.23 ± 3.62
n	26	14	9	0	0	5	4	3

I analysed the effect of season and reproductive state on mass in male *R. bechuanae* of size class 9 (n = 22), accounting for the mass effect of body size. There was no significant difference in body mass seasonally (F = 0.45, p = 0.769, df = 4, 17) or between reproductively active (n = 4) and non-reproductive males (n = 18) (F = 0.06, p = 0.814, df = 1, 20). No difference in body mass was observed for Winter or Spring of different study years (p > 0.05, Tukey HSD test), the only seasons with body mass records for males of size class 9 (Table 21).

3.2.8. Sexual dimorphism in mass

Based on the reproductive characteristics of the individuals trapped, Winter 2015 was identified as the only non-breeding season (i.e. no reproductively active individuals trapped). Body mass records for individuals captured at this trapping session were used to investigate sexual dimorphism of *R. bechuanae* at SO. No males of size class 7 (7 – 7.9 cm) and only 1 female of size class 10 (10 – 10.9 cm) were recorded at this trapping session. Comparisons were therefore made using samples for size classes 8 and 9, respectively. There was no difference in body mass between females and males of size class 8 (F = 3.34, p = 0.098, df = 1, 10) or 9 (F = 0.12, p = 0.739, df = 1, 17).

3.2.9. Regional temperature and rainfall

3.2.9.1. Regional temperature for the 30 days preceding each trapping session:

There were no significant differences in the minimum and maximum temperatures for the 30 days preceding the same seasons of different years (p > 0.05, Tukey HSD test). The lowest mean temperatures were recorded 30 days prior to the Winter 2015 and Winter 2016 trapping sessions (Table

22). The highest mean temperatures were recorded 30 days prior to the Summer 2016 and Spring 2016 trapping sessions (Table 22).

Table 22: Mean ± SD regional temperature recorded during the 30 days preceding each trapping session, including counts of lower- (< 0 °C) and upper extremes (> 35 °C) at SO.

Trapping session	Mean ± SD	Lower extremes	Upper extremes
Autumn 2015	Min.: 7.97 ± 4.66 Max.: 25.92 ± 2.72	2	0
Winter 2015	Min.: 1.32 ± 3.15 Max.: 20.59 ± 3.21	12	0
Spring 2015	Min.: 9.24 ± 3.1 Max.: 30.91 ± 4.52	0	8
Summer 2016	Min.: 17.6 ± 2.14 Max.: 33.4 ± 4.91	0	11
Autumn 2016	Min.: 9.83 ± 2.29 Max.: 26.73 ± 4.12	0	0
Winter 2016	Min.: -0.79 ± 2.51 Max.: 18.48 ± 3.51	22	0
Spring 2016	Min.: 9.96 ± 4.96 Max.: 31.56 ± 4.59	0	10
Summer 2017	Min.: 15.19 ± 2.91 Max.: 31.10 ± 3.59	0	2

3.2.9.2. Regional rainfall for the 30 and 90 days preceding each trapping session:

A strong positive correlation was observed between total rainfall 30- and 90 days preceding each trapping session (r_s = 0.86, p = 0.011). Total annual rainfall, i.e. cumulative rainfall for the 90 days preceding the first four- and the last four seasons respectively, varied significantly (χ^2 = 26.86, p < 0.001, df = 1) between the first- (364.94 mm) and second year (519.03 mm) of the study. Total rainfall for the 30 days preceding each trapping session differed significantly between Autumn (χ^2 = 62.13, adj. p < 0.001, df = 1) and Winter (χ^2 = 11.95, adj. p < 0.001, df = 1) of the different study years. Total rainfall for the 90 days preceding each trapping session differed significantly between Winter (χ^2 = 27.83, adj. p < 0.001, df = 1) and Summer (χ^2 = 7.81, adj. p = 0.005, df = 1) of the different study years. The smallest differences in rainfall between the 30 and 90 days preceding a trapping session was recorded for Spring 2015 (10.92 mm) and Spring 2016 (6.49 mm) and the greatest differences were recorded for Autumn 2015 (137.81 mm) and Summer 2017 (102.42 mm) (Figure 20).

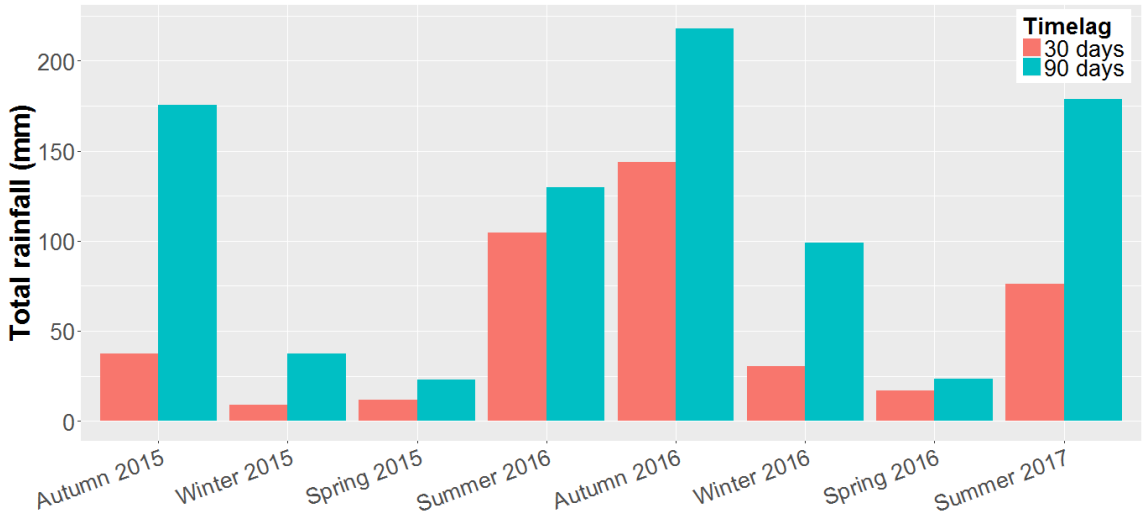


Figure 20. Total rainfall for the 30 and 90 days respectively preceding each trapping session at SO.

3.2.10. Plant cover

A strong positive correlation was observed between median plant cover associated with *R. bechuanae* trap stations and the entire sample at SO (Table 23) for total- (r_s = 0.93, p = 0.002), wood- (r_s = 0.86, p = 0.006) and grass cover (r_s = 0.88, p = 0.007). Due to this correlation, I only discuss here the median plant cover recorded at trap stations that successfully captured *R. bechuanae*, even though the LMM analyses considered the entire sample (successful trap stations as well as randomly sampled trap stations of a similar number) at SO.

Table 23. Number of successful trap stations associated with *R. bechuanae* for which plant cover was sampled during each season and year of the study at SO. Estimates concerning plant cover for the study site were calculated with the reported sample sizes.

Season	Number of successful trap stations	Sample size for study site
Autumn 2015	27	54
Winter 2015	27	54
Spring 2015	24	48
Summer 2016	5	10
Autumn 2016	2	4
Winter 2016	5	10
Spring 2016	5	10
Summer 2017	3	6
Total	98	196

Plant cover associated with R. bechuanae *trap stations*:

The median plant cover at trap stations with *R. bechuanae* varied significantly seasonally for total- (F = 10.87, p < 0.001, df = 7, 90) and grass cover (F = 4.22, p < 0.001, df = 7, 90). Wood cover did not vary significantly in the 8 seasons (F = 1.82, p = 0.092, df = 7, 90). For the first and second study year respectively, median total cover was greatest in Winter 2015 (96.25 %) and Winter 2016 (67.50 %) and lowest in Summer 2016 (57.50 %) and Spring 2016 (60.00 %). Grass cover was more abundant than wood cover only in Autumn 2015 (χ^2 = 8.63, adj. p = 0.003, df = 1). Wood cover was significantly more abundant than grass cover in Summer 2016 (χ^2 = 35.22, adj. p < 0.001, df = 1), Autumn 2016 (χ^2 = 51.21, adj. p < 0.001, df = 1), Winter 2016 (χ^2 = 9.38, adj. p = 0.002, df = 1), Spring 2016 (χ^2 = 42.59, adj. p < 0.001, df = 1) and Summer 2017 (χ^2 = 9.94, adj. p = 0.002, df = 1). Wood and grass contributed equally to cover at trap stations associated with *R. bechuanae* in Winter- and Spring 2015 (p > 0.05, chi-squared test).

4. Discussion

The aim of my study was to evaluate the demography (population size, survival rates, reproductive rates, sex ratio and body size class structure of the population) and basic morphology (body size, mass and dimorphism in mass) of two *R. bechuanae* populations. A critical feature of this research was the analysis of temporal variation in demography and physical characteristics (body size and mass). Finally, through empirical and theoretical investigation, I aimed to elucidate the influence of pertinent extrinsic environmental factors on seasonal fluctuations in population size, survival rates, reproductive rates and body mass. The small sample size of *R. bechuanae* for the Soetdoring Nature Reserve study site made inferences from the data analyses difficult. Therefore, where relevant, I referred to the results for Tussen die Riviere to substantiate my findings on *R. bechuanae*.

4.1. Population size

Peak population density of *R. bechuanae* at Tussen die Riviere (TDR) Nature Reserve (24 individuals/ha; mean of 8 individuals/ha) was 3 times greater than that of the species at Soetdoring (SO) Nature Reserve (7 individuals/ha; mean of 2 individuals/ha) and peak density at both sites was lower than has been recorded in other studies of *Rhabdomys* demography (Brooks 1974; David & Jarvis 1982; Krug 2004; Perrin *et al.* 2001; Schradin & Pillay 2005a, b). At both sites, peak population size, estimated according to full-likelihood models, during the first study year (419 individuals at TDR and 74 individuals at SO, in Autumn 2015) was 8 times greater than the peak size during the second year (50 individuals at TDR and 9 individuals at SO, in Winter 2016). From the data collected here it is apparent that clear inter-annual fluctuations existed in peak population size and that the timing / season of these peaks were not constant between years, similar to *R. pumilio* in the Cape flats, Western Cape Province (David & Jarvis 1985).

Although trapping effort varied across the study period, the timing of peaks in population size was similar between my populations: although not constant between years, both study populations peaked during the same seasons (Autumn of the first study year and Winter of the second). For both populations, the lowest population size was reached toward the end of the study period (Summer 2017), although the minimum number of animals alive at SO was ≤ 7 for the last 5 trapping sessions (Summer 2016 onward). The timing of positive population growth (i.e. an increase in population size) was also similar between the study populations: from Winter- to Spring 2015 and Autumn- to Winter 2016.

Rainfall (for the 30- and 90 days preceding each trapping session), significantly affected variation in population size seasonally for *R. bechuanae* at TDR. The effect of total rainfall in the 90 days preceding the trapping sessions is likely indirect since rainfall promotes an increase in plant cover and food

availability (Ernest *et al.* 2000; Brown & Ernest 2002), in turn promoting reproductive rates and population growth of *Rhabdomys* (Krug 2004; Nater *et al.* 2016). Although the regression analysis did not point to this, I expected a positive correlation with seasonal rainfall, 90 days preceding the trapping sessions, given its importance in determining plant cover and food availability, which is linked to population growth (Ernest *et al.* 2000; Brown & Ernest 2002). A strong negative correlation occurred between population size and total rainfall 30 days prior to each trapping session, which suggests that high rainfall the month preceding a trapping session is associated with a decline in population size. Extreme rainfall events, specifically sheet flooding, are known to cause mortality (and a resultant decline in population size) in small mammals, even capable swimmers such as the Kangaroo rat *Dipodomys spectabilis* (Brown & Ernest 2002). Flooding can also spoil underground seed stores and render nest sites temporarily uninhabitable (Ernest *et al.* 2000). Although *R. bechuanae* is an arid-adapted species, I do not expect flooding to be detrimental to my populations given that the slope in the landscape of the study sites would have resulted in run-off.

Variation in population size at SO was significantly associated with temperature (minimum and maximum) as well as rainfall (30 and 90 days prior to each trapping session), although no correlation was found between these continuous predictors and population size. Given the small sample size available for this study population, the results of this LMM remain tenuous. Nevertheless, the results of the LMM could point to the additive effect of temperature and rainfall in determining the availability of resources and, indirectly, population size at SO (Hone & Clutton-Brock 2007). Ultimately, the effect of extrinsic factors would be indirect in determining population size at TDR and SO. As population dynamics are mediated through changes in demographic rates (i.e. survival and reproduction) responding to environmental conditions (Benton *et al.* 2006), the effect of extrinsic factors on survival and reproductive rates ultimately determine the population size at a given time (Begon *et al.* 1990; Krebs 2013).

4.2. Survival rates and longevity

There was seasonal variation in survival rates for *R. bechuanae* at TDR, independent of sex. According to the most parsimonious CJS model, survival rates varied between 14 % and 54 % (mean of 33 %) and the highest rates coincided with periods of positive population growth from Winter- to Spring 2015 and Autumn- to Winter 2016. At SO, survival rate was constant at 19 %, independent of season or sex. This estimate, and the lack of variation between seasons, may however be confounded by the small sample size at this study site.

Variations in temperature (both minimum and maximum) as well as rainfall (90 days preceding each trapping session) were significantly associated with survival rate of *R. bechuanae* at TDR, although no

correlation existed between these continuous predictors and survival. Minimum temperature could affect survival rates directly through mortality due to hypothermia (Howard 1951). Across the study period, 128 frost days were recorded with 16 and 22 frost days recorded in the 30 days preceding Winter 2015 and Winter 2016, respectively. Nater et. al (2015) found considerable influence of temperature on survival at all life stages of *R. pumilio* with decreasing survival at low temperatures for immatures due to the cost of thermoregulation. Indirectly, minimum temperature could be related to decreased food availability associated with Winter months. Long term (three months preceding a trapping session) total rainfall can act additively in determining the seasonal availability of resources (Brown & Ernest 2002). Total rainfall for the 90 days preceding Winter of both study years was consistently the lowest compared to the other seasons. Similarly, Schradin & Pillay (2005a) linked the mortality rates of *R. pumilio* in the Succulent Karoo to low temperatures and deteriorating food supply in Winter.

Rhabdomys from arid regions are expected to have a high thermoneutral zone (32 ± 1 °C; Haim & le R. Fourie 1979) and the risk of exposure or evaporative water loss should be minor as it concentrates activity to the crepuscular periods of the day, remaining in cover in-between these periods (Christian 1977; Krug 2004; Perrin 1981). However, breeding adult *R. pumilio* are susceptible to high temperatures, an indirect effect coinciding with mortality at old age after the end of the second breeding season and the onset of summer (Nater *et al.* 2015). In *R. bechuanae*, maximum temperature may serve the same purpose. However, given the ecological differences, specifically differences in rainfall pattern and food availability, between *R. pumilio* in the Succulent Karoo (Winter rainfall of ± 150 mm per annum) and *R. bechuanae* in the Dry Highveld Grassland (Spring, Summer rainfall of ± 500 mm per annum; Rutherford *et al.* 2006), I would expect a difference (at least in timing) in the response of *R. bechuanae* survival to maximum temperature. Alternatively, maximum temperature could have an indirect, positive effect on survival and may be associated with increased food availability during Spring and Summer. Temperatures peaked during Spring and Summer of each year, also the seasons where the greatest abundance of green vegetation and flowers were observed (*pers. obs*). At TDR, peaks in total rainfall for the 90 days preceding the trapping sessions were recorded for Summer of both years and Spring of the second year. Therefore, rainfall could act additively with maximum temperature, determining the growing season in *R. bechuanae* habitat.

No correlation occurred between seasonal rainfall and survival rates of *R. bechuanae* at TDR. An interesting observation was that peak survival probabilities ($\Phi = 0.54$ during Winter- to Spring 2015 and $\Phi = 0.44$ during Autumn- to Winter 2016) were preceded by low total seasonal rainfall (≤ 33 mm recorded in the 90 days preceding Spring 2015 and Winter 2016) compared to low survival probabilities ($\Phi = 0.15$ during Summer- to Autumn 2016 and $\Phi = 0.14$ during Spring 2016 to Summer 2017) that

were preceded by high seasonal rainfall (≤ 137 mm recorded in the 90 days preceding Autumn 2016 and Summer 2017). A parsimonious explanation could be that *R. bechuanae* invest in survival during periods of low resource availability, during low rainfall periods, and in reproduction during periods of high resource availability, during periods of high rainfall.

R. bechuanae was observed to live for up to 70 weeks (17 months) at TDR and 30 weeks (7 months) at SO although the majority of individuals (75 % at TDR and 90 % at SO) were only captured once during the two-year study period. The lack of recaptures across trapping sessions could likely be explained by reduced survival, although emigration from the study sites may have been an important contributor. Similarly, David & Jarvis (1985) reported a mean longevity, since first capture, of 1.9 to 2.5 months for *R. pumilio* of the Cape flats with a maximum longevity of 15 months for females and 13 months for males.

4.3. Reproductive rates

At both study sites, potentially reproductively active individuals were observed at 7 of the 8 trapping sessions, with no morphological signs of reproduction recorded for any females or males during Winter 2015. With regards to the SO population, reproduction rates would have been relatively low due to the small sample size and the often biased sex ratio (for 7 out of 8 trapping sessions). Without dissection of the reproductive tracts, I could not determine whether oogenesis / spermatogenesis was taking place in potentially reproductively active individuals (David & Jarvis 1985) but instead refer to theory, and evidence from my data analysis, to delineate the approximate breeding seasons of my study populations.

For *R. bechuanae* at TDR, more than 40 % of the captured population was potentially reproductively active during Autumn (2015 and 2016), Summer (2016 and 2017) and Spring 2016. Peak population size in *Rhabdomys* is expected to reflect the end of the breeding season (David & Jarvis 1985; Nater *et al.* 2015). This trend has also been observed for small rodents, including *Rhabdomys*, at TDR nature reserve (Avenant & Cavallini 2007). For both study populations, peaks in population size were observed for Autumn 2015, Spring 2015 and Winter 2016 thus indicating that reproductive output peaked before these trapping sessions. It would be logical that Autumn 2015 was preceded by a breeding season as I expect *R. bechuanae* to breed when resources are most abundant, i.e. during Spring and Summer. It was also the trapping session where the largest proportion of small (< 9 cm) individuals were observed, possibly recruited through birth. Breeding did not take place in Winter 2015, at either site, and the peak in population size observed for Spring 2015 could therefore not be ascribed to reproductive output but perhaps immigration into the study site. It is plausible that peak breeding activity preceded Winter 2016: 80 % of the individuals captured (n = 30) at TDR during Autumn 2016 were potentially reproductively active and an equal number of potentially reproductive females and males were recorded. Therefore,

the plausible conclusion was that, during the study period, reproduction peaked before Autumn 2015 and Winter 2016.

According to the LMM, temperature (both minimum and maximum), rainfall (both 30- and 90 days *a priori*) and plant cover were associated with the seasonal proportion of the female population at TDR that was potentially reproductive. No relationship was observed between these extrinsic factors and female reproductive activity. In effect, reproductive activity could potentially be affected, positively or negatively, by temperature, rainfall and plant cover (Nater *et al.* 2015). The results of this LMM could point to the importance of seasonality (seasonal pattern of temperature, rainfall and plant cover) in determining reproductive activity. The lack of any linear relationship between female reproductive activity and the extrinsic factors could be a result of temporal desynchrony in peak reproductive activity, having plausibly occurred in Summer 2015 (outside my sampling period) and Autumn 2016.

Plant cover, used here as a proxy for resource availability, is essential to reproduction in providing food, to meet increased energy requirements (Krug 2004), habitat complexity for social interactions between females and males (Krebs 2013) as well as nesting opportunities (Krug 2004) for rearing young. Median total plant cover fluctuated within-year and was greatest during Autumn of each year, following high Summer rainfall, and lowest during Summer trapping sessions. Grass cover was an important feature of *R. bechuanae* habitat at TDR. It was the dominant vegetation type in Autumn 2015, Winter 2015, Spring 2015 as well as Summer 2017 and contributed equally with woody cover to *R. bechuanae* habitat at the other four trapping sessions. All the trapping sessions were preceded by rainfall in the 30 days *a priori*. Annuals or ephemerals, such as grasses, germinate and flower quickly in response to rainfall (Brown & Ernest 2002). The significant effect of all five continuous predictors could point to temperature, rainfall and plant cover acting additively in determining reproductive rates.

Although sex ratios for *R. bechuanae* at TDR were comparable for 6 out of 8 trapping sessions, parity in the number of potentially reproductive females to males was only observed at 2 trapping sessions. This could indicate temporal desynchrony in the change from non-reproductive to reproductive, with females perhaps becoming receptive before males, as observed for *R. pumilio* of the Cape flats (David & Jarvis 1985). However, the adaptive significance of this suggestion on the species' ecology remains unclear.

It remains unclear why the two populations studied were potentially reproductive during Winter 2016 but not Winter 2015. For TDR, statistically similar conditions were experienced prior to Winter 2015 and Winter 2016 and therefore neither temperature (for the month preceding) nor rainfall (for one or three months preceding) could alone explain this observation. However, an extended period of resource

availability, specifically protein rich food (Taylor & Green 1976; Perrin 1980a), may explain the large proportion of potentially reproductively active individuals present in Autumn 2016, resulting in the Winter 2016 peak in population size.

The coefficient of variation of 31 % indicated high variability in expected rainfall in the habitats occupied by *R. bechuanae* in my study sites (Rutherford *et al.* 2006). Indeed, total annual rainfall for SO was significantly higher during the second- compared to the first study-year. As an opportunistic breeder, reproduction in *R. bechuanae* could take place continuously, only ceasing if food availability declines (Jackson & Bernard 1999). As rainfall determines cover- and food availability (Brown & Ernest 2002), I do not expect the timing of the onset and termination of reproduction to be repeated annually.

4.4. Sex ratio

At TDR equal numbers of females to males were captured across the two-year study period and the sex ratio was skewed at only two of the trapping sessions (first towards males in Winter 2016 and towards females in Summer 2017). If recapture rates were indeed equal between females and males, as the most parsimonious CJS model predicted, this parity would provide further support for equal survival rates between the sexes. At SO more females than males were captured across the study period although the sex ratio did not consistently favour one sex: the sex ratio was skewed towards females at 4 of the 8 trapping sessions and towards males at 3 out of 8 trapping sessions, with parity being observed at only the first (Autumn 2015) trapping session. Low trapping effort alone cannot explain the disparate sex ratios at SO since the trapping session with the highest trapping effort still delivered a biased sex ratio. At both sites, the sex ratio deviated from parity only at low population densities. I therefore have to consider that low densities decrease the probability of a mouse visiting a trap station and that trapping effort cannot compensate for this detection threshold.

4.5. Basic morphology of *R. bechuanae* and relative age at reproductive maturity

With regards to morphology, I discussed results for both sites collectively and referred to specific sites where differences were found. As similar growth rates are reported for several species of *Rhabdomys* (Neville Pillay *pers. comm.*), I also compared my findings with the available literature. *R. bechuanae* exhibited sexual dimorphism in body size with males being larger than females. No sexual dimorphism in body mass was apparent between females and males for either populations. This contrasts with the results of Schradin & Pillay (2005a) who found that male *R. pumilio* weighed significantly heavier than females. In both females and males, individuals that were potentially reproductively active were significantly larger in size and mass than non-reproductive individuals. Males reached a maximum

length of 12 – 12.9 cm and mass of 65 g and females reached a maximum length of 11 – 11.9 cm and mass of 70 g. Female *R. bechuanae* reached maturity and had potential to reproduce at a body size of 8 – 8.9 cm and a mass of 18 – 29 g (5 to 7 weeks of age; Henschel *et al.* 1982) compared to male *R. bechuanae* that were potentially reproductively active at a body size of 8 – 9.9 cm and a mass of 28 – 33 g (7 to 8 weeks of age; Henschel *et al.* 1982). Similar to the findings of Brooks (1974), David & Jarvis (1985) and Schradin & Pillay (2005b), females reached maturity earlier than males. *R. bechuanae* therefore reached sexual maturity at ages comparable to *R. dilectus* spp. of mesic grasslands (Brooks 1974; Schradin & Pillay 2005b) and *R. pumilio* of the Cape flats (David & Jarvis 1985). However, signs of reproduction were recorded at a lighter body mass for *R. bechuanae* compared to *R. pumilio* (44 g for females and 41 g for males) of the Succulent Karoo (Schradin & Pillay 2005a). For *R. bechuanae* in my study, this size class made up a comparatively small proportion of the captured population (22 % at TDR and 16 % at SO) and was not always observed among the reproductively active proportion of the population. Accordingly, their contribution to reproductive rates were likely very small.

As expected, the number of individuals within each body size class fluctuated seasonally as large adults disappeared (through dispersal or mortality) and small individuals were recruited (through dispersal or fecundity) to the population. However, size class structure was not constant between the same seasons of different study years and I expect therefore that the effect of survival and reproduction on population structure was not constant across the study period. At both sites, Winter 2015 was the only trapping session where the number of small *R. bechuanae* (< 9 cm in body length) were greater than the number of large individuals (≥ 10 cm).

With regards to seasonal body size-class structure, no clear trend was apparent for either populations. For the last 5 of 8 trapping sessions at TDR, the population consisted of significantly more large compared to small individuals. During this period, recruitment through birth seemed to be minimal, according to the percentage of each population recorded as small individuals. Although I acknowledge that the number of *R. bechuanae* trapped with body sizes of < 9 cm could not reflect the number of mice born into the population (David & Jarvis 1985), the results for both sites point to clear temporal (seasonal and inter-annual) variation in body size class structure.

Mean mass of male *R. bechuanae* fluctuated seasonally, though no clear pattern was observed and mean mass did not consistently peak during the same seasons of different years. This is perhaps reflected in my findings that, according to a LMM, male body mass was not affected by minimum temperature, maximum temperature, rainfall 30 days *a priori*, rainfall 90 days *a priori* or plant cover. I expected minimum temperature to have a negative effect on body mass due to the energetic costs associated with thermoregulation (Nater *et al.* 2015). This effect would be most pronounced during the coldest months

of the year, i.e. late Autumn thru Winter. Mean minimum temperatures of -0.46 °C were recorded during the 30 days preceding Winter 2015 and -1.38 °C preceding Winter 2016. However, mean male body mass during Winter 2016 was comparable to that of Spring 2015. As *Rhabdomys* in arid regions are expected to lose weight with decreasing food availability (Schradin & Pillay 2005a), plant cover, as a proxy for food availability, should have a direct effect on body mass. At TDR, median total plant cover consistently decreased to its lowest point during Summer, regardless of the preceding amount of rainfall. Nonetheless, Winter trapping sessions were preceded in the 90 days *a priori* by comparatively low total rainfall resulting in a general lack of green plant material and invertebrate prey (*pers. obs.*). The lack of any significant effect between male body mass and the extrinsic factors tested here perhaps suggest that a more complex statistical model, such as a General Linear Mixed Effect or Multi-state Mark Recapture model, be used.

4.6. Comparing *R. bechuanae* population size and survival between study sites

The differences in trapping schemes and sample size between study sites make the comparison of results between populations difficult. However, if one were to assume similar ecology of *R. bechuanae* between the study sites then the differences in their apparent demography (i.e. population density and mean survival) would result, at least partly, from differences in their extrinsic environment. Both population density and mean survival probability were higher at TDR (24 individuals/ha, 33%) compared to SO (7 individuals/ha, 19%). I suggest that these differences can perhaps be produced by variation in habitat quality.

Hoffman and Zeller (2005), in their comparison of small mammal diversity and species abundance in a heavily grazed versus lightly grazed rangeland, consistently found small mammals to be more abundant in habitat of higher quality, i.e. the lightly grazed rangeland. Accordingly, habitat quality at TDR should therefore be higher compared SO. They proposed that larger population size in the lightly grazed rangeland was due to the greater availability of cover, promoting food availability and decreasing predation risk (Kotler 1984). However, a lower availability of total plant cover was recorded at TDR compared to SO, at both seasons of peak and lowest total plant cover. Therefore, total plant cover cannot explain the difference in population density between my study sites and does not necessarily predict food availability or habitat quality.

Only qualitative inference can be made with regards to habitat quality at my study sites. At TDR, *R. bechuanae* associated with both wood and grass cover, though the association was stronger with grass cover for 4 of the 8 trapping sessions. At SO, *R. bechuanae* associated significantly more with wood compared to grass cover. I suggest that this variation reflects the differences in plant community composition and habitat structure evident between the study sites (Appendix, Figures A1 & A2) and

not necessarily that the populations varied in their habitat preference. The comparable presence of both grass and wood cover at TDR may point to a greater variety of food plants, both annual and perennial. In contrast, the larger part of the SO study site was qualitatively homogenous with Sweet thorn *Vachellia karroo* being the dominant plant species (*pers. obs.*). Avenant & Cavallini (2007) correlated high quality habitats (those of high plant diversity) with high small mammal diversity. Indeed, small mammal diversity was evidently higher in the TDR study site (11 small mammal species including 8 murid) compared to SO (6 small mammal species including 5 murid) though this could also be contributed to differences in landscape features (Figures 3 & 4). In the case of a granivorous rodent, such as *R. bechuanae*, a more appropriate parameter to estimate habitat quality would be seed / fruit production or recording seasonal changes in plant phenology.

5. Conclusion

In the two-year study, *R. bechuanae* demonstrated cyclic dynamics with peak densities recorded once per year. These peaks were not constant in their timing or amplitude, possibly alluding to variability in seasonal conditions. Though plant cover followed a simple trend, i.e. peak cover in Autumn and least cover in Summer of each year, temperature and rainfall were not consistent between the same seasons of different years. For TDR, temperature preceding Spring 2015 was significantly lower than Spring 2016; temperatures were significantly higher preceding Summer 2016 compared to Summer 2017; total rainfall, for the 30 days preceding each trapping session, varied significantly between Autumn, Spring and Summer of the different study years and total rainfall, for the 90 days preceding each trapping session, varied significantly between Autumn and Summer of the different study years. The effect of variability in weather was seen in the lack of correlations between *R. bechuanae* population parameters (i.e. population size, survival rate, reproductive activity and body mass) and the extrinsic factors (i.e. temperature, rainfall and plant cover) analysed. Therefore, *R. bechuanae* responded non-linearly to extrinsic factors or the extrinsic factors acted additively in determining resource availability, hence determining periods of high survival or reproductive activity. The synthesis of the results of Nater *et al.* (2015) indicate that temperature and food availability did not always influence the demography of *R. pumilio* directly but could also indicate the timing of life-history events, such as the increase in temperature indicating the onset of the dry Summer season and a shift from the breeding to the non-breeding season.

5.1. Future research of *Rhabdomys* population dynamics

The research presented here highlights the high degree of complexity inherent in the dynamics of any organismal population (Benton *et al.* 2006). In short term studies, dynamics are often explained through linear relationships between the environment and the population, i.e. bottom-up regulation (Brown & Ernest 2002). I found, in the interpretation of my data analysis, that non-linearity is ubiquitous and that population parameters rarely fluctuated according to the influence of a single environmental factor. It is therefore essential that, in future research of *R. bechuanae* population dynamics, an analytical approach is adopted that considers the synergistic and sequential influences of each factor, both intrinsic and extrinsic, relevant to the model organism (Lidicker 1988; Wiens 2011).

A need exists to incorporate the interactive effects of causal factors in the analysis of population dynamics (Benton *et al.* 2006; Brown & Ernest 2002). Nater *et al.* (2015) showed that, for *R. pumilio*, interactive effects between temperature, food availability and population density were essential in understanding variation in demographic rates. In my analysis of survival, I did not differentiate between life stages, i.e. immature, philopatric or breeder. Nater *et al.* (2015) showed that individuals from each respective life stage may respond differently in their survival rate (neutral, positive or negative response) to the environment (i.e. temperature, food availability and population density). Additionally, flexibility in individual life-history could be essential in determining dynamics at a population level (Benton *et al.* 2006). For example, alternative reproductive tactics have been identified in male *R. pumilio* of the Succulent Karoo with differences in hormonal physiology and behaviour expressed within each tactic. Compared to breeder group-living males, roamer males expend more energy during mate location (Schradin & Lindholm 2011) and maintain larger home ranges (Schradin *et al.* 2009), with direct survival and fitness implications (Rimbach *et al.* 2016). Therefore, neglecting individual variation could lead to false conclusions drawn from mean seasonal or annual demographic estimates, such as survival and reproductive rates (Benton *et al.* 2006).

Linear relationships rarely occurred in my analyses of fluctuation in population parameters according to extrinsic factors, possibly due to the indirect effect of weather on population dynamics. Alongside abiotic weather variables, analysis of primary productivity, e.g. Normalised Difference Vegetation Index or Soil Adjusted Vegetation index, would be useful in determining the timing of population processes (Andreo *et al.* 2009), such as the breeding season. Though it is rarely considered in studies of population dynamics (Krebs 2013), dispersal through immigration and emigration may be an important intrinsic factor affecting population growth in *R. bechuanae* and should be investigated in future population dynamics studies on the species. Finally, including the effect of predators on

population dynamics could prove important (Krebs 2013), especially given the fact that *R. bechuanae* was the only diurnally active rodent in my study sites.

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Appendix



Figure 21: The southern half of Tussen die Riviere field site, bordering the Caledon river. The most common trees in the site were Blue bush *Diospyros lyciodes* and Firethorn *Searsia pyrroides*. A stretch of evenly spaced Lye ganna *Salsola aphylla* bordered the riparian zone. Photograph taken in Spring 2016



Figure 22: Western half of Soetdoring field site containing a dense stand of shrub-like *V. karroo*, stretching to the far-end of the frame, interspersed with patches of grass and bare-soil. Photograph taken in Summer 2016.

Table 24: List of small mammals trapped at my study site in Tussen die Riviere Nature Reserve, including taxonomic order and family. * I included both the genera of *Crocidura* and *Suncus* as differentiation could not be made based on morphology and their ecology overlap with habitat features at the Tussen die Riviere study site.

Order	**Family**	**Species**	**Common name**	**Number of captures**
Rodentia	Muridae	*Dendromus melanotis*	Grey climbing-mouse	1
		Mastomys spp.	Multimammate mouse	119
		Micaelamys namaquensis	Namaqua rock-mouse	142
		Nannomys minutoides	Pygmy mouse	9
		Otomys saundersii	Saunders' vlei rat	2
		Otomys irroratus	African vlei rat	2
		Rhabdomys bechuanae	African striped mouse	851
		Saccostumus campestris	Pouched mouse	55
Macroscelidea	Macroscelididae	*Elephantulus myurus*	Eastern rock sengi	42
Eulipotyphla	Soricidae *	*Crocidura* spp.	Musk Shrew	1*
		Suncus spp.	Dwarf shrew	1*

Table 25: List of small mammals trapped at my study site in Soetdoring Nature Reserve, including taxonomic order and family.

Order	**Family**	**Species**	**Common name**	**Number of captures**
Rodentia	Muridae	*Gerbilliscus leucogaster*	Bushveld gerbil	143
		Mastomys spp.	Multimammate mouse	145
		Mystromys albicaudatus	White-tailed mouse	2
		Nannomys minutoides	Pygmy Mouse	3
		Rhabdomys bechuanae	African striped mouse	180
Eulipotyphla	Soricidae	*Crocidura* spp.	Musk Shrew	2

Table 26: Capture histories used in the full-likelihood estimation of *R. bechuanae* population size at TDR. Each capture history ends with its frequency of occurrence within the dataset.

Season	Capture history
Autumn 2015	10000000 14; 11010110 1; 11010100 1; 11000110 1; 10100000 1; 11110110 1; 10100010 1; 10000010 3; 10001010 1; 11001000 1; 11010000 1; 10010000 1; 10000100 1; 10000001 1;

	10110010 1; 11010010 1; 01000000 34; 01000011 2; 01010000 10; 01000100 6; 01000010 10; 01110110 1; 01000110 1; 01011000 1; 01110000 1; 01000001 1; 01001010 3; 01001110 1; 01010100 1; 01001000 1; 00100000 8; 00101010 2; 00100010 3; 00110001 1; 00111000 1; 00100110 1; 00110000 1; 00111011 1; 00010000 37; 00010010 7; 00010101 2; 00010001 4; 00010100 5; 00011000 1; 00011010 1; 00010011 2; 00001000 12; 00001110 2;

	00001101 1; 00001100 1; 00001010 1; 00000100 27; 00000101 2; 00000110 3; 00000010 47; 00000001 6;
Winter 2015	10001 6; 10000 9; 10110 2; 10101 2; 11011 1; 11000 1; 10111 2; 10100 4; 11001 3; 10010 2; 10011 3; 01000 16; 01010 5; 01110 2; 01101 1; 01001 5; 01100 4; 00100 19; 00101 6; 00010 17; 00011 1; 00001 28;
Spring 2015	1001000 3; 1000000 3; 1010000 2; 1011010 1;

	1100000 1; 1110100 2; 1001100 1; 1111100 1; 1101100 1; 1001110 1; 1010010 2; 1011110 1; 1000100 1; 0100010 4; 0110000 1; 0100000 17; 0101010 2; 0101100 3; 0101000 7; 0110100 2; 0100100 5; 0100101 1; 0100001 1; 0111000 1; 0010100 6; 0011100 1; 0011000 3; 0010000 21; 0010110 3; 0010010 4; 0010011 1; 0001000 15; 0001010 1; 0001100 1; 0000100 33; 0000010 11; 0000001 1;
Summer 2016	1010 6;

	1001	6;
	1110	2;
	1000	13;
	1100	4;
	1101	1;
	1111	1;
	0110	9;
	0100	8;
	0101	3;
	0010	6;
	0011	1;
	0001	7;
Autumn 2016	10011011	1;
	11101110	1;
	10000100	1;
	11011111	1;
	11000000	1;
	01001110	1;
	01010001	1;
	01000000	1;
	01000110	1;
	00100100	1;
	00100101	1;
	00010010	2;
	00010000	1;
	00010100	1;
	00001011	1;
	00001100	1;
	00000101	1;
	00000100	3;
	00000110	1;
	00000010	6;
	00000001	2;
Winter 2016	100000	1;

	100001	2;
	010000	5;
	010011	2;
	011110	1;
	010101	1;
	010010	2;
	001010	1;
	001001	2;
	001000	2;
	001011	2;
	000110	2;
	000101	2;
	000100	1;
	000010	5;
	000001	8;
Spring 2016	1010011	1;
	1010001	1;
	1000001	1;
	1000000	1;
	0100000	2;
	0101000	3;
	0111011	1;
	0111001	1;
	0101001	1;
	0101011	1;
	0100001	1;
	0110000	1;
	0010000	1;
	0001000	3;
	0000101	1;
	0000100	1;
	0000110	1;
	0000010	1;
	0000001	1;

Summer 2017	0110001	1;
	0010100	2;
	0010000	1;
	0001000	1;
	0001001	1;
	0000010	2;
	0000001	1;

Table 27: Capture histories used in the full-likelihood estimation of *R. bechuanae* population size at SO. Each capture history ends with its frequency of occurrence within the dataset.

Season	Capture history	
Autumn 2015	100000	4;
	100100	1;
	111000	1;
	110000	2;
	101000	1;
	101001	1;
	110100	1;
	010000	5;
	010010	3;
	011001	1;
	010100	1;
	011011	1;
	011111	1;
	010101	1;
	001001	4;
	001000	8;
	001100	1;
	001101	1;
	001110	2;
	000101	1;
	000100	4;
	000010	6;

	000011	1;
	000001	5;
Winter 2015	1000000	5;
	1100100	1;
	0100000	3;
	0110000	2;
	0100101	1;
	0100100	1;
	0011111	1;
	0010111	1;
	0010000	2;
	0000111	1;
	0000100	4;
	0000101	2;
	0000011	1;
	0000010	4;
Spring 2015	1100000	1;
	1010000	1;
	1000000	1;
	1000110	1;
	1000010	1;
	1011000	1;
	1001010	1;
	0100000	2;
	0110110	1;
	0110010	1;
	0010000	5;
	0011000	1;
	0010011	1;
	0001010	1;
	0001000	1;
	0000100	4;
	0000101	1;
	0000010	4;

	0000001	1;
Summer 2016	100000	1;
	010000	1;
	000100	1;
Autumn 2016	00001010	1;
Winter 2016	1100	1;
	1001	1;
	1000	1;
	0100	2;
	0001	1;
Spring 2016	1000000	1;
	0010100	1;
	0001010	1;
	0000100	2;
Summer 2017	010000	1;
	001000	1;

Table 28: Capture histories used in the Cormack-Jolly-Seber estimation of *R. bechuanae* survival for the TDR and SO populations, respectively. Female capture histories end in "1 0" and those of males "0 1".

TDR	SO
10000000 1 0;	10000000 1 0;
11100000 1 0;	10000000 1 0;
10000000 1 0;	10000000 1 0;
11000000 1 0;	10000000 1 0;
10000000 1 0;	10000000 1 0;
10000000 1 0;	10000000 1 0;
10000000 1 0;	10000000 1 0;
10000000 1 0;	10000000 1 0;
11000000 1 0;	10100000 1 0;
10000000 1 0;	11000000 1 0;
10000000 1 0;	11000000 1 0;
10000000 1 0;	10000000 1 0;

10000000 1 0;	10000000 1 0;
10000000 1 0;	10000000 1 0;
10000000 1 0;	10000000 1 0;
10000000 1 0;	10000000 1 0;
10000000 1 0;	10000000 1 0;
11000000 1 0;	11000000 1 0;
10000000 1 0;	11100000 1 0;
10110000 1 0;	10000000 1 0;
10000000 1 0;	10000000 1 0;
10000000 1 0;	00100000 1 0;
10000000 1 0;	01000000 1 0;
11010000 1 0;	01000000 1 0;
10110000 1 0;	01000000 1 0;
11100000 1 0;	01000000 1 0;
10110000 1 0;	00100000 1 0;
10000000 1 0;	00100000 1 0;
10010000 1 0;	00100000 1 0;
11000000 1 0;	00100000 1 0;
10000000 1 0;	00100000 1 0;
11000000 1 0;	00100000 1 0;
10000000 1 0;	00110000 1 0;
10000000 1 0;	00100000 1 0;
10000000 1 0;	00100000 1 0;
10000000 1 0;	00100000 1 0;
10000000 1 0;	00110000 1 0;
10000000 1 0;	00100000 1 0;
10000000 1 0;	00100000 1 0;
10000000 1 0;	00010000 1 0;
10000000 1 0;	00010000 1 0;
10000000 1 0;	00001100 1 0;
10100000 1 0;	00000100 1 0;
10000000 1 0;	00000010 1 0;
10000000 1 0;	10000000 0 1;
10000000 1 0;	11100000 0 1;

11000000 1 0;	10000000 0 1;
10000000 1 0;	10000000 0 1;
11100000 1 0;	10000000 0 1;
10000000 1 0;	10000000 0 1;
10000000 1 0;	10000000 0 1;
10000000 1 0;	10000000 0 1;
10000000 1 0;	10000000 0 1;
10000000 1 0;	10000000 0 1;
11110000 1 0;	10000000 0 1;
10000000 1 0;	10000000 0 1;
10100000 1 0;	10000000 0 1;
11000000 1 0;	10000000 0 1;
10000000 1 0;	10000000 0 1;
10000000 1 0;	10000000 0 1;
10000000 1 0;	10000000 0 1;
11000000 1 0;	10000000 0 1;
10000000 1 0;	10000000 0 1;
10000000 1 0;	10000000 0 1;
10000000 1 0;	10000000 0 1;
11000000 1 0;	01000000 0 1;
10000000 1 0;	01000000 0 1;
11100000 1 0;	01000000 0 1;
11111100 1 0;	01000000 0 1;
11000000 1 0;	01000000 0 1;
10000000 1 0;	01000000 0 1;
10000000 1 0;	01000000 0 1;
10000000 1 0;	01000000 0 1;
10000000 1 0;	00100000 0 1;
10000000 1 0;	00100000 0 1;
10000000 1 0;	00100000 0 1;
11100000 1 0;	00000100 0 1;
10000000 1 0;	00000100 0 1;
10100000 1 0;	00000100 0 1;
11000000 1 0;	00000100 0 1;

10000000 1 0;	00000010 0 1;
10000000 1 0;	00000010 0 1;
10010000 1 0;	00000010 0 1;
10000000 1 0;	00000010 0 1;
11100000 1 0;	00000001 0 1;
10000000 1 0;	00000001 0 1;
10000000 1 0;	00000001 0 1;
10000000 1 0;	
10000000 1 0;	
10000000 1 0;	
10000000 1 0;	
10000000 1 0;	
10000000 1 0;	
01000000 1 0;	
00100000 1 0;	
00100000 1 0;	
01000000 1 0;	
00010000 1 0;	
01000000 1 0;	
01000000 1 0;	
01000000 1 0;	
00100000 1 0;	
00010000 1 0;	
00110000 1 0;	
00110000 1 0;	
01000000 1 0;	
01000000 1 0;	
01000000 1 0;	
01000000 1 0;	
01000000 1 0;	
01000000 1 0;	
01000000 1 0;	
01000000 1 0;	
01100000 1 0;	

01000000 1 0; 01110000 1 0; 01100000 1 0; 01000000 1 0; 01100000 1 0; 01000000 1 0; 01000000 1 0; 01110000 1 0; 01000000 1 0; 01100000 1 0; 01000000 1 0; 01000000 1 0; 01000000 1 0; 01000000 1 0; 01000000 1 0; 01000000 1 0; 01100000 1 0; 01000000 1 0; 00100000 1 0; 00100000 1 0; 00100000 1 0; 00100000 1 0; 00110000 1 0; 00100000 1 0; 00100000 1 0; 00100000 1 0; 00100000 1 0; 00110000 1 0; 00100000 1 0; 00100000 1 0; 00100000 1 0; 00100000 1 0; 00100000 1 0; 00100000 1 0;	

00100000 1 0; 00100000 1 0; 00100000 1 0; 00100000 1 0; 00111000 1 0; 00100000 1 0; 00100000 1 0; 00100000 1 0; 00100000 1 0; 00100000 1 0; 00100000 1 0; 00100000 1 0; 00100000 1 0; 00100000 1 0; 00100000 1 0; 00010000 1 0; 00010000 1 0; 00010000 1 0; 00010000 1 0; 00010000 1 0; 00010000 1 0; 00010000 1 0; 00010000 1 0; 00010000 1 0; 00010000 1 0; 00010000 1 0; 00010000 1 0; 00010000 1 0; 00010000 1 0; 00010000 1 0; 00010000 1 0; 00010000 1 0; 00010000 1 0; 00001110 1 0; 00001000 1 0; 00001000 1 0; 00001000 1 0; 00000110 1 0;	

00000100 1 0; 00000100 1 0; 00000100 1 0; 00000100 1 0; 00000100 1 0; 00000100 1 0; 00000100 1 0; 00000011 1 0; 00000010 1 0; 00000010 1 0; 00000011 1 0; 00000010 1 0; 00000010 1 0; 00000010 1 0; 00000001 1 0; 00000001 1 0; 10000000 0 1; 10000000 0 1; 11000000 0 1; 11000000 0 1; 10000000 0 1; 10000000 0 1; 11000000 0 1; 11000000 0 1; 10000000 0 1; 10000000 0 1; 11011000 0 1; 11000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 11000000 0 1;	

10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 11000000 0 1; 10000000 0 1; 10000000 0 1; 11000000 0 1; 11000000 0 1; 10000000 0 1; 10000000 0 1; 11000000 0 1; 10000000 0 1; 10000000 0 1; 11000000 0 1; 10100000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 11100000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10110000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 11000000 0 1;	

10000000 0 1; 10000000 0 1; 10100000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 11000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10100000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 11100000 0 1; 10000000 0 1; 10000000 0 1; 11110000 0 1; 10100000 0 1; 10000000 0 1; 10000000 0 1; 10010000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 10000000 0 1; 01000000 0 1; 01100000 0 1;	

01100000 0 1; 01000000 0 1; 01100000 0 1; 01100000 0 1; 00100000 0 1; 00110000 0 1; 00010000 0 1; 01000000 0 1; 01100000 0 1; 01100000 0 1; 01000000 0 1; 01000000 0 1; 00110000 0 1; 01000000 0 1; 01000000 0 1; 01100000 0 1; 01100000 0 1; 01110000 0 1; 01000000 0 1; 01100000 0 1; 01000000 0 1; 01100000 0 1; 01000000 0 1; 01000000 0 1; 01000000 0 1; 01000000 0 1; 01000000 0 1; 01000000 0 1; 01100000 0 1; 01100000 0 1; 01000000 0 1; 01000000 0 1; 01100000 0 1; 01000000 0 1; 01000000 0 1;	

01000000 0 1; 01000000 0 1; 01100000 0 1; 01000000 0 1; 01100000 0 1; 01000000 0 1; 01100000 0 1; 01000000 0 1; 01100000 0 1; 00100000 0 1; 00110000 0 1; 00100000 0 1; 00110000 0 1; 00100000 0 1; 00110000 0 1; 00100000 0 1; 00100000 0 1; 00100000 0 1; 00100000 0 1; 00100000 0 1; 00100000 0 1; 00100000 0 1; 00100000 0 1; 00110000 0 1; 00100000 0 1; 00100000 0 1; 00110000 0 1; 00100000 0 1; 00100000 0 1; 00100000 0 1; 00100000 0 1; 00111110 0 1; 00111100 0 1; 00100000 0 1; 00100000 0 1;	

00100000 0 1; 00100000 0 1; 00100000 0 1; 00100000 0 1; 00100000 0 1; 00100000 0 1; 00100000 0 1; 00100000 0 1; 00011000 0 1; 00010000 0 1; 00010000 0 1; 00010000 0 1; 00010000 0 1; 00010000 0 1; 00010000 0 1; 00010000 0 1; 00010000 0 1; 00010000 0 1; 00010000 0 1; 00010000 0 1; 00010000 0 1; 00011000 0 1; 00010000 0 1; 00010000 0 1; 00010000 0 1; 00010000 0 1; 00010000 0 1; 00011000 0 1; 00010000 0 1; 00010110 0 1; 00001000 0 1; 00001000 0 1; 00001100 0 1; 00000100 0 1; 00000100 0 1; 00000100 0 1;	

00000110 0 1; 00000110 0 1; 00000100 0 1; 00000110 0 1; 00000100 0 1; 00000100 0 1; 00000100 0 1; 00000100 0 1; 00000100 0 1; 00000010 0 1; 00000010 0 1; 00000010 0 1; 00000010 0 1; 00000010 0 1; 00000001 0 1; 00000001 0 1;	