ABUNDANCE, SPECIES COMPOSITION AND DIVERSITY OF SMALL MAMMALS AND THE PREVALENCE AND INTENSITY OF INFESTATION OF ASSOCIATED FLEAS (SIPHONAPTERA) ACROSS AN ALTITUDINAL GRADIENT ALONG THE UGAB RIVER, NAMIBIA

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ABSTRACT

The objectives of the study were to determine and compare the abundance, species composition and diversity of small mammals and the associated fleas and to determine and compare the prevalence and intensity of infestation of fleas across an altitudinal gradient along the Ugab River, Namibia. Three sampling sites at different altitudes were selected, Outjo (high altitude site) at about 1300 m above sea level (a.s.l.), Vingerklip (middle altitude site) at about 1000 m a.s.l. and Brandberg (low altitude site) at 400 m a. s. l. Small mammals were trapped in January (hot wet season) and May (cold dry season) in 2018. A total of 159 small mammals belonging to seven rodents and two insectivore species were trapped during the entire study. Small mammals trapped included: Namaqua rock mouse *(Micaelamys namaquensis)*, Natal multimammate rat *(Mastomys natalensis)*, Red rock rat *(Aethomys chrysophilus)*, lesser Red musk shrew *(Crocidura hirta)*, pouched mouse *(Saccostomus campestris)*, bushveld gerbil *(Gerbiliscus leucogaster)*, black-tailed tree rat *(Thallomys nigricauda)*, Acacia rat *(Thallomys paedulcus)* and bushveld elephant shrew *(Elephantulus intufi)*. The abundance, species composition and diversity of small mammal hosts were not significantly different among the sampling sites during the two seasons (hot wet and cold dry seasons). A total of 139 fleas were collected from small mammals during the study. Three flea species were recorded from small mammal hosts during the study, namely: *Xenopsylla cheopis*, *Xenopsylla brasiliensis* and *Listropsylla dorripae*. The overall intensity of flea infestation (median) per host was not significantly different among the three sampling sites during the hot wet and the cold dry season. Overall infestation prevalence of fleas for the three sites during the hot wet season revealed no significant difference. However, the infestation prevalence of fleas of small mammals was significant among the three sites during the cold dry season. Altitude affects vegetation structure and cover, which in turn affect the small mammal and flea communities. Altitude also affects several climatic factors (temperature, rainfall, humidity), which affect small mammal and flea communities.

Keywords: small mammals, fleas, infestation prevalence, the intensity of flea infestation, abundance, species composition, diversity, altitudinal gradient, Ugab River, Namibia

DEDICATION

I dedicate this Thesis to my late brother Fillipus Simaneka Shipanga and son Festus Haitange Frans.

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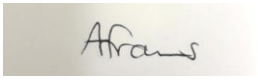
The Department of Biological Sciences at the University of Namibia is thanked for allowing me to use the laboratory facilities.

DECLARATION

I, Alma Inga Frans, hereby declare that this study is my own work and is a true reflection of my research and that this work or any part thereof has not been submitted for a degree at any other institution.

Alma Inga Frans		21/09/2021
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M. namaquensis - *Micaelamys namaquensis*

M. natalensis - *Mastomys natalensis*

A. chrysophilus - *Aethomys chrysophilus*

C. hirta - *Crocidura hirta*

S. campestris - *Saccostomus campestris*

G. leucogaster - *Gerbilliscus leucogaster*

E. intufi - *Elephantulus intufi*

T. nigricauda - *Thallomys nigricauda*

T. paedulcus - *Thallomys paedulcus*

X. cheopis - *Xenopsylla cheopis*

X. brasiliensis - *Xenopsylla brasiliensis*

L. dorripae - *Listropsylla dorripae*

LAS - Low altitude site

MAS - Middle altitude site

HAS - High altitude site

OJ - Outjo (1300 m a.s.l.)

VK - Vingerklip (1000 m a.s.l.)

BB - Brandberg (400 m a.s.l.)

Jan - January

CD - Cold dry season

HW - Hot wet season

OCD - Outjo cold dry season

VCD - Vingerklip cold dry season

BCD - Brandberg cold dry season

OHW - Outjo hot wet season

VHW - Vingerklip hot wet season

BHW - Brandberg hot wet sea

a.s.l. - above sea level

m - meters

M - Male

F - Female

AT - Ascended Testicles

DT - Descended Testicles

OV - Open Vagina

CV - Closed Vagina

ANOSIM - Analysis of similarities

HCA - Hierarchical cluster analysis

PAST - Paleontological statistics

GPS - Global positioning system

CHAPTER 1

INTRODUCTION

1.1. Background of the study

Understanding the processes that shape the diversity of organisms along elevational gradients has become a vital issue in biogeographical studies (Reiss *et al*., 2009; Fleishman, 2010). Elevational gradients are essential when evaluating the potential effects of global climate change and the local extinction risk of vulnerable species (Reiss *et al*., 2009; Fleishman, 2010; Novillo & Ojeda, 2014). Biodiversity patterns along gradients result from contemporary biophysical interactions (climate, heterogeneity, and biotic factors) and historical factors such as dispersal, extinction, and speciation (Rahbek & Graves, 2001; Jetz & Rahbek, 2002; Novillo & Ojeda, 2014). There is confusion between altitude, elevation, and height; they are used interchangeably in the literature (McVicar & Korner, 2012). Elevation is described as the vertical distance between a point on the land surface and a reference point, usually taken to be the mean sea level (Rahbek, 1995; McVicar & Korner, 2012), while altitude refers to the vertical distance (elevation) between an object and a reference point where the object is not in direct contact with the reference point (McVicar & Korner, 2012). In this study, altitude was used, but studies on elevational gradients were also cited.

Studies of different groups of organisms have identified pronounced variation in species richness along elevational gradients (Kessler, 2000; Sanchez-Cordero, 2001; Vetaas & Grytnes, 2002). Several factors have been identified as underlying causes of elevational

diversity gradients (Rahbek, 1995; Odland & Birks, 1999). Some of the most commonly tested factors are climate and productivity (Rahbek, 1995; Odland & Birks, 1999; Grytnes, 2003; Fu *et al*., 2006; Rowe, 2009; Wang *et al*., 2009), source-sink dynamics (Kessler *et al*., 2011), area (Rahbek, 1995; Sanders, 2002; Jones *et al*., 2003; Bachman *et al*., 2004; Herzog, *et al*., 2005), and evolutionary history (Machac *et al*., 2011). Different historical and climatic variables have been used to describe species richness variations along elevational gradients (Lomolino, 2001; Grytnes, 2003). Climatic variables influence species richness along elevational gradients for all kinds of living organisms (Heaney, 2001; Nor *et al*., 2001; Whittaker *et al*., 2001). The climatic factors that differ with elevation include temperature, potential evapotranspiration, length of the growing season, humidity, air pressure, nutrient availability, ultraviolet radiation and rainfall (Whittaker *et al*., 2001). Elevational gradients in the species richness of organisms offer many characteristics that make them more suitable for uncovering the mechanisms that shape biodiversity patterns (Nogues-Bravo *et al*., 2008; Sanders, 2012; Yu *et al*., 2013). When contrasted with a monotonic decrease of species richness and the elevation-richness relationship, the elevational pattern of species richness with complexity depends on the particular taxonomic group and the scale and extent of the elevational gradients (Lomolino, 2001; Rahbek, 2004). A unimodal (mid-elevation peak) pattern and monotonic decline in richness with increasing elevation are the two most commonly observed species richness patterns (Rahbek, 1995; Lomolino, 2001; Rahbek, 2004; Nogues-Bravo, *et al*., 2008; Rowe, 2009). These peaks are predicted to occur either at the point of optimal environmental conditions, at mid-domains where species overlap or locations where distinct vegetation communities occur nearby (Lomolino, 2001; Currie & Kerr, 2008; Bateman *et al*., 2010). Species diversity patterns change

across spatial gradients in response to changes in climate, area, latitude, altitude, productivity, available resources and habitat complexity and evolutionary history, and the extent of disturbance amongst many other factors at a global scale (Lomolino, 2001; Rowe, 2009).

The productivity hypothesis, the harsh environment hypothesis, the species-area hypothesis and the resources diversity hypothesis have been proposed to explain elevational patterns of diversity (Heaney, 2001; Lomolino, 2001; McCain, 2009). Contemporary climatic factors, including temperature and precipitation, spatial factors, including geometric constraints (mid-domain effect) and area size, vary along altitudinal gradients (Rowe, 2009). Biological processes such as habitat heterogeneity, productivity and interspecific interactions and the evolutionary and historical processes such as niche conservation, isolation, speciation, endemism and evolutionary diversification may differ across gradients, which in turn affects patterns of biodiversity (Lomolino, 2001; Hawkins *et al*. 2007; Li *et al*., 2009; Machac *et al*., 2011). Therefore, biological communities are expected to differ according to environmental gradients, either gradually or abruptly (Caceres *et al*., 2011). One of these gradients is altitude (Caceres *et al*., 2011). Species diversity can be considered a phenomenon that reflects the landscape's quality and functionality (Li *et al*., 2009). The more diverse and natural the landscape is, the higher the biodiversity (Lomolino, 2001).

Climate is the most widely supported predictor of biodiversity worldwide (Rowe, 2009). Its influence in shaping diversity can be direct and indirect (Rowe, 2009). Climate can directly set limits on species distributions by exceeding species physiological tolerance

(Currie & Kerr, 2008; Hawkins *et al*., 2007; Rowe, 2009). Indirectly, temperature and rainfall gradients establish trends in energy availability (primary productivity), affecting photosynthetic activities and the rates of biological processes and are thus considered a primary driver of biological patterns (Hawkins *et al*., 2007; Currie & Kerr, 2008; Rowe, 2009). Numerous studies along elevational gradients have found strong support for the role of climate in structuring species richness patterns (Bhattarai *et al*., 2004; Fu *et al*., 2006; Sanders, 2011). Habitat heterogeneity is another form of environmental variability that influences the production and maintenance of diversity (Rowe, 2009). An increase in the number of habitat types of greater structural complexity in the vegetation will provide more resources than a more uniform environment and may support a more significant number of species (Rowe, 2009).

Small mammals are a suitable model group to assess environmental quality because of their excellent reproductive capacity and invasive ability (Slabova *et al*., n.d.). The diversity of small mammals can indicate the presence of specific habitat requirements such as microhabitats and food sources and, in turn, indicate the health of an ecosystem (Anon., 2012). Small mammals serve as indicator species (Aplin *et al*., 2003) because they are abundant enough to allow meaningful statistical analysis of data, they belong to different trophic levels and are easily studied (Van Deventer & Nel, 2006). The community characteristics of small mammals could signal ecological disturbance, especially in conservation areas (Van Deventer & Nel, 2006). A biological indicator is an organism whose characteristics such as presence or absence, population density, dispersion, reproductive success is used as an instrument to measure the health of an ecosystem (Mohammadi, 2010). Mohammadi (2010) emphasized that small mammals

are an indicator group because they have essential ecosystem roles, such as being primary consumers, and further urged that after a disturbance such as fire, pioneering small mammals may be important seed sources for plant regeneration. Changes in small mammals' habitats are associated with changes in their diversity (Mohamaddi, 2010). For example, Avenant (2011) reported a decrease in small mammals' species richness with their habitats' ecological disturbance. Furthermore, some human activities alter habitat characteristics with cascading effects on faunal communities (Gbogbo *et al*., 2017). These human activities include refuse dumping, vegetation trampling by off-road driving, increased fire frequencies, and infrastructure development that alters natural habitats' environmental conditions to influence species diversity and community composition of small mammals (Gbogbo *et al*., 2017).

Livestock grazing has been identified as a significant threat to the biodiversity of small mammals in Namibia (Hoffmann & Zeller, 2005). Mining, agriculture and alien invasive plants also pose significant threats (Hoffmann & Zeller, 2005). Small mammals are often ignored in the planning and conservation of an area (Mena & Vazquez-Dominguez, 2005). Mena & Vazquez-Dominguez (2005) indicated that rodents have been very useful in the studies of environmental gradients, mainly because they form more or less conspicuous assemblages along such gradients as a result of adaptations to, among others, elevation, vegetation and because of historical factors such as dispersal, extinction, and speciation (Mena & Vazquez-Dominguez, 2005). Several studies have documented a frequent peak in species richness of non-volant small mammals at some elevation intermediate between the base and peak of a mountain; the hump-shaped pattern (Mena & Vazquez-Dominguez, 2005). The influence of altitude on the

abundance, richness and diversity of small mammals in Namibia is mostly unknown despite many studies that have been conducted on the ecology and conservation of small mammals (Amutenya, 2004; Hoffmann & Zeller, 2005; Erkie, 2007; Shihepo *et al*., 2008; Mfune *et al*., 2013). Several studies on small mammals and other organisms along altitudinal/elevational gradients have been done in South Africa and other African countries (Kasangaki *et al*., 2003; Mulungu *et al*., 2008; Curran *et al*., 2012; Datiko & Bekele, 2013; Linden *et al*., 2014).

The distributions of parasite communities across populations of hosts are influenced by many factors and tend to be combined, with only a few host individuals carrying most parasites (Archer *et al*., 2014). Froeschke *et al*. (2010) highlighted that environmental conditions play a vital role in regulating the distribution, transmission and developmental success of parasites and pathogens. Meteorological parameters can influence both the parasite species richness and the intensity of infection and infestation on the host species (Froeschke *et al*., 2010). Therefore, it is clear that the ecology of small mammals is partly driven by parasites, which in some instances may directly be responsible for natural population fluctuations (Shepherd & Leman, 1983). For example, some parasites that infest four-striped grass mouse (*Rhabdomys pumilio*) are essential in the aetiology of zoonotic diseases in humans and may involve the transmission of domestic and wild animals (Matthee *et al*., 2007). A survey conducted between 1972 and 1981 of rodent species associated with plague in the Eastern Cape Province in South Africa revealed antibodies to the plague bacterium *Yersinia pestis* in *R. pumilio* and other rodents (Shepherd & Leman, 1983).

The composition of parasite communities varies across host individuals, populations, species and communities (Krasnov *et al*., 2006). This variation is due to both the diversity of host biotic and abiotic environments. Unlike endoparasites, ectoparasites are influenced not only by the host but also by the host's environment (Krasnov *et al*., 2006). An ectoparasite habitat is not just a particular host but a particular host in a particular habitat (Krasnov *et al*., 2006). Many factors have been postulated to affect flea parasitism's prevalence and intensity among and within-host species (Krasnov *et al*., 2002). Most factors fall broadly into a host and environmental factors (Stanko *et al*., 2002; Young *et al*., 2015). Host factors include individual-level properties such as sex, age, body condition and health, species-level properties such as taxonomy and life history (e.g., body size, longevity sociality) and community level properties such as host density and host composition and diversity (Stanko *et al*., 2002; Young *et al*., 2015).

Ectoparasites live on or burrow into the surface of their hosts' epidermis. They spend all or some portion of their lives on animals (hosts) (Wall & Shearer, 2001). Apart from fleas, other ectoparasites include ticks, lice and mites. Generally, the growth of ectoparasites and maturation from egg to adult may be accomplished via several developmental paths. The juveniles called nymphs are usually similar to the adults in appearance, feeding habits and habitat (Wall & Shearer, 2001). A typical flea life cycle includes egg, larva, pupa, and adult (Wall & Shearer, 2001). Ectoparasites tend to be more exposed to the environment than other parasites (Young *et al*., 2015), such as nematodes. Environmental factors may be particularly critical in determining prevalence, intensity and the richness of ectoparasites such as fleas. The direct impacts of fleas' environment include the effects of rainfall and substrate texture on flea larvae's

success and development rates (Young *et al*., 2015). Indirect effects of flea parasitism's environment include instances where the environment may change host behaviour such as social contact, grooming rates or burrowing behaviour, physiology via immune investment or community composition and density (Young *et al*., 2015). The influence of altitude/elevation on species diversity and richness on the small mammals and on the prevalence and intensity of infestation of associated fleas is mostly unknown in Namibia.

1.2. Statement of the problem

Altitude is an essential parameter to understand the abundance, species composition, diversity and distribution of animals, especially small mammals (Aplin *et al*., 2003). Bateman *et al*. (2010) argued that altitudinal gradients are significant as there is a strong relationship between the changing altitude and the changing environmental variables such as climate and vegetation. There is a lack of studies directed at small mammal diversity across altitudinal/elevational gradients in Namibia. Such studies are essential to enhance knowledge by determining the influence of altitude on small mammal species in Namibia. The topographic differences along altitudinal gradients may influence the diversity patterns of small mammals (Magige, 2013). Rodents are mostly known to have ecological, economical, social and cultural values among communities (Habtamu & Bekele, 2012); hence they were assessed during this study.

Namibia is a land of contrast in terms of the diversity of vegetation types and biomes, and landscapes that occur at different altitudes (Mendelsohn *et al*., 2002). While many

studies have been undertaken in Namibia on the ecology and host-parasite interactions of small mammals (Shipanga, 2007; Shihepo *et al*., 2008; Mfune *et al*., 2013), the effects of altitude on the species diversity of small mammals is mostly unknown. Similarly, patterns of prevalence and intensity of flea infestation on small mammals at different altitudes remain poorly understood. This knowledge gap has important implications for biodiversity conservation and the fitness of animals directly impacted by fleas and wildlife and humans' health in communities affected by fleas. Furthermore, high densities of parasites such as fleas facilitate the likelihood of disease transmission among hosts and drive the emergence of flea-borne epizootics and other emerging diseases among humans (Young *et al*., 2015). The present study investigated the abundance, species composition and diversity of small mammals and the prevalence and intensity of infestation of associated fleas across an altitudinal gradient along the Ugab River in Namibia. Therefore, the study will allow meaningful insights into how small mammals and their associated fleas respond to altitudinal gradients in the Namibian context, which is lacking in the literature. It is unknown whether small mammals in Namibia follow the same most commonly observed and reported mid-altitudinal peak pattern observed worldwide (Rahbek, 1997; Nor *et al*., 2001; Sanchez-Cordero, 2001; Colwell *et al*., 2004; McCain, 2004).

1.3. Research objectives

The objectives of the study were:

1. To determine and compare:

   (1) the abundance;

(2) species richness;

(3) species composition; and

(4) species diversity of small mammal hosts among the three selected sampling sites across an altitudinal gradient along Ugab River, Namibia.

2. To determine and compare:

   (5) the abundance;

   (6) species richness;

   (7) species composition;

   (8) species diversity of fleas harboured by small mammal hosts among the three selected sampling sites across an altitudinal gradient along the Ugab River, Namibia.

3. To determine and compare:

   (9) the prevalence; and

   (10) the intensity of infestation of fleas harboured by small mammal hosts among the three selected sites across an altitudinal gradient along the Ugab River, Namibia.

1.4. Research questions

The study attempted to address the following research questions:

1. (a) What are the patterns of:

   (1) abundance;

   (2) species richness;

   (3) species composition; and

(4) species diversity of small mammal hosts among the three selected sampling sites across an altitudinal gradient along Ugab River, Namibia?

(b) Is there a significant difference in the:

(1) abundance;

(2) species richness;

(3) species composition; and

(4) species diversity of small mammal hosts among the three selected sampling sites across an altitudinal gradient along Ugab River, Namibia?

2. (a) What are the patterns of:

(5) abundance;

(6) species richness;

(7) species composition;

(8) species diversity of fleas harboured by small mammal hosts among the three selected sampling sites across an altitudinal gradient along the Ugab River, Namibia?

(b) Is there a significant difference in the:

(5) abundance;

(6) species richness;

(7) species composition;

(8) species diversity of fleas harboured by small mammal hosts among the three selected sampling sites across an altitudinal gradient along the Ugab River, Namibia?

3. (a) What are the patterns of:

(9) prevalence; and

(10) intensity of infestation of fleas harboured by small mammal hosts among the three selected sampling sites across an altitudinal gradient along the Ugab River, Namibia?

(b) Is there a significant difference in the:

(9) infestation prevalence and

(10) the intensity of infestation of fleas harboured by small mammal hosts among the three selected sampling sites across an altitudinal gradient along the Ugab River, Namibia?

1.5. Research hypotheses

The following hypotheses were tested:

1. H_0: There is no significant difference in:

(1) the abundance;

(2) species richness;

(3) species composition; and

(4) species diversity of small mammal hosts among the three selected sampling sites across an altitudinal gradient along the Ugab River, Namibia.

H_a: There is a significant difference in:

(1) the abundance;

(2) species richness;

(3) species composition, and

(4) species diversity of small mammal hosts among the three selected sampling sites across an altitudinal gradient along the Ugab River, Namibia

2. H_0: There is no significant difference in:

   (5) the abundance;

   (6) species richness;

   (7) species composition; and

   (8) species diversity of fleas harboured by small mammals among the three selected sampling sites across an altitudinal gradient along the Ugab River, Namibia.

   H_a: There is a significant difference in:

   (5) the abundance;

   (6) species richness;

   (7) species composition; and

   (8) species diversity of fleas harboured by small mammals among the three selected sampling sites across an altitudinal gradient along the Ugab River, Namibia.

3. H_0: There is no significant difference in:

   (9) the flea infestation prevalence; and

   (10) the intensity of infestation of fleas harboured by small mammals among the three selected sampling sites across an altitudinal gradient along the Ugab River, Namibia.

   H_a: There is a significant difference in:

   (9) the flea infestation prevalence; and

   (10) the intensity of infestation of fleas harboured by small mammals among the three selected sampling sites across an altitudinal gradient along the Ugab River, Namibia.

1.6. Significance of the study

Altitudinal gradients are characterized by rapid environmental changes over short horizontal distances (Quasin & Uniyal, 2011), and are therefore known to be ideal for investigating diversity patterns. The present study was conducted at three different altitude/elevation sites. The three sites (high altitude site, middle altitude site and the low altitude site) are likely to have different vegetation structures, different climates, temperatures, and rainfall may also vary. Different land-use practices, such as mining, agriculture, and tourism, occur along the Ugab River (Jacobson *et al*., 1995). These human activities are likely to alter the habitats in which the small mammals live. When the small mammals' habitats are altered, species diversity of small mammals at different habitats and altitudes will likely affect the prevalence and intensity of infestation of small mammals' associated fleas. This information is vital in the conservation practices of small mammals because of their roles in the environment and as vectors of various pathogens significant to both humans and wildlife health, such as plague, murine typhus, cat flea typhus and bartonellosis (Young *et al*., 2015).

CHAPTER 2

LITERATURE REVIEW

2.1. Patterns of altitudinal/elevational diversity gradients

Previous studies have been undertaken along elevational/altitudinal gradients on small mammals, bats, plants and other organisms (Rahbek, 1997; Vetaas & Grytnes, 2002; Kasangaki *et al*., 2003; Bhattacharyya *et al*., 2009; Li *et al*., 2009; Williams *et al*., 2010; Yu *et al*., 2013; Linden *et al*., 2014; Zhang *et al*., 2016). Many studies have shown unique/different results (Vetaas & Grytnes, 2002; Li *et al*., 2009; Linden *et al*., 2014; Zhang *et al*., 2016). Sinha *et al*. (2018) revealed that species richness of plants showed a negative correlation with altitude and attributed this to climatic variables such as actual evapotranspiration, potential evapotranspiration, and the moisture index as the measures of available environmental energies that drive the final shape of the forest community structure. These factors showed a significant relationship with species richness and the forest's altitude, which present the current shape of the forest community composition structure of Singalila National Park, India (Sinha *et al*., 2018). However, Zhang *et al*. (2016) revealed that the species richness of plants across temperate mountain forests had a monotonically decreasing pattern, and the tree richness had a unimodal pattern along the elevational gradients in two mountain areas. The altitudinal patterns in shrub and herb richness were not consistent on the two mountains. Anthropogenic disturbances contributed to increased plant diversity, especially for shrubs and herbs in understory layers, which are more sensitive to microenvironmental changes at low elevations (Zhang *et al*., 2016). The phylogenetic structure of plant communities exhibited an inverted hump-shaped pattern along the elevation gradient on Mount Tai, China which

demonstrates that environmental filtering is the primary driver of plant community assembly at high and low elevations, and interspecific competition may be the primary driver of plant community assembly in the middle elevations (Zhang *et al*., 2016).

A study by Martins *et al*. (2015) showed a variation in bat species richness and composition along an altitudinal gradient in the Atlantic Forest of southeastern Brazil, and a change in habitat heterogeneity was noted along the altitudinal gradient. Factors including climate, area, low productivity, evolutionary processes, and niche partitioning and roost microclimate affected the species richness of bats and functional composition (Martins *et al*., 2015). Species richness peaked around low elevations (500 - 1000 m a.s.l.), and there was a decrease in bats species richness at high elevation. There was a significant difference in the bat's species composition along an elevational gradient. Bat species richness and abundance were negatively correlated with altitude (Martins *et al*., 2015). Activity, species richness and diversity significantly decreased with increasing altitude in the Soutpansberg Range, South Africa (Linden *et al*., 2014). The changes in species richness and diversity over altitude were caused by factors correlated with altitudes such as vegetation type, area size, energy availability and climatic differences. These authors demonstrated that lower altitudes were richer and more diverse in bat species (Linden *et al*., 2014).

Magige (2013) reported a higher species richness of rodents in the woodland habitats than in the grasslands in northern Serengeti, Tanzania. Woodlands served as a haven for rodents that occupy suitable available niches (Magige, 2013). In contrast, however, Kasangaki *et al*. (2003) found that the small mammals' species richness decreased with

an increase in altitude. The main factors that accounted for the observed variations were wide altitudinal variation and a complex array of vegetation types. Changes in altitude resulted in a series of vegetation zones (Kasangaki *et al*., 2003). Increasing altitude resulted in a decline in grass biomass and growth, a decrease in the number of small mammals, and the numerical dominance of a single species of small mammals also decreased with an increase in altitude (Kasangaki *et al*., 2003).

Mulungu *et al*. (2008) investigated the diversity and distribution of rodent and shrew species associated with altitude variations on Mount Kilimanjaro, Tanzania. They revealed that the number of individuals captured varied with altitude and vegetation. The distributional patterns and species diversity of the rodents and shrews were influenced by habitat complexity and heterogeneity (Mulungu *et al*., 2008). The diversity of species varied with vegetation type, highest in the forest and lowest in the lowland area (Mulungu *et al*., 2008). More individuals were captured in the disturbed forest habitats than the moorland, fallow land and bushland (Mulungu *et al*., 2008). The abundance and distribution of small mammals depended on vegetation's nature and density, influencing food and shelter availability for small mammals (Mulungu *et al*., 2008). The vegetation in the studied areas with high trap success was forest and tall grasses (Mulungu *et al*., 2008). The lowest trap success was in the moorland (high altitude) (Mulungu *et al*., 2008). They reported that living conditions in moorland (high altitude) were unfavourable; hence the abundance of rodents and shrews was lower than in a disturbed and intact forest (Mulungu *et al*., 2008). Habitats with short and sparse grass on the slopes of Mt. Elgon in Tanzania have been reported to have comparatively low species diversity and abundance of small mammals (Mulungu *et al*., 2008).

Bateman *et al*. (2010) reported that the richness of small volant mammals peaked towards the summit of the altitudinal gradient in north-eastern Australia. They observed a positive non-linear relationship between altitude and mammal species richness. Abundance peaked at the 800 - 900 m range (Bateman *et al*., 2010). Such skews in richness peaks towards the higher altitudes indicate climatic influences that are often associated with vegetation changes (Bateman *et al*., 2010). Peak richness occurred at the point of optimal environmental conditions (high productivity and structural diversity) and the rapid transition zone between distinct vegetation communities (Bateman *et al*., 2010). There was a strong correlation between altitude and broad vegetation group, canopy cover, sub-canopy cover, shrub cover, canopy height, and sub-canopy height (Bateman *et al*., 2010). The initial categorization of the small mammal assemblage using altitude bands was strong for broad vegetation groups (Bateman *et al*., 2010). Ferro & Barquez (2009) recounted that variation in species richness along the elevational gradient was unimodal. The study also revealed a positive relationship between habitat heterogeneity and small mammal abundance with species richness.

Andrade & Monjeau (2014) revealed that while relative abundance and richness of small mammal assemblages increased at the intermediate levels, these two parameters decreased towards the upper and lower altitudes. Furthermore, differences in species composition of small mammals along the altitudinal gradient were evident (Andrade & Monjeau, 2014). They concluded that the sharp altitudinal gradient in the Somuncura plateau in semi-arid Patagonia, Argentina, influenced plant communities, shaping the small mammal assemblage composition along the gradient (Andrade & Monjeau, 2014).

Similarly, the species richness of non-volant small mammals on Mount Nuang, Hulu Langat, Selangor in Argentina decreased gradually from 500 - 1350 m a.s.l. due to elevational gradient (Andrade & Monjeau, 2014). Nor *et al*. (2001) attributed the elevational decrease to the following reasons: a decline in habitat area with increasing elevation, decreased resource diversity with increasing elevation, unfavourable climatic conditions at a higher elevation and decrease in primary productivity (Nor *et al*., 2001). Generally, the pattern of species diversity across a geographical gradient was determined by the change in the physical environment (Nor *et al*., 2001). They reported that physical parameters such as temperature, precipitation, and atmospheric pressure, which usually changes drastically across elevations, shape the local diversity and abundance of plants and animals (Nor *et al*., 2001).

Species composition and diversity of small mammal assemblages in agricultural areas were significantly affected by a degree of naturalness and landscape complexity (Gentili *et al*., 2014). This was investigated in a study on decreased small mammal species diversity and increased population abundance along a gradient of agricultural intensification in northeast Italy (Gentili *et al*., 2014). Species diversity decreased, and the number of generalist species increased with increasing agricultural intensification (Gentili *et al*., 2014). Brook *et al*. (2010) concluded a peak in species richness of small non-volant mammals towards the altitudinal gradient's summit at the point of optimal environmental conditions and greatest vegetation juxtaposition (Brook *et al*., 2010). With increasing altitude, the steep gradient caused a gradual overlap and replacement of species and increased species diversity. Species richness was influenced by local effects such as the relationship between certain species and habitat resources and a combination

of anthropogenic effects and low primary productivity at the lowest altitude sites (Brook *et al*., 2010).

Caceres *et al*. (2011) revealed that altitude and vegetation were the two factors that affect small mammal communities with an interaction between them. Species that are significantly influenced by altitude and vegetation will occur in a given altitudinal zone and habitat type with a specific probability (Caceres *et al*., 2011). Their significant finding was the interaction between altitude and vegetation in determining small mammals' community diversity pattern. The lack of forests on the high-altitude mountain tops can be understood as an effective barrier to forest-dwelling small mammals occupying mountain tops, although some forest species occur in the high altitude forests (Caceres *et al*., 2011). Correlation and regression analyses indicated that vegetation should change according to altitude, partially explaining the community variation (Caceres *et al*., 2011). In the Urucum mountains western Brazil, forests at high altitudes are near the transition to grassland, becoming less complicated, shorter and with an open understorey (Caceres *et al*., 2011). The high altitude contains a mixture of forest and grassland small mammal species but tends to show lower species richness (Caceres *et al*., 2011).

The overall significant difference in rodents' abundance among the habitats at different altitudes was reported by Kassa & Bekele (2008). There was no significant difference among the captures of rodents between species and season. The difference in the number of individual rodents between the dry and wet seasons was significant. The Shannon-Wiener diversity index (H') and Simpson's similarity index (SI) was high for the 3101 -

3400 m a. s. l. zone and the second-most diverse altitudinal zonations 3701 and 4100 m a.s.l. (Kassa & Bekele, 2008). The altitudinal zonation of a given area had different vegetation zones; thus, different species were distributed along different altitudinal gradients (Kasso *et al*., 2010). The vegetation height is the most crucial factor influencing the number of individuals rodents captured (Kok *et al*., 2012). It was hypothesized that the high species richness and diversity of small mammals observed in the Sneeuberg Mountain complex (SMC) were because SMC was located in the grassland and Nama Karoo biomes transition zone. These studies have shown different results/outcomes. Some have shown high diversity and richness of different organisms at middle elevations (Nor *et al*., 2001; Andrade & Monjeau, 2014; Sinha *et al*., 2018), while others have shown high diversity and richness of different organisms either at low or high elevations (Kasangaki *et al*., 2003; Bateman *et al*., 2010; Linden *et al*., 2014; Martins *et al*., 2015). This study predicted that species richness and small mammal hosts' diversity would be high at high altitude sites. It is also predicted that the intensity of flea infestation and flea infestation prevalence will be high at the high altitude site and low at the low altitude site. Although several studies have been undertaken on small mammals and ectoparasites in Namibia, no study investigated small mammals and fleas along altitudinal/elevational gradients. This study was conducted along the altitudinal/elevational gradient across the Ugab River, Namibia. Many studies on altitudinal/elevational gradients were done on mountain ranges (Nor *et al*., 2001; Mulungu *et al*., 2008; Kok *et al*., 2012; Andrade & Monjeau, 2014).

2.2. Small mammals

Small mammals are a dominant group of mammals and comprise about 42% of mammal species known to occur on earth (Aplin *et al*., 2003). They comprise small free-living rodents, such as moles, rats, mice, lemmings, gerbils, jerboas, dormice and squirrels, and insectivores (Delany, 1974) as shrews. Small mammals weigh less than 5 kg and are host to diverse communities of both ectoparasites and endoparasites (Delany, 1974). Rodents are a very successful and well defined assemblage of mammals, occurring throughout the world (De Graaf, 1981; Hoffmann & Zeller, 2005). Aplin e*t al*. (2003) stated that rodents occupy a wide range of natural habitats, including forests and grasslands and agricultural landscapes, villages, and townships. This group of animals (small mammals) shows a wide range of adaptations for successfully colonizing and inhabiting almost any habitat type. They are among the essential components of nearly all terrestrial fauna (De Graaf, 1981; Leis *et al*., 2007). Small mammals are of great importance to humans, and knowledge of these animals is of great value. In many cases, they are pests, feeding on and destroying crops and the damage they cause to food is well known where food is consumed and spoilt in silos, warehouses and individual homes (Delany, 1974).

2.3. Importance of small mammals in ecosystems

Small mammals play an essential role in maintaining natural ecosystems because of their large numbers, short generation intervals, and rapid and sustained population growth capacity. Small mammals, especially rodents, are abundant, widely distributed, and essential components of nearly all terrestrial ecosystems, especially in semi-arid or arid

areas (Van Deventer & Nel, 2006). Hoffmann & Zeller (2005) highlighted that small mammals are essential components of arid and semi-arid ecosystems where they serve as consumers, predators and dispersers of seeds, burrowers and as prey for carnivores and raptors. They further state that changes in habitat structure and complexity are associated with changes in small mammal community structure and species richness (Hoffmann & Zeller, 2005). Small mammal communities often respond rapidly to change in habitat structure and plant composition, and they occupy vital positions in food webs, making them informative biological indicators of change (Leis *et al*., 2007). Small mammals are sufficiently mobile to disperse to suitable sites and leave unsuitable sites, yet they are dependent on resources from a reasonably definitive localized area. They are found almost in every type of habitat and have a high reproduction rate and, therefore, a valuable tool for managers assessing conditions such as soil type and vegetation structure across landscapes (Leis *et al*., 2007). The high diversity of rodent species in many agroecosystems provide an opportunity to identify species that can indicate whether the ecosystem is in a poor (degraded landscape) or good condition where there is sustainable production. Numerous species of small mammals are adapted to live in agroecosystems, therefore represent an essential element of the ecosystem as they can significantly affect the diversity of higher trophic levels (Gentili *et al*., 2014). Species diversity can be considered a phenomenon that reflects the quality and functionality of a landscape. The more diverse and natural the landscape is, the higher the biodiversity of small mammals. Because of their good reproductive capacity and invasive ability, small mammals are a suitable model group to assess environmental quality (Slabova *et al*., n.d.). The relationship between the environment and small mammals is complex and reflects the physiological, nutritional, social and anti-predator

requirements of the small mammals in question. Small mammal community structure and species richness have been related to biotic and abiotic variables such as habitat structure and complexity, area, productivity, predation, trampling and grazing, surrounding landscape and the distance between similar habitats, maturing of the habitat/succession of the vegetation and the presence of exotics (Avenant, 2011).

2.4. Fleas

Fleas (Order Siphonaptera) are a monophyletic group that evolved from mecopteran (scorpionfly) winged ancestors during the early Cretaceous 120 - 130 million years ago in parallel with marsupials and insectivore hosts (Durden & Hinkle, 2019). More than 2000 species of fleas have been described so far, about 90% of which are parasitic on placental mammals, especially rodents (Gillot, 1980). Siphonaptera comprises families with 32 genera and 98 species in the Southern African subregion (Segerman, 1985). Fleas are small, dark, wingless, laterally compressed parasitic insects with long legs that enable them to jump considerable distances (Segerman, 1985). Most fleas in the adult stages depend on the blood of warm-blooded vertebrates for nourishment (Triplehorn & Johnson, 2005). However, the larvae of fleas are relatively free-living and feed on organic material in the host nest. Some fleas visit the host only for short periods to feed and are otherwise found in the host's nest burrow. They are called nest fleas (Segerman, 1985). While many flea species are only a biting nuisance, few are disease vectors, serve as the intermediate host of certain tapeworms, and few others burrow into their host's skin (Borror *et al*., 1989). Dobler & Pfeffer (2011) stated that fleas are among the most important ectoparasites of humans in that several species are vectors of several important infectious diseases such as the plague.

In general, fleas are not very host-specific, although they have preferred hosts. Mfune *et al*. (2013) found that the flea species *Listropsylla aricinae* infested their mammal host, hairy-footed gerbil (*Gerbillurus paeba*) only, and *Dinopsyllus ellobius* was only recorded from bushveld gerbil (*Gerbilliscus leucogaster*). Most fleas can transfer from their primary host to either another or a host of a different species. Mfune *et al*. (2013) recorded *X. brasiliensis* and *X. cheopis* from three different host species (*G. leucogaster, G. paeba and T. nigricauda*) in high abundance in each case. *Xenopsylla brasiliensis and X. cheopis* are therefore not host-specific. The flea common names, rat fleas, chicken fleas, and human fleas, refer only to their preferred host and do not imply that they attack that host exclusively (Roberts & Janovy Jr, 2009). Although few flea species are cosmopolitan (including some that attack humans) and attack a wide range of hosts, most species are restricted to their hosts and geographic distribution (Borror *et al*., 1989). They are highly modified for their ectoparasitic lifestyle, a feature that has made the determination of their relationship with other Insecta extremely difficult (Gillot, 1980). Gillot (1980) further stated that adults between 1 and 10 mm in length are highly compressed laterally and heavily sclerotized. The many hairs and spines on the body are directed posterior to facilitate forward movement (Segerman, 1985). The adult head capsule may be 'fracticipit', with a transverse inter antennal groove connecting the antennal fossae dorsally, or inter gricipit in which the inter antennal groove is absent. It usually bears a single frontal tubercle mesally on the frontal margin and a variable number of pre-antennal setal rows (Triplehorn & Johnson, 2005). The head is broadly attached to the body and carries the 3-segmented short antennae in grooves. The mouthparts are modified to piercing the host's skin and sucking blood. The thoracic

segments are mobile and increase in size posteriorly (Gillot, 1980). The thorax consists of 3 distinct and separate segments. The pronotum is demarcated and may have one to three rows of setae and frequently a distinct comb along its caudal margin (Triplehorn & Johnson, 2005). The propleurites and prosternum have lost their identities and form a composite, L-shaped structure called the prosternosome devoid of setae (Triplehorn & Johnson, 2005). Legs are adapted for jumping and clinging to the host. All bodily functions, such as breathing, mating, egg-laying, and defecation, occur at the small opening at the posterior end (Segerman, 1985). High humidity tends to favour egg-laying in adults and is considered a prevalent condition in nests and burrows (Roberts & Janovy Jr, 2009). The abdomen of adult fleas consists of 8 distinct segments plus a compound terminal area in which segmentation is indistinct (Triplehorn & Johnson, 2005).

Some fleas are of significant medical importance as they transmit *Yersinia pestis*, the causative agent of plague. Besides some other diseases that fleas are suspected of transmitting, there are irritating flea bites that may cause quite severe medical conditions in hypersensitive people (Segerman, 1985). The most crucial disease transmitted by fleas is a plague or Black Death, an acute infectious disease caused by the bacillus *Pasteurella pestis* (Borror *et al*., 1989). The cosmopolitan rat flea, *X. cheopis*, is responsible for transmitting bubonic plague and typhus, typically diseases of rodents, to humans (Gillot, 1980). Fleas are also the intermediate hosts of dog and rodent tapeworms that can infect humans (Gillot, 1980).

Two broad trends in the life cycle of fleas are evident (Wall & Shearer, 2001). A simple association with the nesting habitat is preserved in many groups of the family Ceratophyllidae, characterized by infrequent and brief associations with the host and often considerable adult movement between hosts and nests. In contrast, many groups of the family Pulicidae show prolonged adult associations with the host. However, within these broad categories, a high degree of co-evolution between individual flea species and their hosts may exist, and the variation in the flea life cycle may be considerable (Wall & Shearer, 2001).

2.5. Studies on fleas

Host-specificity, prevalence, and intensity of infestation of fleas of small mammals at selected sites in Windhoek, Namibia, were investigated (Mfune *et al*., 2013). The study revealed that the flea species *Dinopsyllus ellobius* and *Xenopsylla trispinis* exclusively infested the bushveld gerbil (*G. leucogaster).* The species diversity and richness of fleas did not vary significantly between the bushveld gerbil (*G. leucogaster)* and hairy-footed gerbil (*G. paeba)* and between male and female hosts (Mfune *et al*., 2013). The study also revealed that the prevalence of fleas was highest in the hairy-footed gerbil (*G. paeba)* followed by the bushveld gerbil (*G. leucogaster)* and black-tailed tree rat (*Thallomys nigricauda*) (Mfune *et al.,* 2013). It also showed that the prevalence was higher in males than in females while there was no significant difference in the flea intensity of infestation between the bushveld gerbil (*G. leucogaster)* and the hairy-footed gerbil (*G. paeba)* (Mfune *et al*., 2013).

A comparison of the prevalence and intensity of infestation and species diversity of fleas of small mammals from different localities and altitudes in Namibia was conducted by Litubezi (2013), who concluded that the prevalence of infestation of fleas varied between hosts and among different sites due to differences in climatic conditions among sites and the faunal habitat of the small mammal hosts. The intensity of flea infestation did not vary significantly amongst the sites in *Micaelamys namaquensis* and *G. leucogaster*. The species diversity of fleas was higher in *M. namaquensis* than in *G. leucogaster* and among different sites because *M. namaquensis* provides a suitable habitat for different flea species (Litubezi, 2013). Litubezi (2013) elaborated that M. *namaquensis* provides suitable habitat for different flea species, thus a high diversity of fleas.

The current study was undertaken over two seasons; the hot wet season (January) and the cold dry season (May). A study on the seasonal occurrence of fleas and other ectoparasites of small mammals at Waterberg Plateau Park, Namibia, was undertaken by Uusiku (2007). Species diversity was higher during summer (December) and lower during autumn (March) and winter (June), most probably because of pronounced seasonality in terms of temperature and precipitation. There was also a significant difference in fleas' prevalence between summer and autumn and between summer and winter. The lower prevalence of fleas during autumn and winter was attributed to heavy precipitation during autumn and lower winter temperatures. There was a positive relationship between host sample size and host relative density (Uusiku, 2007). Stanko *et al*. (2002) also reported a positive relationship between flea species richness and host density estimates. Linear regression analysis showed a positive effect of host density on

flea species richness for five species of the small mammal species examined and no effect for Ural field mouse (*Apodemus uralensis)* and European pine vole (*Microtus subterraneus)* (Stanko *et al*., 2002).

Froeschke *et al*. (2010) reported that environmental variables such as rainfall and temperature have an essential role in parasite transmission and infestation patterns. They reported a strong positive correlation between the mean annual precipitation (rainfall and relative humidity) and the nematode infestation rate of four-striped grass mice *(Rhabdomys pumilio)* and a negative correlation with temperature. There were associations between precipitation and different parasite burden measurements (mean nematode species richness, the mean number of nematode worms and infection intensity per individual host). Parasite burden was higher in wetter climates than the dries ones (Froeschke *et al*., 2010).

The composition of flea species in a habitat is determined by species composition and the habitat's environmental parameters (Shihepo *et al*., 2008). This was reported by Shihepo *et al*. (2008) in the study on the fleas associated with small mammals in selected areas in northern Namibia. The number of fleas and flea species richness at Omatjene Research Station (99 individuals and seven species) and Okawikenga Farm area (86 individuals and seven species) was due to specific environmental conditions offering various suitable habitats to host species. Omatjene Research Station had a denser grass and vegetation cover, an advantage for fleas, as ectoparasites are subjected to the host's external and internal environment (Shihepo *et al*., 2008).

Larger individual hosts are predicted to host a higher abundance of fleas because they present a larger food resource for ectoparasites (Young *et al*., 2015). These authors reported that the factors that influence the intensity of flea infestation among individuals in a population are body size, sex, and season. Heavily parasitized hosts had poor body conditions as a result of high levels of parasitism. The most consistent and vital variables identified in predicting flea parasitism's intensity and prevalence across host species populations were host abundance and vegetation cover (Young *et al*., 2015).

Guernier *et al*. (2014) reported the heterogeneous distribution of fleas over the Reunion Island, with no *Xenopsylla* flea collected along the windward humid eastern coast because of excessive rainfall. They also argued that temperature, rainfall, and relative humidity directly affected fleas' development and survival. The direct effect of rainfall occurs when high-intensity rainfall causes flooding of rodent burrows. Warm moist weather has been described to provide high flea indices (Guernier *et al*., 2014).

Laudisoit *et al*. (2009) reported that flea species composition increased during the dry and rainy seasons with an increase in the similarity in host species composition in their investigation of host and flea species composition across different habitats during dry and rainy seasons in the western Usambara Mountains in Tanzania. Nevertheless, between-season within-habitat and within-season between-habitat similarity in host species composition was higher than similarity in flea species composition. According to their host and flea species composition, their ordination of habitats demonstrated that the pattern of between-habitat similarity in both host and flea species composition varied seasonally (Laudisoit *et al*., 2009).

A study by Zimba *et al*. (2011) on seasonal abundance of *X*. *brasiliensis* from rodent hosts sampled from selected habitat types of two peri-urban suburbs of Harare; Zimbabwe reported that *X. brasiliensis* is an essential vector of plague in Zimbabwe. In both formal and informal settlements, the highest percentage incidence index (PII) of *X. brasiliensis* was attained for *M. natalensis*, followed by the black rat (*Rattus rattus*). *Gerbilliscus leucogaster* recorded the highest indices and *R. pumilio,* the lowest in the cultivated habitat (Zimba *et al*., 2011). *Xenopsylla brasiliensis* was found to cohabitate with *Dinopsyllus lypusus* and *Ctenophthalmus calceatus* on *M. natalensis, R. rattus,* and *G. leucogaster*. For all the rodent species sampled, both PII and specific flea index (SFI) of *X. brasiliensis* were highest during the hot dry season, followed by the hot wet season, with the cold dry season recording the lowest indices. The overall cohabitation was highest during the hot dry season and lowest during the hot wet season (Zimba *et al*., 2011).

CHAPTER 3

MATERIALS AND METHODS

3.1. Study Area

The study was conducted at three sampling sites (Figure 1) selected over an altitudinal gradient along the Ugab River, Namibia, which runs through different biomes, namely: Namib Desert, Nama Karoo and the Acacia tree and Savanna (Mendelsohn *et al*., 2002). These biomes have different vegetation types and cover at different altitudes along the river. The Ugab River is about 450 km long and has an elevation range between 0 and 1865 m with a catchment area of about 28 400 km^2 (Jacobson *et al*., 1995). The Ugab river is ephemeral and originates near Otavi yet supports a wide range of land uses, including mining, tourism and agriculture. Typical vegetation along the Ugab River include the ana tree (*Faidherbia albida),* camelthorn (*Vachellia erioloba),* Mustard tree (*Salvadora persica)*, Mopane (*Colophospermum mopane)*, leadwood (*Combretum imberbe)*, *Euclea* species*, Tamarix* species, *Cyperus* species and *Phragmites* species (Jacobson *et al*., 1995).

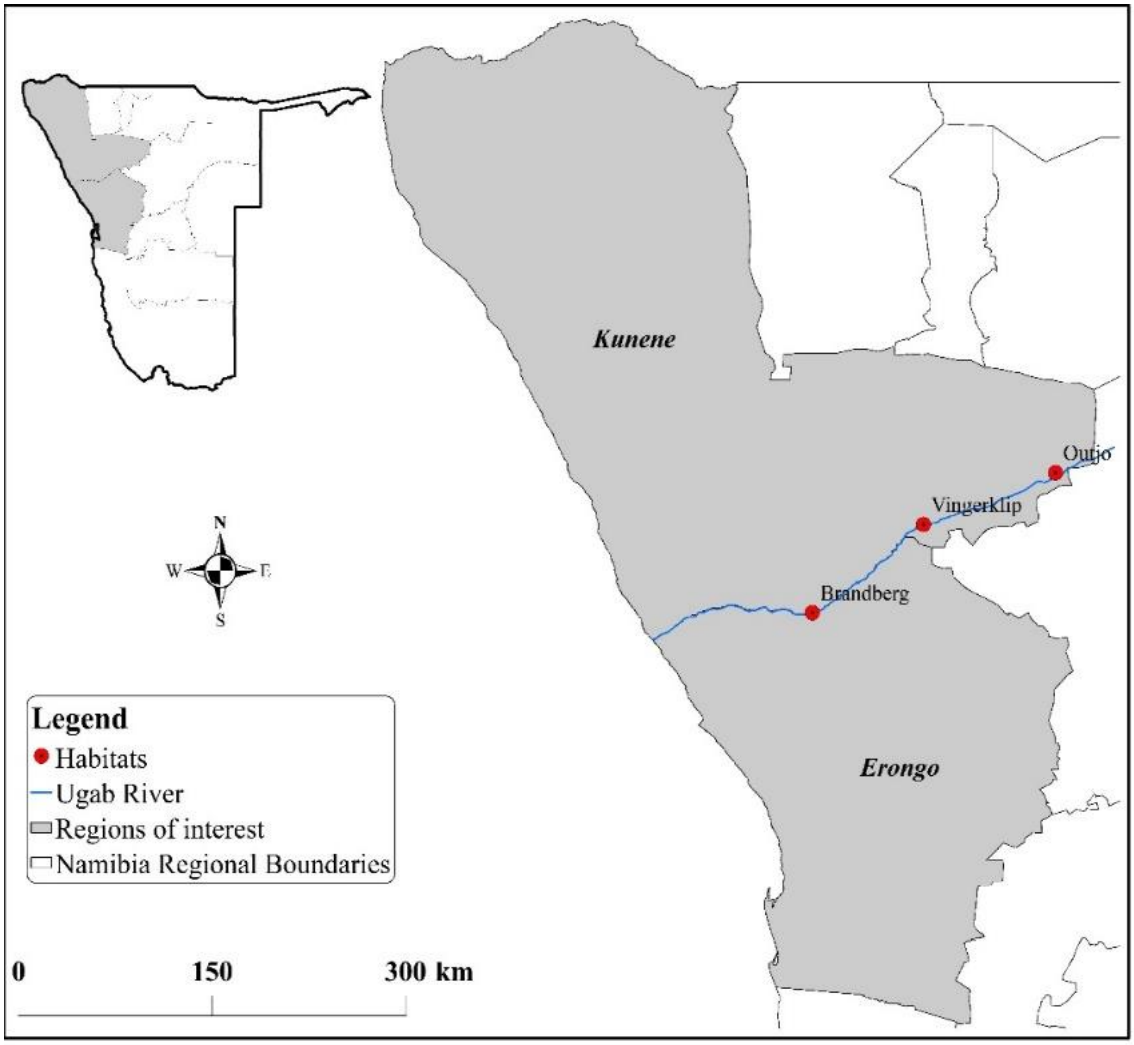


Figure 3.1.1: Map of Namibia showing the sampling sites, Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.).

The first site was in Outjo (1300 m a.s.l.) area (S20.05083˚/E016.43684˚), located in Kunene Region, situated on the C38 road 90 km southwest of the Anderson Gate of the Etosha National Park. The average annual temperature for Outjo is 21.4° C, and the average rainfall is about 394 mm per year (Anon. n.d). The second site was in the Vingerklip area (1000 m a.s.l.) in Damaraland in the Erongo Region (S20.34783˚/ E01.54510˚), 70 km west of Outjo town. The Ugab River meanders through the

landscape between Outjo and Khorixas. The third site was in Brandberg (400 m a.s.l.). It is located in Damaraland in the Erongo Region in the southwestern Namib Desert near the coast (S21.00464˚/E014.74156˚. The study site in Brandberg was near the Brandberg white lady lodge along the Ugab River.

3.2. Small mammals sampling

Two line transects, 290 m long each, spaced 100 m apart, were laid at each site. Thirty Sherman live traps (H. B. Sherman traps Inc., Florida, United States of America) baited with a mixture of rolled oats and peanut butter to attract a wide range of small mammal species were set. Transects were placed 10 m apart from each other. Sherman live traps are commonly used to trap small mammals. Lee (1997) found the Sherman live traps to be effective in trapping small mammals than snap traps. Nicolas & Colyn (2006) found that pitfall traps were more effective than Sherman and Snap traps for capturing shrews. In contrast, pitfall traps were less efficient in capturing rodents. Traps were set in the late afternoon from 17h00 and inspected the next morning from 08h00. Traps were set for three consecutive nights at each site during the hot wet season (January) and cold dry season (May) 2018 (Uusiku, 2007; Laudisoit *et al*., 2009; Zimba *et al*., 2011). Traps were set in microhabitat with suspected small mammal occurrence, including under tree logs, along rodent runs, in thick grass or under shaded vegetation, as stated by Musila *et al*. (2019). The small mammals were sampled under Research Permit number 2287/2017.

3.3. Recording of standard small mammal hosts data

Live small mammals were removed from the Sherman live traps and individually placed in zip-lock plastic bags and sacrificed using cotton wool saturated with chloroform placed in the plastic bag (Zimba *et al*., 2011; Mfune *et al*., 2013). This was done to ensure that there was no mixing up of host animals. The use of chloroform to euthanize small mammals is a standard human method commonly used for such studies (Mfune *et al*., 2013). The sacrificed animals were then carefully transferred onto a white tray. Standard data that included reproductive status (breeding/non-breeding), sex, body mass (to the nearest g using a spring scale), body length, tail length, ear length, foot length all to the nearest mm were recorded.

3.4. Identification of host species

Host specimens were identified using Southern African small mammal identification keys by Skinner & Chimimba (2005) and The Field Guide to Mammals of Southern Africa (Stuart & Stuart, 2015). Each small mammal host was also given an identification number to ensure that they do not get mixed up.

3.5. Collection of fleas from small mammal hosts

The whole body of the sacrificed small mammal host was brushed thoroughly and carefully with a fine toothbrush (to ensure that all fleas are removed from the host) while holding the animal above the white tray to dislodge and remove the ectoparasites. Ectoparasites, including fleas, were collected in petri-dishes and the fleas were stored in labelled (host identification number, site, date) vials containing 70% ethanol using a fine

jeweller's forceps for later processing and identification. Seventy percentage ethanol is used to preserve samples until they can be processed. Lung, heart and liver tissues were dissected out for later screening of hantaviruses in the Department of Biological Sciences at the University of Namibia, Windhoek. The gut of each animal was dissected out for further studies on endoparasites and genetic analysis. The extracted organ tissues were placed in separate two mL cryovials and appropriately labelled with the host animals' identification numbers and immediately frozen in a -20^{o} C mobile freezer and transported to the laboratory (University of Namibia) for processing and long-term storage.

3.6. Processing and identification of small mammal fleas

The standard procedure by Peterson (1981) was used to prepare the fleas for identification (Mfune *et al*., 2013). Fleas were removed from storage vials in 70% ethanol and were placed in distilled water for one hour to rinse alcohol off the specimens. Flea species were then transferred into petri-dishes containing 15% Potassium Hydroxide (KOH) and incubated at room temperature for four days to clear/dissolve the endodermal and the mesodermal tissues, leaving only the exoskeleton, which is required for the identification of fleas. Flea specimens were placed in distilled water for one hour to remove KOH and neutralized using 10% acetic acid for 30 minutes. Rinsing of KOH in distilled water was repeated once. The specimens were subsequently dehydrated using different strengths of alcohol: -70% for 30 minutes, 80% for 30 minutes, 96% for 30 minutes and absolute alcohol for an hour. Flea specimens were placed in oil of cloves and mounted permanently onto microscopes glass slides

using Canada balsam. The slides were then air-dried, ready for identification to species level. A standard identification key by Segerman (1995) was used to identify flea species known to occur in the southern Africa sub-region, including Namibia. The flea specimens were examined under a compound microscope at the University of Namibia, Department of Biological Sciences and identified to species level.

3.7. Vegetation assessment

At each of the three trapping sites, six 10 m x 10 m quadrats were laid, 30 m apart from each other, and all the trees and shrubs were recorded per species in the following height (m) classes: <1 m, 1 m-1.5 m, 1.6 m-2 m, 2.1 m-2.5 m, 2.6 m-3 m, and >3. Grass cover in each of the six quadrats was visually estimated according to the following percentage cover classes according to the modified Braun-Blanquet and Domin cover scales: 0-25%, 26-50%, 51-75%, 76-100% (Kent, 2012).

3.8. Statistical/data analysis

Species richness for woody vegetation, small mammal hosts and fleas recorded from small mammals were recorded for each site per season. Species richness is the number of species in a community (Krebs, 1994; Molles, 2016). Molles (2016) explained that a community with 20 species is less diverse than a community with 80 species. Species diversity for woody vegetation, small mammals and fleas were calculated using the Shannon-Wiener diversity index (H'). The index is given by $H' = -\sum pi \ln pi$, where H is diversity index, pi is the proportion of individuals belonging to the ith species, and ln is the natural log (Krebs, 1994). Data were analysed using the PAST (Paleontological

Statistics) software and XLSTAT. The Pearson's chi-square (χ^2) test was used to compare the species diversity of woody vegetation, small mammal hosts and fleas recorded from small mammal hosts between the three sites across the two seasons. Quinn & Keough (2002) stated that the Pearson's chi-square (χ^2) test is a fundamental statistical analysis of categorical data. They further urged that the Pearson's chi-square (χ^2) test compare observed and theoretical frequencies of the categories. Species composition of woody vegetation, small mammal hosts and fleas were analysed using the Hierarchical cluster analysis dendrogram based on the Bray-Curtis similarity single linkage. Hierarchical clustering techniques proceed by a series of successive mergers or a series of successive divisions. The most similar objects are first grouped and are merged according to their similarities (Johnson *et al*., 2007). One Way ANOSIM (analysis of similarities) was used to compare species composition of woody vegetation, small mammal hosts and fleas recorded from small mammals in selected sites across the two seasons. ANOSIM is a distribution-free multivariate test that compares the average ranked distances of (dis)similarity measures based on multiple species and their abundances within and between groups. It generates an *R*-value, which indicates the magnitude of separation between the groups, and this value ranges between 0 and 1 (Chapman & Underwood, 1999; Ramette, 2007). The Generalized linear models (GLM) compared the relationship between species richness of small mammal hosts and fleas recorded from small mammals with altitude. GLM uses a link function to establish a relationship between the mean of the response variable and a function of the explanatory variable(s). GLMs are more flexible and better suited for analyzing ecological relationships (Guisan *et al*., 2002).

The median number of fleas per infested host was used to represent the intensity of the infestation of fleas as described by Mfune *et al*. (2013). Shapiro-Wilk test was used to test for the normality of flea intensity of infestation per host. A Kruskal-Wallis test was used to compare flea intensity of infestation per site and host sex. The Kruskal-Wallis test is the nonparametric test equivalent to the one-way ANOVA and has a null hypothesis that all samples are taken from populations with the same median (Dytham, 2003). In this study, the flea infestation prevalence was defined as the percentage or proportion of the hosts (small mammals) that were infested with ectoparasites (fleas) irrespective of the number of fleas recorded per host as described by Stanko *et al*. (2002); Durden & Hinkle (2019); Durden *et al*. (2004). Thus prevalence was calculated based on the presence or absence of ectoparasites. The Pearson's chi-square (χ^2) test was used to compare fleas' infestation prevalence recorded from small mammals between the three sites during the two seasons. The Tukey's HSD test was used to compare flea infestation prevalence among sites, small mammal host species and small mammal host sex. Tukey's HSD test is a simple and reliable multiple comparison test that compares each group mean with every other group mean in a pairwise manner and controls the family-wise Type 1 error rate to no more than the nominal level (Quinn & Keough, 2002).

CHAPTER 4

RESULTS

4.1. Vegetation assessment (species richness, abundance, diversity and composition of woody plants and grass cover)

The Shapiro-Wilk normality test showed that the abundance of woody plants in different height classes was not normally distributed ($W_{(17)} = 0.44$, $n = 18$, $P < 0.05$). Therefore the Kruskal-Wallis test for the mean abundance of woody plants per height classes of these non-normally distributed data revealed that abundance was significantly different among the different height classes for different species across the two seasons ($H_{(17)} = 15.59$, $n = 18$, $P < 0.05$). Pearson's chi-square (χ^2) test showed that the Shannon-Wiener diversity (H') index of woody plants did not differ significantly among the sampling sites across the two seasons ($\chi^2_{(5)} = 0.267$, $n = 6$, $P = 0.998$).

Twelve species of woody plants were recorded in Outjo (1300 m a.s.l.) during the hot wet season, and ten species were recorded in Vingerklip (1000 m a.s.l.) for both seasons (hot wet and cold dry seasons). Brandberg (400 m a.s.l.) recorded six woody plants species during the hot wet season and seven during the cold dry season (Figure 4.1.1).

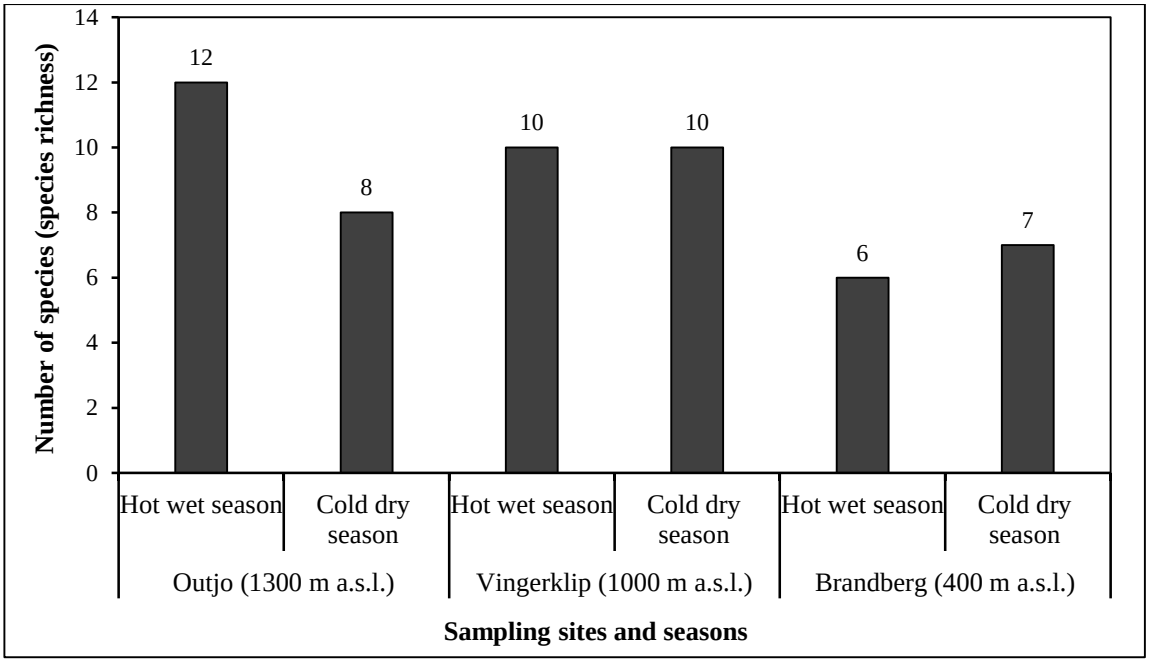


Figure 4.1.1: Species richness of woody plants recorded at the three sampling sites, Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.), during the hot wet and dry cold seasons, Namibia, 2018.

The mean abundance (standard error (S.E.±)) of woody plants (< 1 m) at the Outjo site (1300 m a.s.l.) during the hot wet season was 6.83 (Table 4.1.1. (a)) and 4.08 during the dry cold season (Table 4.1.1. (b)). Brandberg (400 m a.s.l.) had a mean abundance of 9.13 for woody plants > 3 m during the hot wet season and 4.71 during the cold dry season.

Table 4.1.1: Mean abundance (standard error (S.E.±)) of woody plants per height classes recorded at the three sampling sites, namely: Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.), during the hot wet (a) and cold dry season (b) Namibia, 2018. OHW = Outjo hot wet season, VHW = Vingerklip hot wet season, BHW = Brandberg hot wet season, OCD = Outjo cold dry season, VCD = Vingerklip cold dry season, and BCD = Brandberg cold dry season

(a)

Woody plants height classes	Mean abundance of woody plants per height class	S.E.
OHW <1 m	6,83	3,08
OHW 1 m - 1.5 m	4,33	1,77
OHW 1.6 m - 2 m	2,50	1,48
OHW 2.1 m - 2.5 m	1,54	1,17
OHW 2.6 m - 3 m	0,92	0,48
OHW >3 m	3,67	1,63
VHW <1 m	0,04	0,04
VHW 1 m - 1.5 m	2,25	1,15
VHW 1.6 m - 2 m	0,00	0,69
VHW 2.1 m - 2.5 m	0,96	0,59
VHW 2.6 m - 3 m	0,04	0,04
VHW >3 m	6,33	3,66
BHW <1 m	0,00	0,00
BHW 1 m - 1.5 m	0,00	0,00
BHW 1.6 m - 2 m	0,96	0,96
BHW 2.1 m - 2.5 m	0,29	0,29
BHW 2.6 m - 3 m	0,79	0,53
BHW >3 m	9,13	6,53

(b)

Woody plants height classes	Mean abundance of woody plants per height class	S.E.
OCD <1 m	4,08	0,83
OCD 1 m - 1.5 m	2,50	0,51
OCD 1.6 m - 2 m	0,38	0,08
OCD 2.1 m - 2.5 m	0,08	0,02
OCD 2.6 m - 3 m	0,08	0,02
OCD >3 m	0,13	0,03
VCD <1 m	0,63	0,13
VCD 1 m - 1.5 m	0,96	0,20
VCD 1.6 m - 2 m	0,29	0,06
VCD 2.1 m - 2.5 m	0,04	0,01
VCD 2.6 m - 3 m	1,83	0,37
VCD >3 m	3,13	0,64
BCD <1 m	0,00	0,00
BCD 1 m - 1.5 m	0,08	0,02
BCD 1.6 m - 2 m	0,04	0,01
BCD 2.1 m - 2.5 m	0,33	0,07
BCD 2.6 m - 3 m	0,38	0,08
BCD >3 m	4,71	0,96

The species diversity of woody plants for the Outjo site (1300 m a.s.l.) was 1.95 during the hot wet season and 1.80 during the cold dry season. Vingerklip (1000 m a.s.l.) had a species diversity value of 2.00 during the cold dry season, while Brandberg (400 m a.s.l.) had a species diversity value of 1.22 during the hot wet season (Figure 4.1.2.).

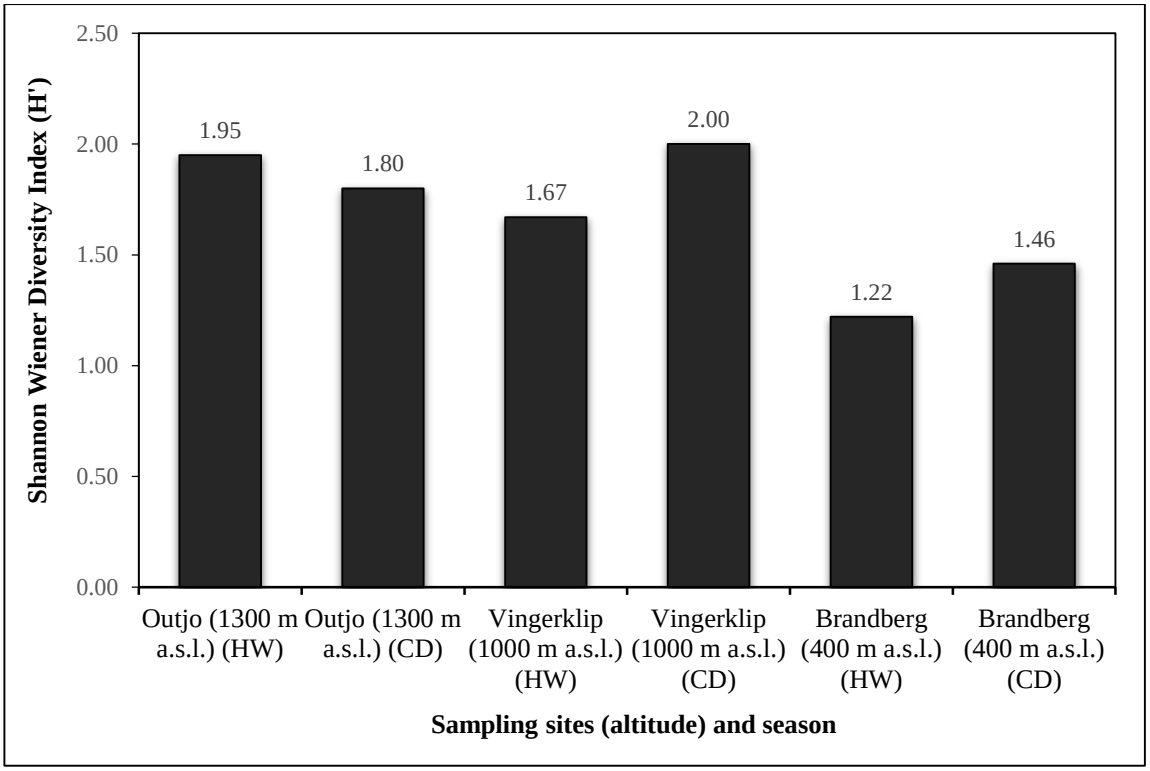


Figure 4.1.2: The Shannon-Wiener diversity (H') index of woody plants at the three sampling sites, Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.) per season (HW = hot wet season, and CD = cold dry season), Namibia, 2018.

The Hierarchical cluster analysis (HCA) for species composition of woody plants revealed two main clusters, namely: (a) Brandberg hot wet and cold dry season and (b) Vingerklip (hot wet and cold dry) and Outjo (hot wet and cold dry seasons). The two main clusters have a similarity distance of 0.2 (20% similarity) in species composition. Cluster b is further divided into Outjo (hot wet and cold dry seasons) and Vingerklip (hot wet and cold dry seasons). A similarity distance of about 0.33 (33% similarity) in species composition was observed between the species composition for Outjo (hot wet and cold dry) and Vingerklip (hot wet and cold dry). Species composition for Vingerklip for both seasons (hot wet and cold dry) was closely associated with a similarity distance of 0.68 (68% similarity) in species composition (Figure 4.1.3). The Outjo (1300 m a.s.l.) sites were characterized by short sickle bushes *(Dichrostachys cinerea),* blackthorns (*Senegalia mellifera),* velvet raisins (*Grewia flava)* and shepherd tree (*Boscia albitrunca)* plants during both seasons while Vingerklip (1000 m a.s.l.) was dominated by tall apple ring acacias (*Faidherbia albida),* mopanes (*Colophospermum mopane)* and sweet thorn (*Vachellia karoo*) plants. Kamelthorns (*Vachellia erioloba),* apple ring acacias (*Faidherbia albida),* and silver Terminalia (*Terminalia prunioides)* plants dominated the Brandberg (400 m a.s.l.) study sites. In general, Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.) sites were characterized by tall trees such as *F. albida* and *V. erioloba*, while the Outjo (1300 m a.s.l.) site was characterized by short woody plants, which were less than 3 m such as *B. albtrunca, G. flava* and *S. mellifera*. The ANOSIM results revealed no significant difference in the species composition amongst the 3 sites for the 2 seasons ($R_{(5)} = 1$, $n = 6$, $P = 0.067$).

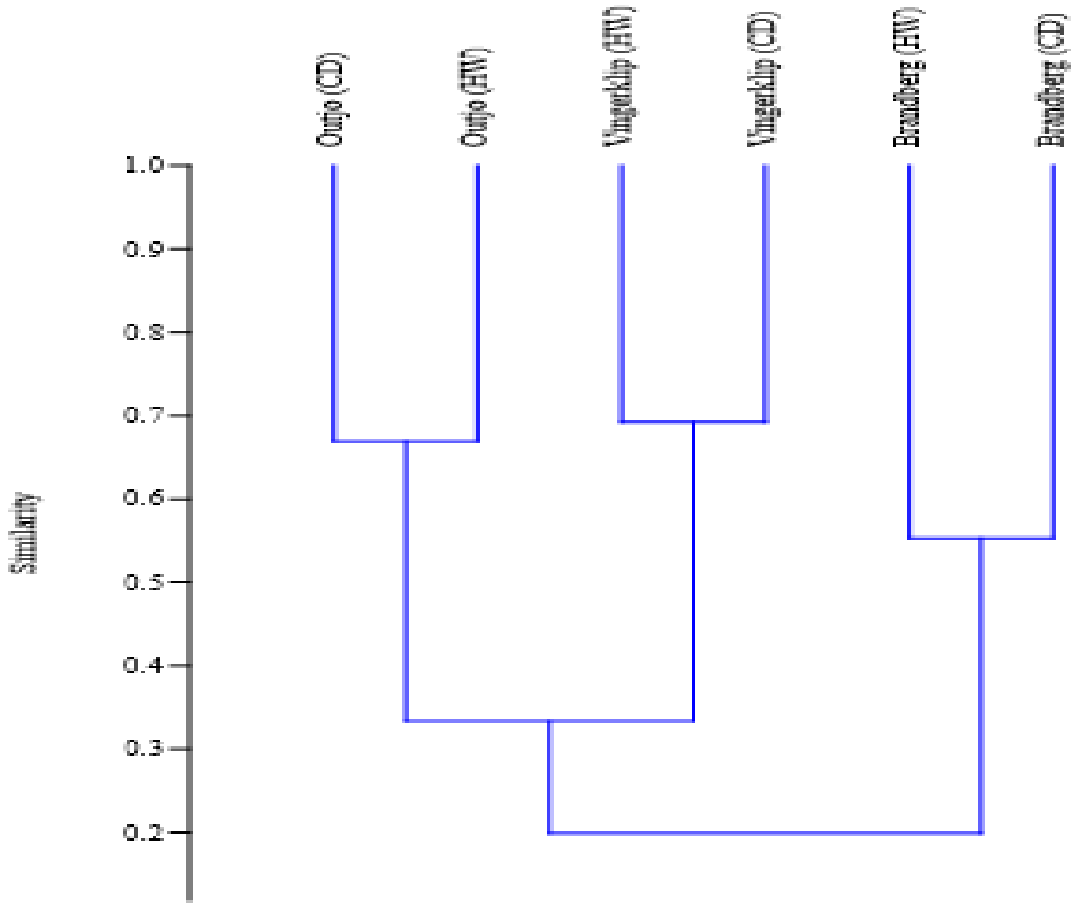


Figure 4.1.3: Hierarchical Cluster Analysis (HCA) using single linkage showing differences in woody plants species composition amongst the sampling sites, Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.), Namibia, 2018 per season (HW = hot wet season, CD = cold dry season). The y-axis shows the Bray-Curtis similarity distance from 0 - 1, and the x-axis shows the clusters and the sampling sites per season.

Fifty percentage of the quadrats assessed for grass cover in Vingerklip (1000 m a.s.l.) during the cold dry season had 76 - 100% grass cover, and 50% had 0 - 25% grass cover, none of the quadrats studied/assessed had 26 - 50% and 51 - 75% grass cover. However, in Brandberg (400 m a.s.l.), all of the quadrats assessed had 0 - 25% grass cover. No quadrat studied had 26 - 50%, 51 - 75% and 76 - 100% grass cover. Twenty-five percent of the quadrats studied in Outjo (1300 m a.s.l.) during the cold dry season had 0 - 25% grass cover. Forty-two percentage of the quadrats had 76 - 100% grass cover, while 8% of the quadrats had 51 - 75% grass cover (Figure 4.1.5.). Grass cover for all the sampling sites Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.) was in the 0 - 25% category during the hot wet season.

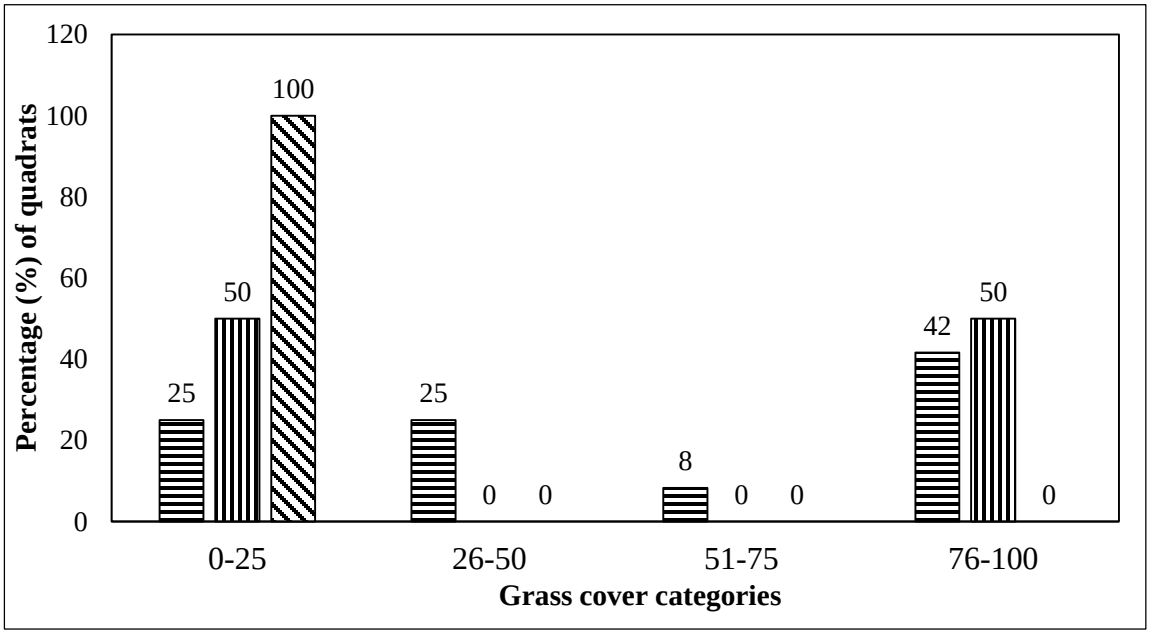


Figure 4.1.4: Percentage (%) grass cover for the 3 sites, Outjo (1300 m a.s.l.) ( ) Vingerklip (1000 m a.s.l.) ( ) and Brandberg (400 m a.s.l.) ( ), during the cold dry season (CD), Namibia, 2018.

4.2. Abundance, species composition, richness and diversity of small mammals

4.2.1 Abundance of small mammals

A total of 159 small mammal hosts representing nine species (seven rodents and two insectivore species) were recorded during the entire study. Eighty-nine animals were trapped in Outjo (1300 m a.s.l.) during the hot wet season and 33 during the cold dry season. Vingerklip (1000 m a.s.l.) recorded 15 individuals, while Brandberg (400 m a.s.l.) recorded six during the hot wet season. Natal multimammate rat (*Mastomys natalensis)* had 58 individual animals in the hot wet season, while the Red rock rat *(Aethomys chrysophilus)*) had 16 individuals during the hot wet season. Outjo (1300 m a.s.l.) recorded five species each during the hot wet and cold dry season, Vingerklip (1000 m a.s.l.) recorded four species during the hot wet season, three species during the cold dry season, while Brandberg (400 m a.s.l.) recorded two species during the hot wet season and three species during the cold dry season. Rodent species trapped in the study included the following species: *Micaelamys namaquensis* (Namaqua rock mouse), *Mastomys natalensis* (Natal multimammate rat), *Aethomys chrysophilus* (Red rock rat), *Saccostomus campestris* (Pouched Mouse), *Gerbilliscus leucogaster* (bushveld gerbil), *Thallomys nigricauda* (black-tailed tree rat) and *Thallomys paedulcus* (Acacia rat). Two insectivore species captured in the present study include *Crocidura hirta* (Lesser Red Musk Shrew) and *Elephantulus intufi* (bushveld elephant shrew) (Table 4.2.1). The Shapiro-Wilk Normality test showed that the abundance of small mammal hosts at different sampling sites across the two seasons was not normally distributed ($W_{(10)} = 0.267$, $n = 11$, $P < 0.050$). Therefore the non-parametric Kruskal-Wallis test for the abundance of small mammal hosts from this non-normally distributed revealed that the

abundance of small mammal hosts was not significantly different among the sampling sites across the two seasons ($H_{(53)} = 11.36$, $n = 54$, $P = 0.072$). However, it can be observed that the high altitude site (Outjo) recorded a high abundance of small mammals during the hot wet season followed by the cold dry season. The low altitude site (Brandberg) recorded a low abundance of small mammals during the wet hot, and cold dry seasons.

Table 4.2.1: Abundance of small mammal hosts sampled during the hot wet and cold dry season at Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.), Namibia, 2018. WH = hot wet season, CD = cold dry season

Host species	**Outjo (1300 m a.s.l.)**		**Vingerklip (1000 m a.s.l.)**		**Brandberg (400 m a.s.l.)**		**Total**
	WH	CD	WH	CD	WH	CD	
Mastomys natalensis	58	5	0	0	0	0	63
Micaelamys namaquensis	8	12	11	2	0	2	35
Aethomys chrysophilus	16	13	0	0	0	0	29
Gerbilliscus leucogaster	6	2	2	5	2	0	17
Thallomys nigricauda	0	0	1	0	4	0	5
Thallomys paedulcus	0	0	0	0	0	4	4
Elephantulus intufi	0	0	1	2	0	0	3
Saccostomus campestris	0	1	0	0	0	1	2
Crocidura hirta	1	0	0	0	0	0	1
Total	89	33	15	9	6	7	159

4.2.2 Small mammal species composition

The Hierarchical cluster analysis (HCA) for small mammal hosts species composition is presented in Figure 4.2.1. The HCA comprised two main clusters that included: (a) Brandberg (CD) and (b), which comprises the rest of the sites and seasons, Brandberg (HW), Vingerklip (CD), Vingerklip (HW), Outjo (CD) and Outjo (HW). The two main clusters had a similarity distance of 0.3 (30% similarity). Cluster b is further divided into (a) Brandberg (HW), (b) Vingerklip HW and CD and (c) Outjo (HW and CD) (Figure 4.2.1). *Mastomys natalensis, A. chrysophilus, M. namaquensis* and *G. leucogaster* dominated the Outjo sites during the hot wet and cold dry seasons. *Micaelamys namaquensis* and *G. leucogaster* mostly dominated Vingerklip during the two seasons. *Gerbilliscus leucogaster* and *T. nigricauda* dominated the Brandberg site during the hot wet season while *T. paedulcus* and *M. namaquensis* dominated Brandberg during the cold dry season. The ANOSIM results revealed no significant difference in the species composition of small mammals among the three sites across the two seasons ($R_{(5)}$ = 0.22, n = 6, P = 0.34).

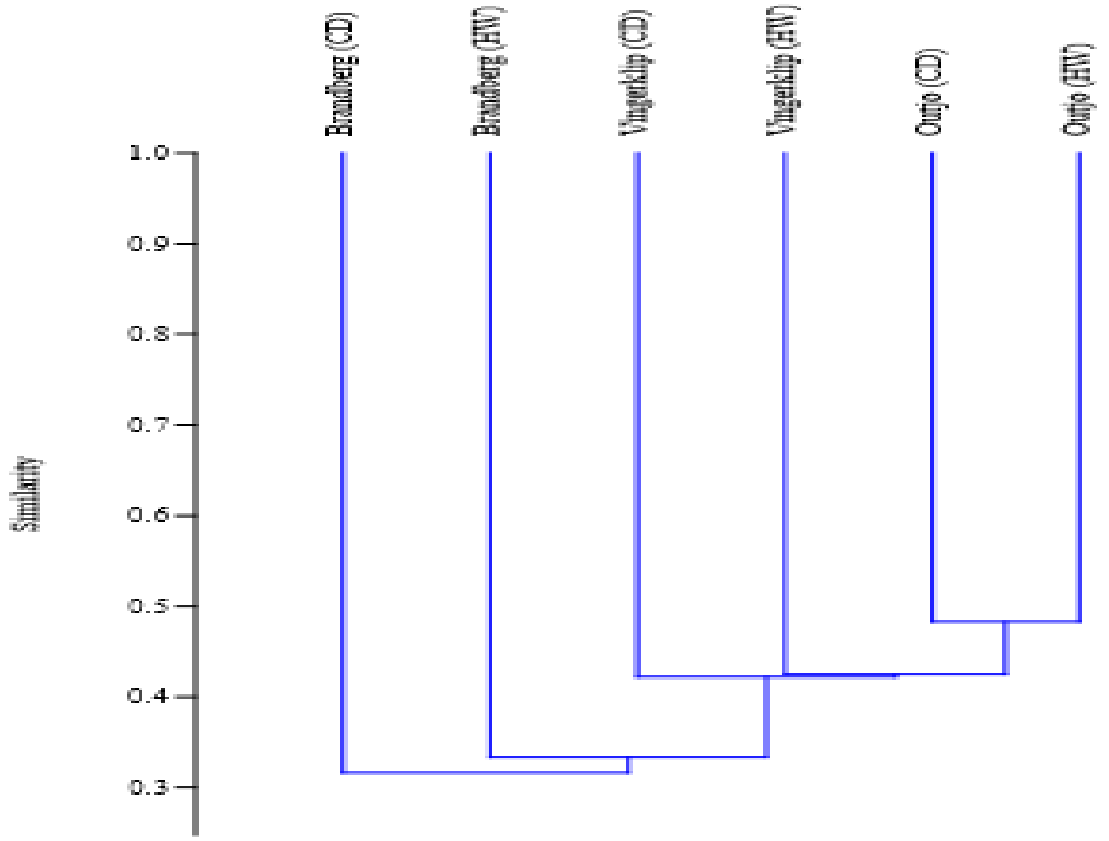


Figure 4.2.1: Hierarchical Cluster Analysis (HCA) using single linkage showing differences in the small mammal host species composition between the sampling sites, Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.), Namibia, 2018 per season (HW = hot wet season, CD = cold dry season). The y-axis shows the Bray-Curtis similarity distance from 0 - 1, and the x-axis shows the clusters and the sampling sites per season.

4.2.3 Small mammal species richness and diversity

A general linear model (GLM) using identity link function showed a strong and positive significant relationship between small mammal hosts' species richness and altitude ($G_{(5)}$ = 14,67, n = 6, P < 0.05). The small mammal hosts' high species richness was associated with an increase in altitude (Figure 4.2.2.). Pearson's chi-square (χ^2) test showed that the Shannon-Wiener diversity (H') index of small mammal hosts did not differ significantly among the three sampling sites during the hot wet ($\chi^2_{(2)}$ = 0.11, n = 3, P = 0.95) and cold dry season ($\chi^2_{(2)}$ = 0.267, n = 3, P = 0.97).

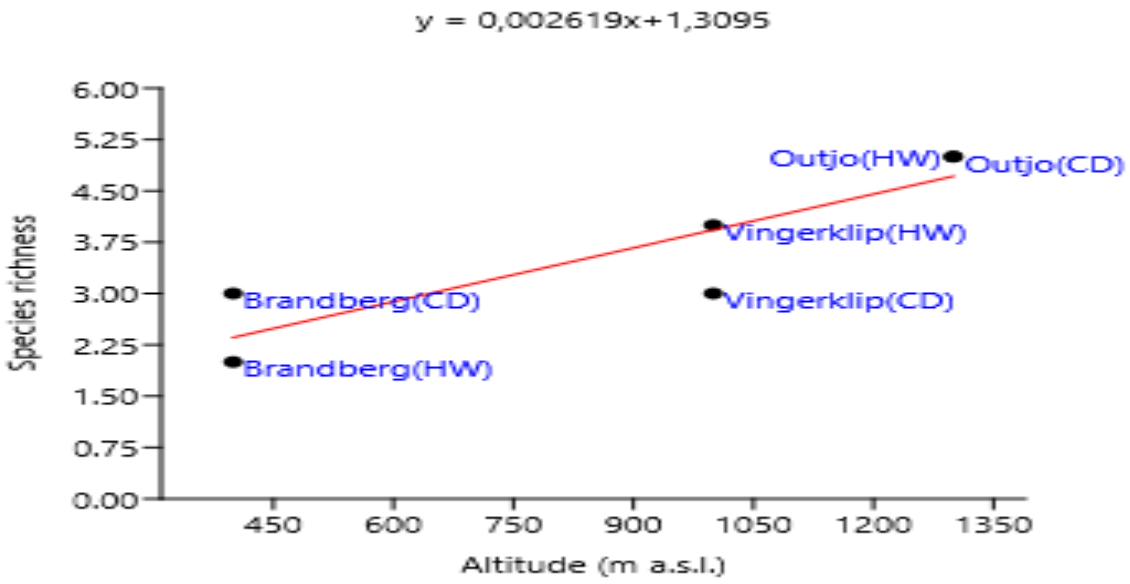


Figure 4.2.2: A Generalized Linear Model (GLM) showing a relationship between species richness of small mammal hosts and altitude at the three sampling sites, Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.), during the hot wet (HW) and cold dry (CD) seasons, Namibia, 2018.

Outjo (1300 m a.s.l.) had a species diversity value of 1.3 during the cold dry season and 1.0 during the hot wet season. The species diversity of small mammal hosts was 0.6 during the hot wet season and 1.0 during the dry cold season in Brandberg (400 m a.s.l.). Vingerklip (1000 m a.s.l.) had 1.0 during cold dry season (Figure 4.2.3.).

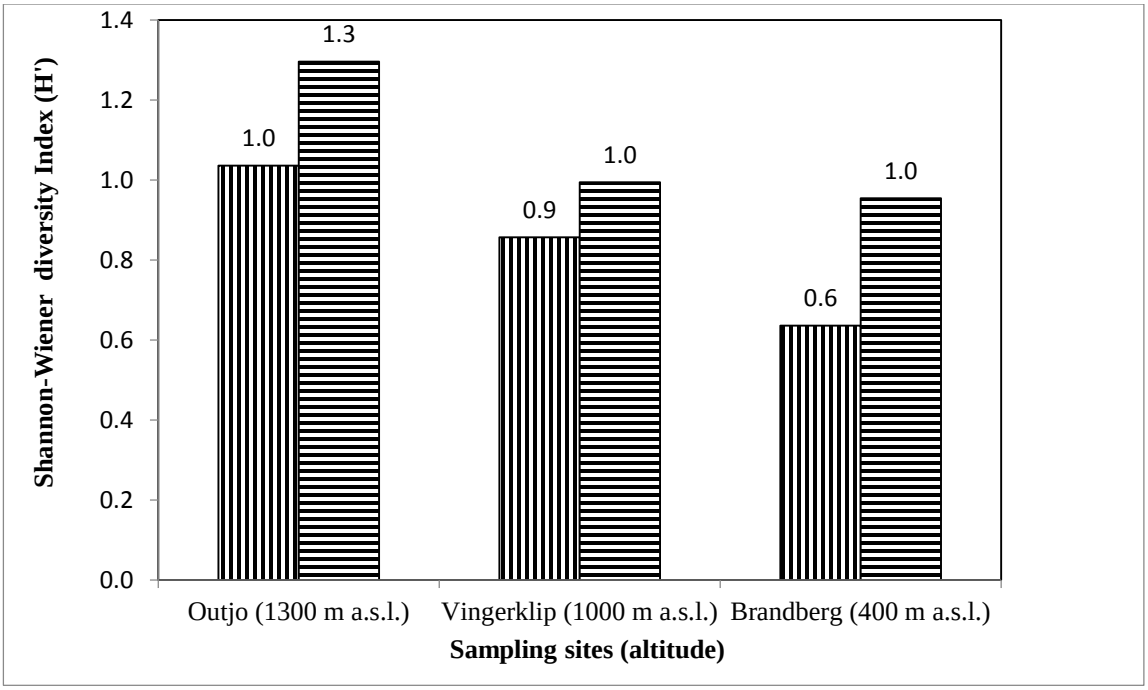


Figure 4.2.3: Shannon-Wiener diversity (H') index for small mammal hosts captured at the three sampling sites, Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.), during the hot wet ( ) and cold dry ( ) seasons, Namibia, 2018.

4.3. Abundance, species composition, richness and diversity of fleas collected from small mammal hosts

4.3.1 Flea abundance

A total of 139 individual fleas were collected from small mammal hosts captured at the three sampling sites during the two seasons (hot wet and cold dry seasons), representing three flea species, *Xenopsylla cheopis*, *Xenopsylla brasiliensis* and *Listropsylla dorripae*. *Xenopsylla cheopis* recorded 34 individuals in Outjo (1300 m a.s.l.) during the hot wet season and 27 during the cold dry season. No fleas were recorded at the three sampling sites during the hot wet season. *Listropsylla dorripae* was only recorded in Outjo (1300 m a. s. l) during the cold dry season, with five individuals (Table 4.3.1). A Shapiro-Wilk Normality test showed that the abundance of fleas collected from small mammals at different sampling sites during the two seasons was not normally distributed ($W_{(2)} = 0.86$, $n = 3$, $P < 0.05$). A Kruskal-Wallis test revealed that the abundance of fleas of these non-normally distributed data was not significantly different among the sampling sites across the two seasons ($H_{(17)} = 5.06$, $n = 18$, $P = 0.06$).

Table 4.3.1: Abundance of fleas collected during the hot wet season and the cold dry seasons in Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.), Namibia, 2018

Sampling sites	*Xenopsylla cheopis*		*Xenopsylla brasiliensis*		*Listropsylla dorripae*		Total	Composition (%)
	Hot wet season	Cold dry season	Hot wet season	Cold dry season	Hot wet season	Cold dry season		
Outjo (1300 m a.s.l.)	34	27	29	26	0	5	121	87.1
Vingerklip (1000 m a.s.l.	9	1	2	0	0	0	12	8.6
Brandberg (400 m a.s.l.)	1	0	1	4	0	0	6	4.3
Total	44	28	32	30	0	5	139	100

The majority of the fleas were recorded from *M. natalensis*, *G. leucogaster* and *M. namaquensis* during the hot wet season, with each recording 32, 24 and 9 flea individuals, respectively. No fleas were recorded from *Thallomys paedulcus*, *Elephantulus intufi*, *Crocidura hirta* and *Saccostomus campestris* during the hot wet season (Table 4.3.2.).

Table 4.3.2: Number of flea species collected from different species of small mammals that were captured at the three sampling sites (Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.), Namibia during the hot wet season, 2018

	Flea species									
	Xenopsylla cheopis			***Xenopsylla brasiliensis***			***Listropsylla dorripae***			
Host species	Outjo	Vingerklip	Brandberg	Outjo	Vingerklip	Brandberg	Outjo	Vingerklip	Brandberg	Total
Mastomys natalensis	20	0	0	12	0	0	0	0	0	32
Gerbilliscus leucogaster	13	9	1	1	0	0	0	0	0	24
Aethomys chrysophilus	1	0	0	8	0	0	0	0	0	9
Micaelamys namaquensis	1	0	0	7	1	0	0	0	0	9
Thallomys nigricauda	0	0	0	0	1	1	0	0	0	2
Crocidura hirta	0	0	0	0	0	0	0	0	0	0
Saccostomus campestris	0	0	0	0	0	0	0	0	0	0
Thallomys paedulcus	0	0	0	0	0	0	0	0	0	0
Total	35	9	1	28	2	1	0	0	0	76

The majority of the fleas were recorded from *M. namaquensis*, *M. natalensis* and *A. chrysophilus* during the cold dry season. The number of fleas collected was 26, 12 and 16, respectively. No fleas were recorded from *T. nigricauda*, *E. intufi* and *C. hirta* (Table 4.3.3.).

Table 4.3.3: Number of flea species collected from different species of small mammal hosts captured at the three sampling sites, Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.), Namibia, during the cold dry season, 2018

	Flea species									
	Xenopsylla cheopis			***Xenopsylla brasiliensis***			***Listropsylla dorripae***			
Host species	Outjo	Vingerklip	Brandberg	Outjo	Vingerklip	Brandberg	Outjo	Vingerklip	Brandberg	Total
Micaelamys namaquensis	15	0	0	9	0	0	2	0	0	26
Aethomys chrysophilus	2	0	0	11	0	0	3	0	0	16
Mastomys natalensis	9	0	0	3	0	0	0	0	0	12
Saccostomus campestris	0	0	0	4	0	0	0	0	0	4
Thallomys paedulcus	0	0	0	0	0	4	0	0	0	4
Gerbilliscus leucogaster	0	1	0	0	0	0	0	0	0	1
Crocidura hirta	0	0	0	0	0	0	0	0	0	0
Elephantulus intufi	0	0	0	0	0	0	0	0	0	0
Thallomys nigricauda	0	0	0	0	0	0	0	0	0	0
Total	26	1	0	27	0	4	5	0	0	63

4.3.3 Flea species composition

The HCA shows that the species composition of fleas collected from small mammal hosts at the three sampling sites, Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.). The y-axis displays the Bray-Curtis similarity distance from 0 - 1, and the x-axis shows the clusters and the sampling sites per season. The HCA revealed two main clusters: namely: (a) Vingerklip hot wet, Outjo cold dry and Outjo hot wet, and (b) comprises of Brandberg hot wet, Vingerklip cold dry and Brandberg cold dry. The two clusters have a similarity distance of 0.3 (30% similarity). In cluster (a), species composition of fleas for Outjo hot wet and cold dry were closely associated with a similarity distance of 0.8 (80% similarity) in the cluster (b) species composition of fleas for Brandberg hot wet and Vingerklip cold dry have a similarity distance of 0.6 (Figure 4.3.1.). *Xenopsylla cheopis* and *X. brasiliensis* dominated Outjo (1300 m a.s.l.) during the hot wet and cold dry seasons. *Listropsylla dorripae* was only collected from small mammals during the cold dry season in Outjo (1300 m a.s.l.). Only three species of fleas were collected from small mammal hosts. Brandberg (400 m a.s.l.) mainly was dominated by *X. brasiliensis*. *Xenopsylla cheopis* dominated Vingerklip during the cold dry season. ANOSIM revealed that the species composition of fleas of small mammals was not significantly different ($R_{(5)} = 0.67$, $n = 6$, $P < 0.14$).

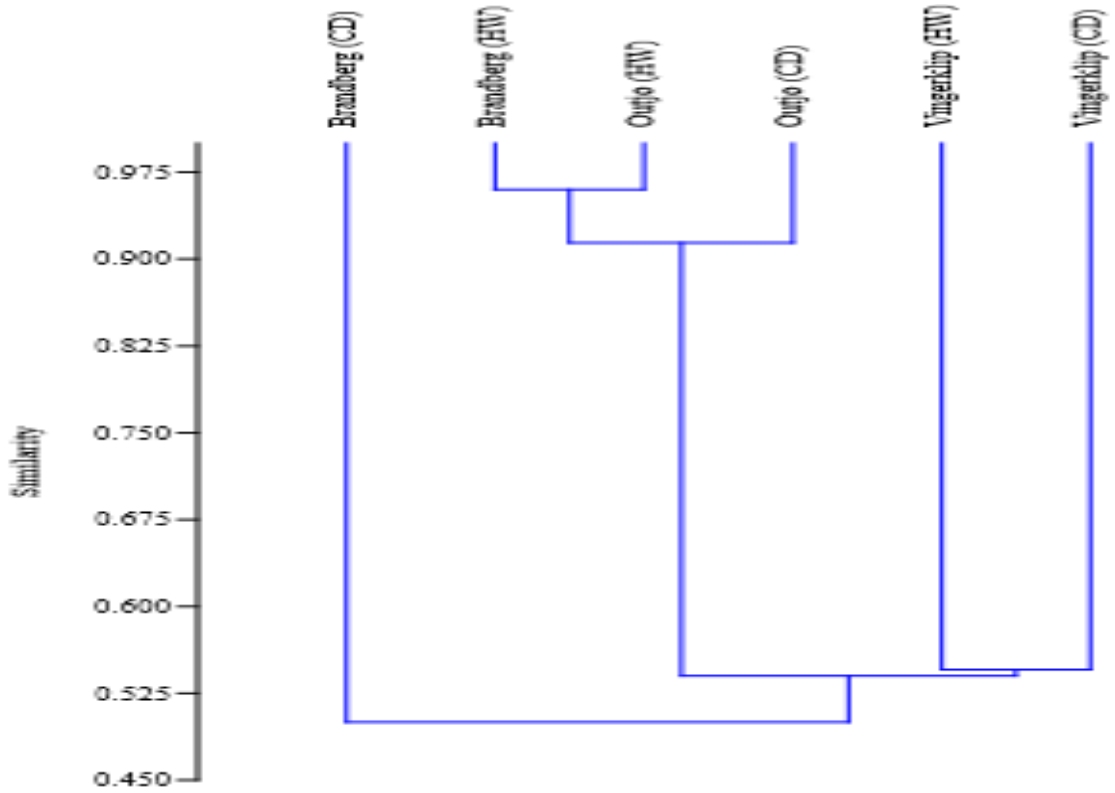


Figure 4.3.1: Hierarchical Cluster Analysis (HCA) using single linkage showing differences in fleas collected from small mammal hosts between the sampling sites (Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.) per season (HW = hot wet season, CD = cold dry season). The y-axis displays the Bray-Curtis similarity distance from 0 - 1, and the x-axis shows the clusters and the sampling sites per season.

4.3.4 Flea species richness and diversity on small mammal hosts

A GLM using identity link function revealed a weak but significant relationship between fleas species richness recovered from small mammals and altitude ($G_{(5)}$ = 0.068, n = 6, P = 0.794) (Figure 4.3.2). A Pearson's chi-square (χ^2) test showed that the Shannon-Wiener diversity (H") index of fleas of small mammals hosts did not differ significantly

among sites during the hot wet ($\chi^2_{(2)} = 0.043$, $n = 3$, $P = 0.98$) and cold dry season ($\chi^2_{(2)} = 1.86$, $n = 3$, $P = 0.40$). The species diversity of fleas of small mammal hosts for Outjo (1300 m a.s.l.) and Brandberg (400 m a.s.l.) was 0.69 each during the hot wet season. Vingerklip (1000 m a.s.l.) has a Shannon-Wiener diversity (H') index value of 0.49.

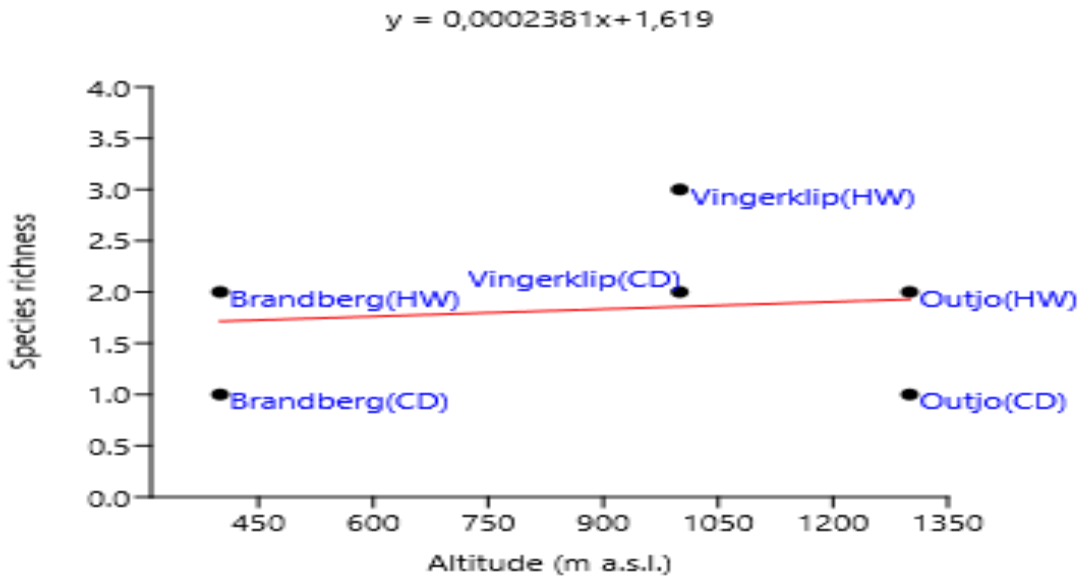


Figure 4.3.2: The Generalized Linear Model (GLM) showing a relationship between species richness of fleas collected from the small mammal hosts and altitude at the three sampling sites, Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.), Namibia, 2018 during the hot wet (HW) and cold dry (CD) seasons.

Species diversity of fleas recorded from small mammals was 0.72 during the cold dry season and 0.69 during the hot wet season for the Outjo site (1300 m a.s.l.). Brandberg (400 m a.s.l.) had a species diversity of 0.69 and Vingerklip (1000 m a.s.l.) 0.47 during the hot wet season. Only one or zero species were recorded in Vingerklip and Brandberg during the cold dry season, thus 0 species diversity values (Figure 4.3.3.)

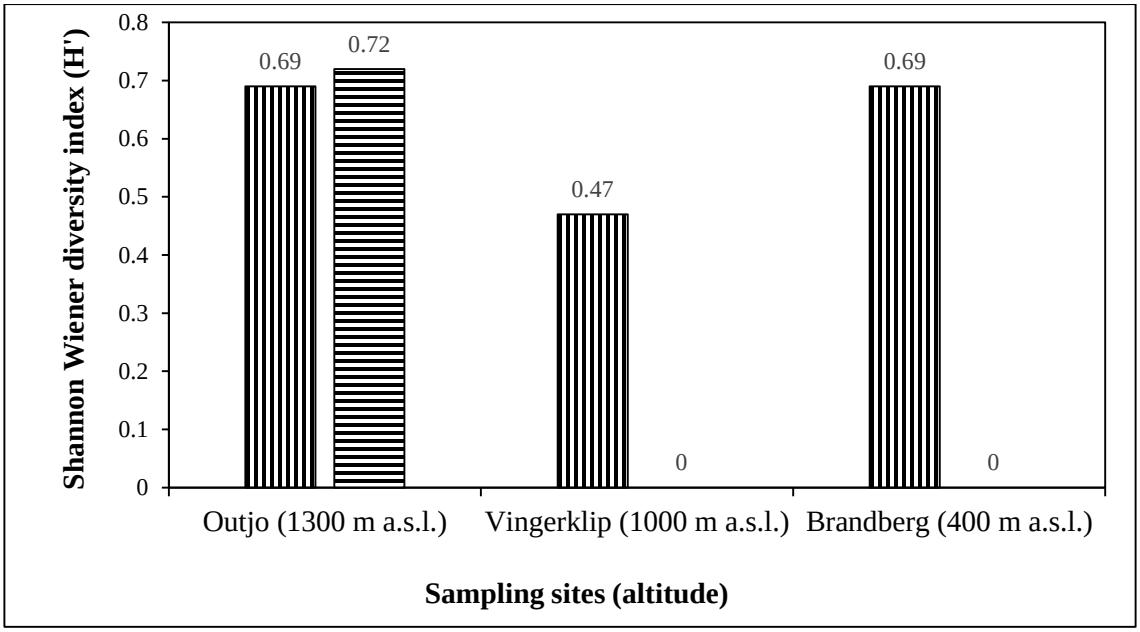
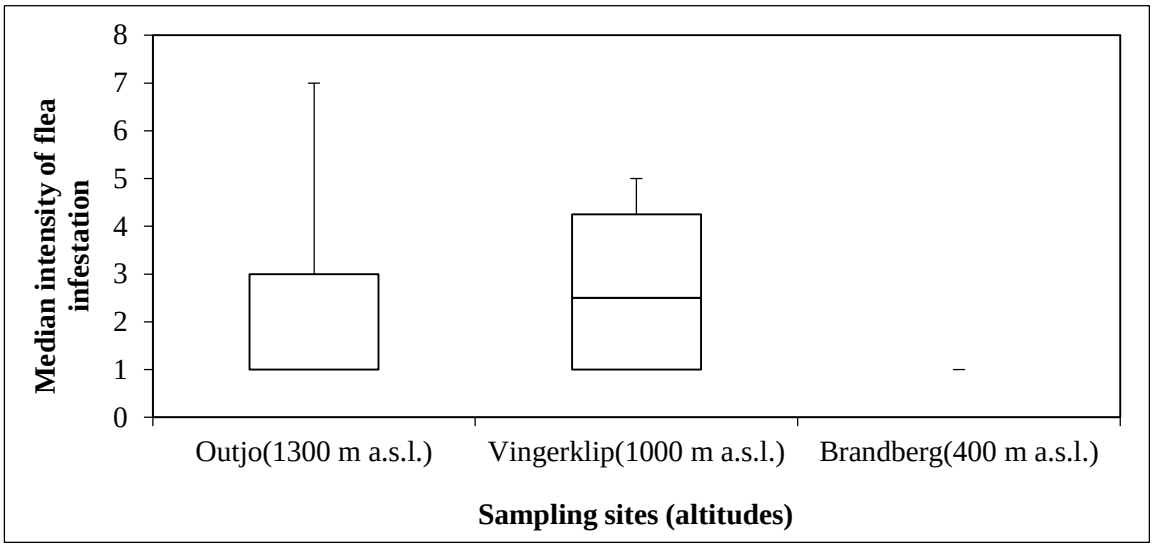


Figure 4.3.3: Shannon-Wiener diversity (H') index of fleas collected from small mammal hosts at the three sampling sites, Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.), and Brandberg (400 m a.s.l.), Namibia, during the hot wet ( ) and cold dry ( )seasons, 2018. Values on each bar represent the Shannon-Wiener Diversity (H") index value.

4.4. Intensity of flea infestation on small mammals

The flea intensity of infestation per host species was not normally distributed, as revealed by the Shapiro-Wilk Test ($W_{(6)} = 0.75$, $n = 7$, $P < 0.05$). A Kruskal-Wallis test of these non-normally distributed data revealed no significant difference in the overall intensity of infestation of fleas among the three sites during hot wet ($H_{(6)} = 2$, $n = 7$, $P = 0.37$) and cold dry ($H_{(6)} = 2$, $n = 7$, $P = 0.36$). However, the median intensity of infestation of fleas was high in Vingerklip and Outjo and low in Brandberg for the hot wet season. The median intensity of infestation of fleas was low in Brandberg during the cold dry season (Figure 4.4.1.).

(a)



(b)

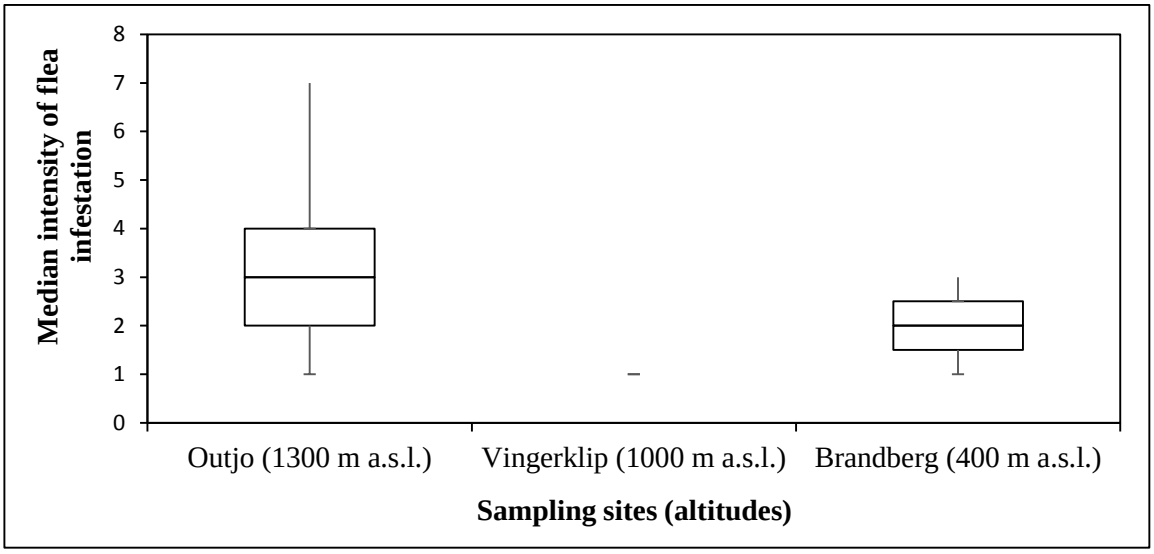
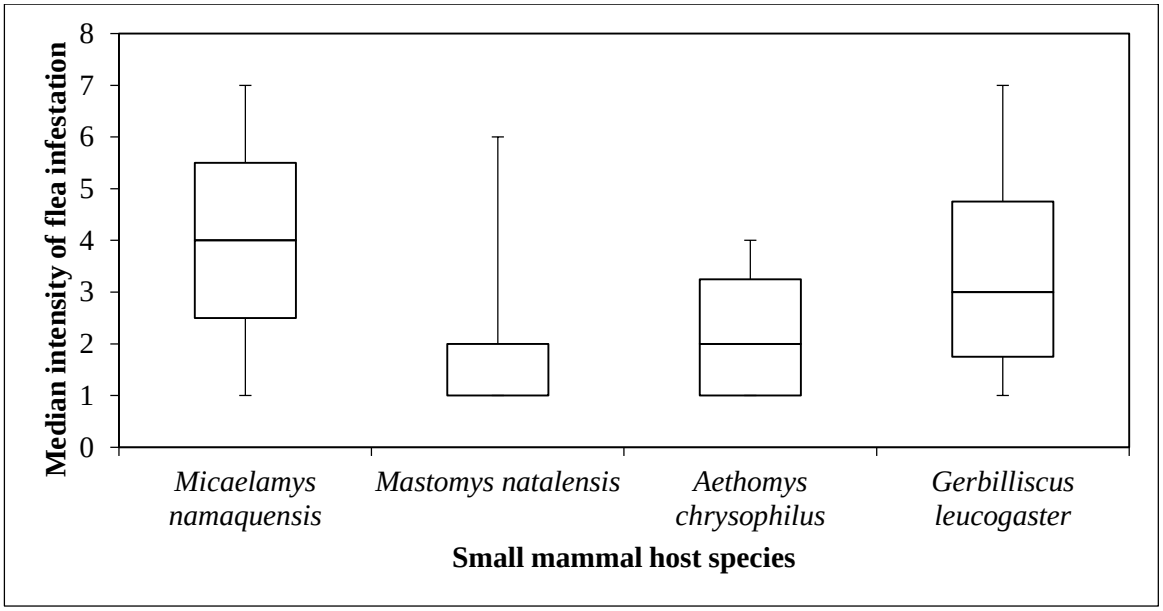


Figure 4.4.1: The overall median number of fleas infesting small mammal hosts at Outjo (1300 m a.s.l.**),** Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.), Namibia, 2018 during the hot wet (a) and the cold dry (b) seasons. The line in the open box represents the median. The top part of each box represents the upper quartile, while the lower part of the box represents the lower quartile.

A Kruskal-Wallis test of the non-normally distributed data revealed no significant difference in the intensity of the infestation of fleas among the host species in Outjo (1300 m a.s.l.) during the hot wet season ($H_{(3)} = 4$, $n = 4$, $P = 0.41$) and cold dry ($H_{(3)} = 4$, $n = 4$, $P = 0.42$) (Figure 4.4.2.).

(a)



(b)

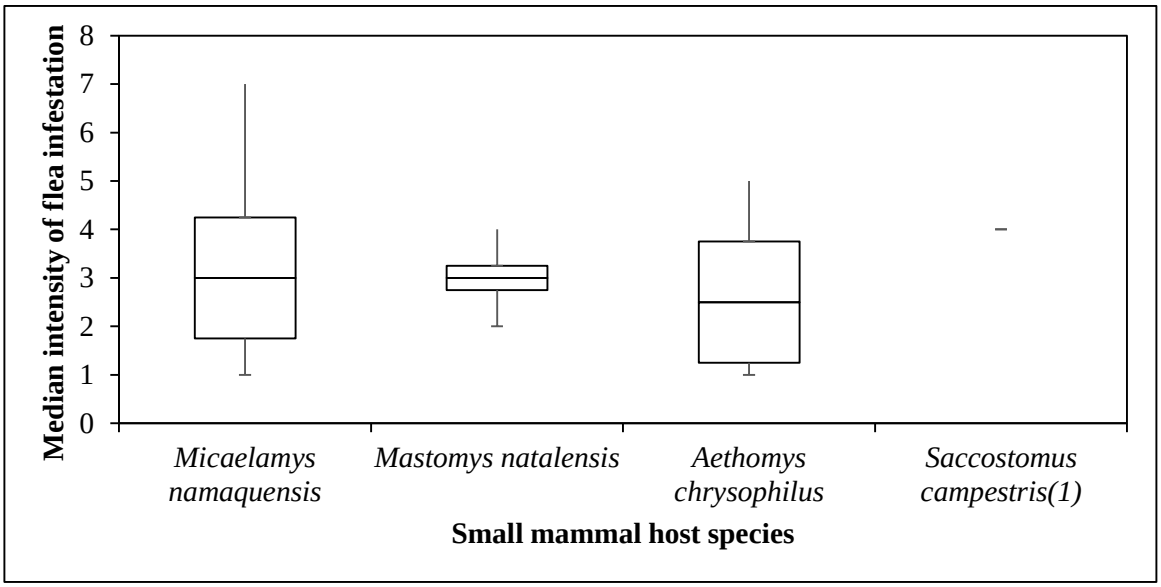
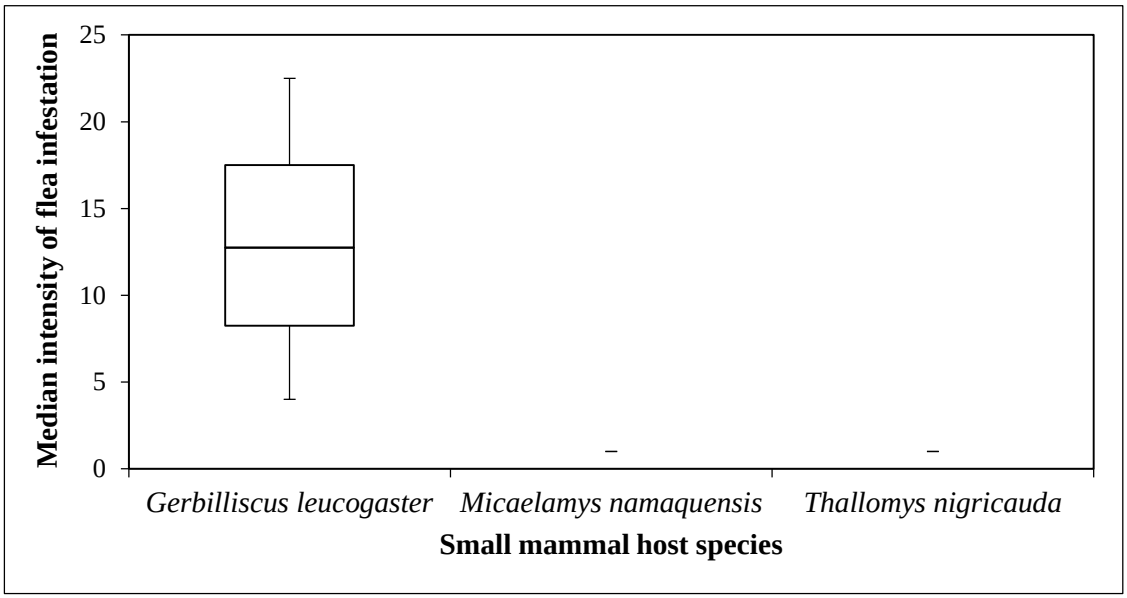


Figure 4.4.2: The median number of fleas infesting small mammal host species in Outjo (1300 m a.s.l.), Namibia, during the hot wet season (a) and cold dry season (b). The line in the open box is the median. The top part of each box represents the upper quartile, while the lower part of the box represents the lower quartile.

A Kruskal-Wallis test revealed no significant difference in the intensity of infestation of fleas among the different small mammal host species from Vingerklip (1000 m a.s.l.) during the hot wet season ($H_{(2)} = 4$, $n = 3$, $P = 0.40$) (Figure 4.4.3). Kruskal-Wallis test for the cold dry season could not be undertaken because only one species had the median infestation intensity among other species. In other words, the median intensity of infestation of fleas could not be computed because only one individual host per species per site was recorded. The median intensity of infestation of fleas recorded from small mammal host species at Brandberg (400 m a.s.l.) could not be computed because the sample sizes of small mammal and fleas were too small for the wet hot, and cold dry seasons.

(a)



(b)

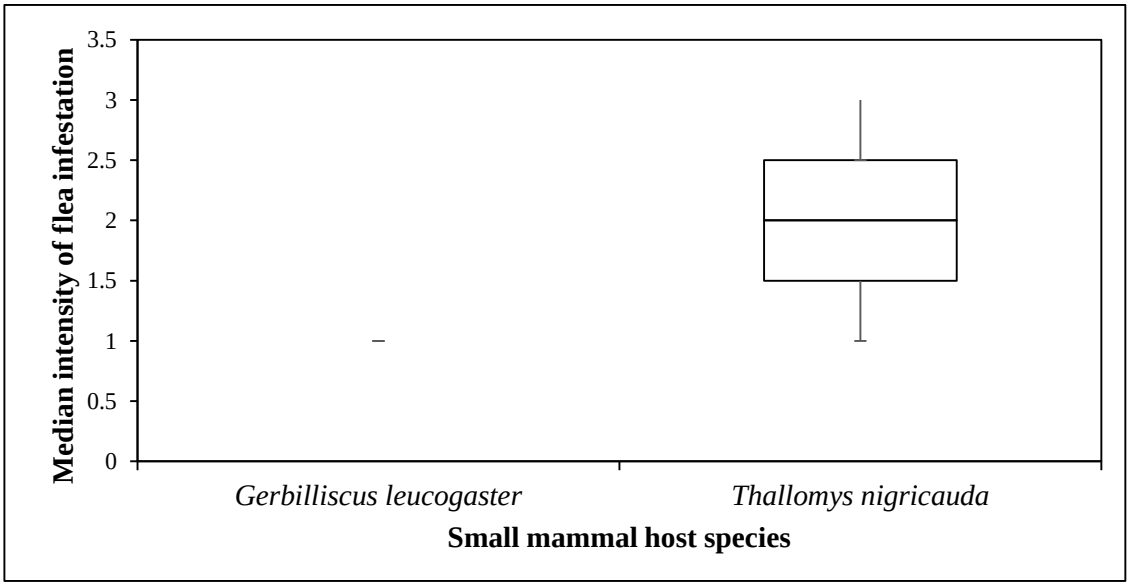


Figure 4.4.3: The median number of fleas collected from small mammal host species in Vingerklip (1000 m a.s.l.), Namibia, during the hot wet season (a) and cold dry season (b), 2018. The line in the open box represents the median. The top part of each box represents the upper quartile, while the lower part of the box represents the lower quartile.

4.5. Flea infestation prevalence in small mammals

The overall flea infestation prevalence on small mammal hosts at Outjo (1300 m a.s.l.) during the cold dry season was 45.5% and 33.7% during the hot wet season. Pearson's chi-square (χ^2) test for the overall prevalence of infestation for the three sampling sites revealed no significant difference in the flea infestation on small mammal hosts ($\chi^2_{(1)}$ = 1, n = 2, P = 0.61) during the hot wet season (Figure 4.5.1). However, the prevalence of infestation of fleas was significantly different among the three sites ($\chi^2_{(2)}$ = 20.78, n = 3, $P < 0.05$) during the cold dry season.

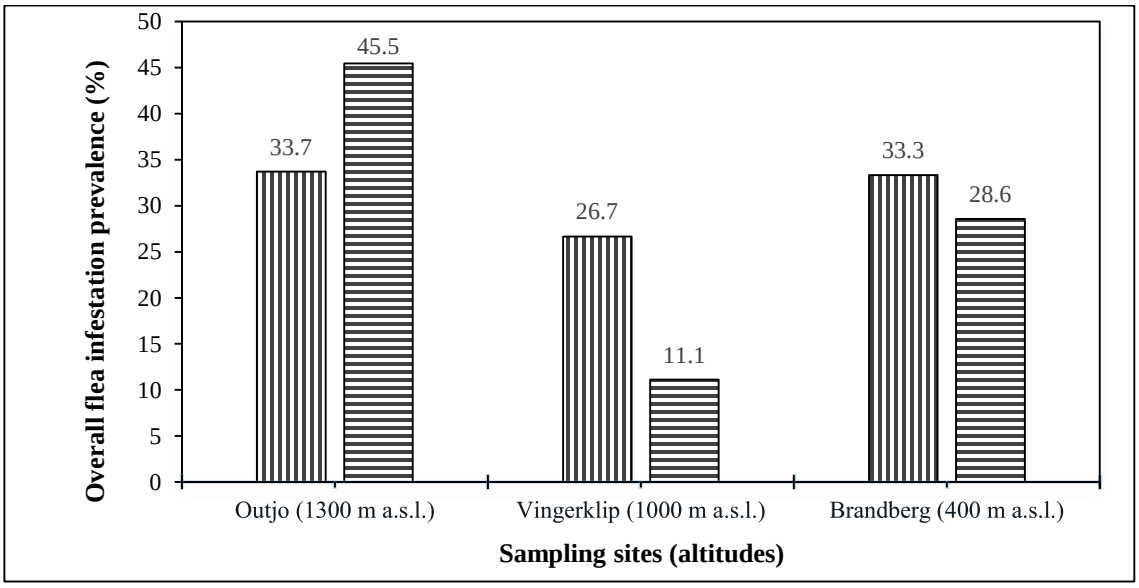
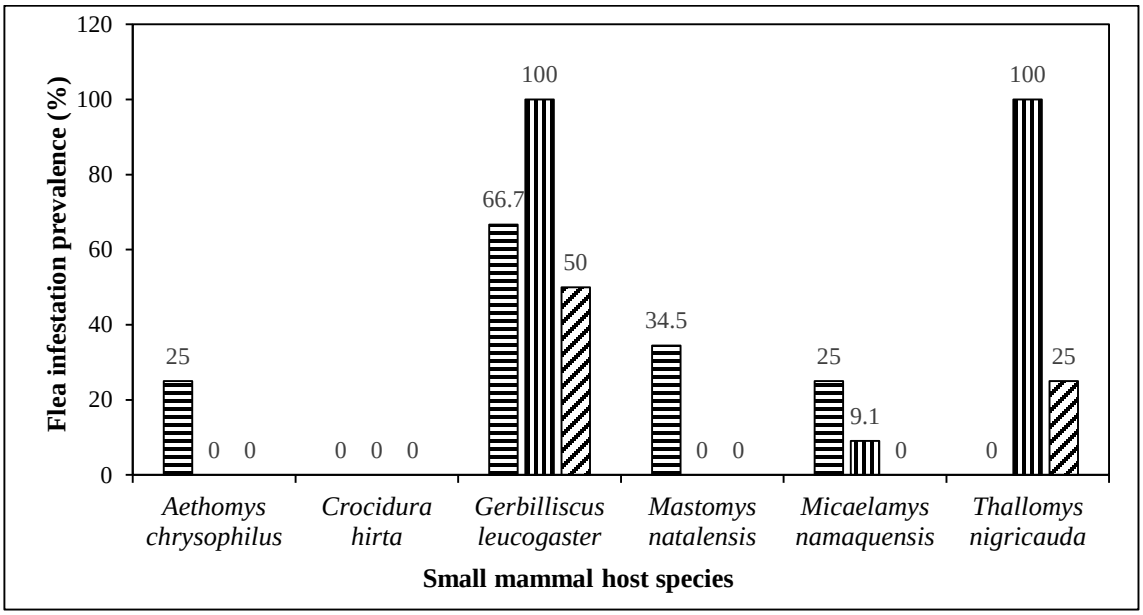


Figure 4.5.1: Overall flea infestation prevalence (%) on small mammal hosts in the hot wet (▥) and cold dry (▤) season at Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.), Namibia, 2018.

The prevalence of small mammal fleas per host species captured during the hot wet and cold dry seasons is presented in Figure 4.5.2. Fleas infested *G. leucogaster* at the three sites Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.) during the hot wet season. However, *M. natalensis* and *A. chrysophilus* were only recorded at Outjo (1300 m a.s.l.) with the prevalence of infestation of 34.5% and 25%, respectively.

(a)



(b)

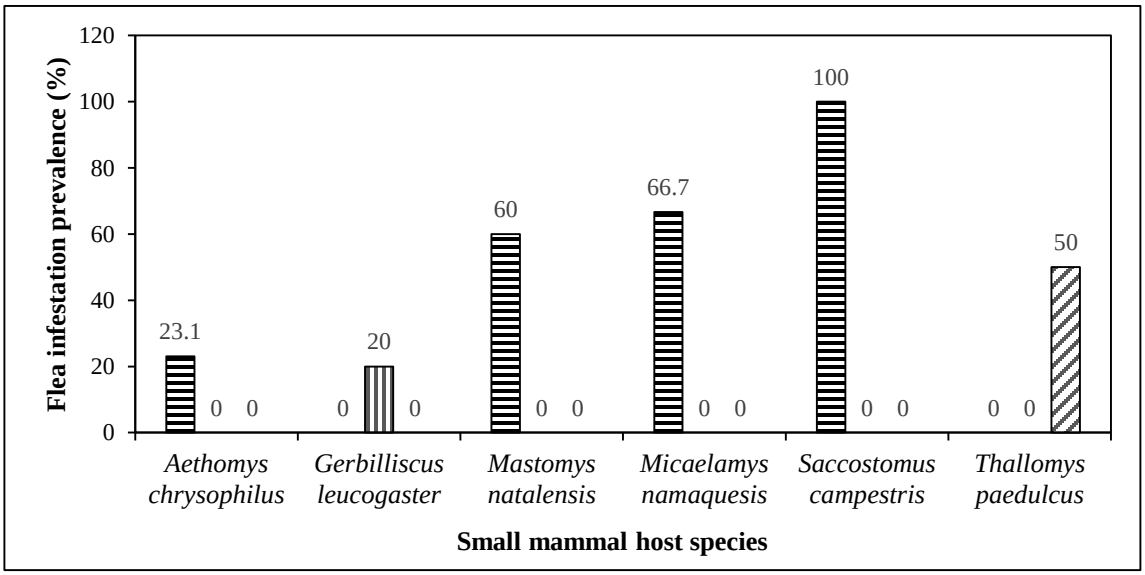


Figure 4.5.2: Prevalence (%) of infestation of fleas per small mammal host species trapped at the three sampling sites, Outjo (1300 m a.s.l.) (▤), Vingerklip (1000 m a.s.l.) (▥) and Brandberg (400 m a.s.l.) (▨), Namibia during the hot wet (a) and cold dry (b) seasons.

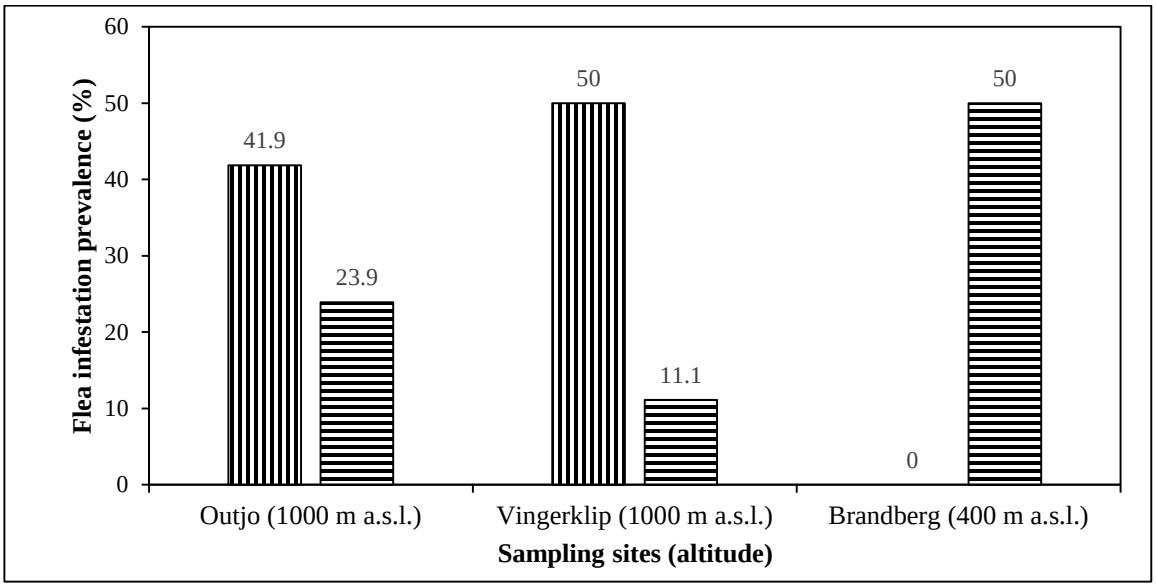
A Pearson's chi-square (χ^2) test results revealed a significant difference in the prevalence of infestation of fleas among the small mammal host species at the three sampling sites for the hot wet season (Figure 4.5.2) - (a): Outjo (1300 m a.s.l.) ($\chi^2_{(4)} = 76.56$, $n = 5$, $P < 0.05$), Vingerklip (1000 m a.s.l.) ($\chi^2_{(3)} = 175.1$, $n = 4$, $P < 0.05$), Brandberg (400 m a.s.l.) ($\chi^2_{(1)} = 8.33$, $n = 2$, $P < 0.05$). Tukey's HSD post hoc test revealed that the prevalence of infestation of fleas was significantly high in *G. leucogaster* followed by *T. nigricauda* and low in *C. hirta* during the hot wet season.

A Pearson's chi-square (χ^2) test for the cold dry season revealed a significant difference in the prevalence of infestation of fleas among the host species at the 3 sampling sites: Outjo(1300 m a.s.l.) ($\chi^2_{(4)} = 122.17$, $n = 5$, $P < 0.05$), Vingerklip (1000 m a.s.l.) ($\chi^2_{(2)} = 40$, $n = 3$, $P < 0.05$), Brandberg (400 m a.s.l.) ($\chi^2_{(2)} = 100$, $n = 3$, $P < 0.05$) (Figure 4.5.2 (b). *Saccostomus campestris* had the highest prevalence in Outjo (1300 m a.s.l.), followed by *M. natalensis*. *Thallomys paedulcus* had the lowest prevalence in Outjo (1300 m a.s.l.). Prevalence was high in *T. nigricauda*, followed by *G. leucogaster*, while *M. natalensis*, *S. campestris*, *C. hirta* and *A. chrysophilus* had the lowest prevalence in Vingerklip (1000 m a.s.l.). *Thallomys paedulcus* had the highest prevalence in Brandberg (400 m a.s.l), *S. campestris* had the lowest prevalence in Brandberg (400 m a.s.l.).

The flea infestation prevalence in female hosts was about 50% at Vingerklip (1000 m a.s.l.). No fleas were recorded from male hosts in Brandberg (400 m a.s.l.). However, male hosts had the highest prevalence of infestation of fleas at Outjo (1300 m a.s.l.) and Vingerklip (1000 m a.s.l.) during the wet hot season (Figure 4.5.3). The male hosts

recorded a prevalence of 100% at Brandberg (400 m a.s.l.) during the dry cold season. No fleas were recorded at Brandberg (400 m a.s.l.) during the cold dry season. Outjo (1300 m a.s.l.) recorded a high prevalence of infestation of 61.11% for female hosts and 53.33% for male hosts. Female hosts recorded a prevalence of 16.67% at Vingerklip (1000 m a.s.l.).

(a)



(b)

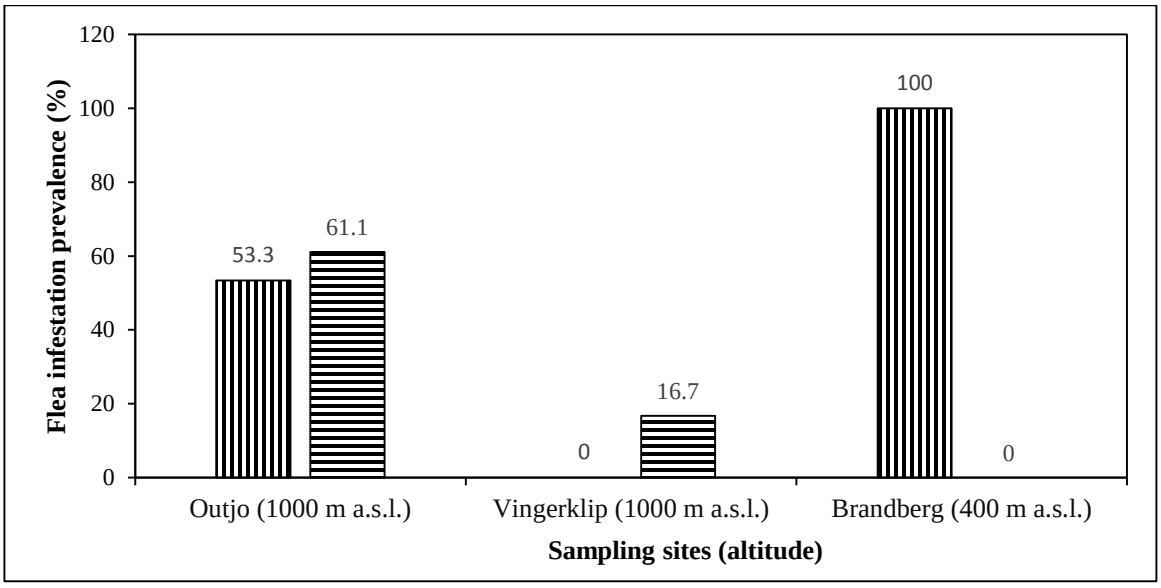


Figure 4.5.3: Prevalence (%) of infestation of fleas per small mammal host sex, males (▤) and females (▥) at the three sampling sites, namely: Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.), Namibia during the hot wet season (a) and cold dry season (b), 2018.

A Pearson's chi-square (χ^2) test revealed a significant difference in the prevalence of infestation of fleas of small mammals between male and female hosts in Outjo (1300 m a.s.l.), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.) during the hot wet season: Outjo (1300 m a.s.l.) ($\chi^2_{(1)} = 4.90$, $n = 2$, $P < 0.05$), Vingerklip (1000 m a.s.l.) ($\chi^2_{(1)} = 24.75$, $n = 2$, $P < 0.05$), Brandberg (400 m a.s.l.) ($\chi^2_{(1)} = 50$, $n = 2$, $P < 0.05$) (Figure 4.5.3(a).

There was no significant difference in the prevalence of infestation of fleas at Outjo (1300 m a.s.l.) site during the cold dry season, ($\chi^2_{(1)} = 0.53$, $n = 2$, $P = 0.47$). However, the prevalence of infestation of fleas was highly significant among male and female hosts at Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.) during the cold dry season: Vingerklip (1000 m a.s.l.) ($\chi^2_{(1)} = 16.67$, $n = 2$, $P < 0.05$), Brandberg (400 m a.s.l.) ($\chi^2_{(1)} = 50$, $n = 2$, $P < 0.05$) (Figure 4.5.3 (b).

A Tukey's HSD post hoc test revealed that the prevalence of infestation of fleas was high in males during the cold dry season and low in female hosts. Prevalence was the same (25%) during the hot wet season for male and female hosts. In Outjo (1300 m a.s.l.), the prevalence was the same for male and female hosts. Male hosts had the highest prevalence than females in Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.).

CHAPTER 5

DISCUSSION

5.1. Small mammal abundance, species composition, richness and diversity

5.1.1. Small mammal abundance

The results of the present study showed that the abundance of small mammal hosts was not statistically significantly different among the three sampling sites at different altitudes during the cold dry and hot wet seasons. The null hypothesis that there is no significant difference in the abundance of small mammal hosts was therefore accepted. However, it could be observed that small mammal hosts abundance was generally high at the high altitude site (Outjo) and low at the low altitude site (Brandberg). There was insufficient evidence to suggest that the abundance of small mammals was affected by altitude. Small sample sizes especially in Brandberg (low altitude site) may have caused bias which affected the statistics outcomes. The vegetation assessment results for the three sampling sites showed that the mean abundance of woody plants was significantly different among the three altitudinal sampling sites during the two seasons (hot wet and cold dry). According to the statistics outcome, changes in the mean abundance of woody plants across the altitudinal gradient did not affect the abundance of small mammal hosts along the altitudinal gradient. The high altitude site (Outjo) had high species richness of woody plants during the hot wet season than the middle and low altitude sites.

Wen *et al*. (2018) reported a significant positive relationship between the mean abundance of small mammals and an elevational gradient. They also observed a positive relationship between the abundance of small mammals and the middle of the elevation

gradient due to the local specialization of the middle and high elevation species and low species richness at higher elevation sites (Wen *et al*., 2018). Williams *et al*. (2010) hypothesized that lower net primary productivity at the high elevations of more than 500 m a.s.l. was limiting bird abundance and energy use. However, the statistics of the current study revealed that altitude did not affect the abundance of small mammals at the three altitude sampling sites during the two seasons sampled because there was no significant difference. Although the statistics revealed no significant difference in the abundance of small mammal hosts along the altitudinal gradient, abundance was generally high at the high altitude site (Outjo) and lower at the low altitude site (Brandberg). Habtamu & Bekele (2012) reported that the abundance of small mammals is linked to high habitat quality, including food resources and high cover. Caceres *et al*. (2011) reported that altitude and vegetation type affect small mammal abundance with interactions between them. Therefore, some species are significantly influenced by altitude, and vegetation will occur at a given altitudinal zone and habitat type and nowhere. This implies that altitude is associated with vegetation changes. Caceres *et al*. (2011) argued that the variation in small mammals' community structure might be explained by both altitude and vegetation type based on individual species.

The current study showed that although the mean abundance of woody plants differed significantly across the altitudinal gradient, a high abundance and richness of short woody plants at the high altitude site (Outjo) implies that the vegetation was denser and heterogeneous, mostly preferred by small mammals; hence they will thrive by reproducing rapidly. Adam *et al*. (2015) noted a significant variation in the small mammal abundance among different habitat types. They attributed the vegetation

diversity and the level of human interference as significant factors that affect the abundance of small mammals in the Hugumdurda Forest, Ethiopia. Bhattacharyya *et al*. (2009) suggested that rock cover and food availability were the main factors shaping the abundance of the Royle's pika populations along an altitudinal gradient in Uttarakhandi, Western Himalaya. It uses the rocky area as the nest site and as a temporary refuge to escape from predators (Bhattacharyya *et al*., 2009). Bateman *et al.* (2010) noted an increase in the abundance of small mammals with increasing altitude. A high abundance of small mammals in the high altitude site was strongly related to high productivity. A high abundance of small mammals was recorded in the high altitude site and low in the low altitude site. However, the statistics revealed that the abundance of small mammals did not differ significantly with altitude. Currie & Kerr (2008) also reported that species abundance increased with increasing altitude, a typical relationship where high abundance is strongly related to high productivity. Hence, the low altitude sites on the gradient and the associated low species abundance may be a function of low environmental suitability and productivity (low rainfall leads to low vegetation structural diversity) (Currie & Kerr, 2008). Ralaizafisoloarivony *et al*. (2014) also supported Currie & Kerr (2008) that an increase in elevation is accompanied by an increase in the abundance of small mammals due to increased water and food availability. However, a decrease of small mammal abundance with elevation has been reported under the Mediterranean climate and was attributed to a decrease in food availability and increasing dryness and cool weather conditions at low elevation sites (Ralaizafisoloarivony *et al*., 2014).

Small mammal community structure often correlates with the vegetation structure's general characteristics (Hoffmann & Zeller, 2005). Diverse vegetation structures are a source of food which in turn shapes the small mammals abundance. In the present study, grass cover was between 0 - 25% during the hot wet season at all sampling sites varied during the cold dry season between the four groups (0 - 25%, 26 - 50%, 51 - 75% and 76 - 100%). Despite the significant difference in the abundance of woody plants at the three sampling sites, grass cover remained the same at the three sampling sites during the hot wet season. This may explain why the abundance of small mammals was not significantly different among the three sampling sites. Hoffmann & Zeller (2005) highlighted that loss of grass cover results in a smaller abundance of small mammals in overgrazed areas. This is due to loss of food resources, disruption of habitat structures and increased predation risk.

5.1.2. Species composition, richness and diversity of small mammals

Rodent species trapped in the present study include the Namaqua rock mouse (*M. namaquensis),* Natal multimammate rat (*M. natalensis),* Red rock rat (*A. chrysophilus),* pouched mouse (*S. campestris),* bushveld gerbil (*G. leucogaster),* black-tailed tree rat (*T. nigricauda)* and Acacia rat (*T. paedulcus).* Two shrew species were captured in the present study, and these included the Lesser Red Musk shrew (*C. hirta)* and the bushveld elephant shrew (E. *intufi).* All small mammal host species recorded in this study have been recorded before in Namibia at different localities (Hoffmann & Zeller, 2005; Shipanga, 2007; Uusiku, 2007; Shihepo *et al*., 2008; Karuaera, 2011; Litubezi, 2013; Mfune *et al*., 2013; Hoveka, 2015; Kapia, 2018). *Mastomys natalensis, A. chrysophilus* and *C. hirta* were only recorded in the high altitude site (Outjo, 1300 m

a.s.l.). *Thallomys paedulcus* was only recorded in the low altitude site (Brandberg, 400 m a.s.l.). However, *M. namaquensis* and *G. leucogaster* were recorded at all three sampling sites (high, middle and low altitude sites).

HCA results revealed that small mammal species recorded at the three different altitudinal sampling sites comprised of two main clusters that included (a) Brandberg (CD) and (b) the rest of the sites and seasons (Brandberg (HW), Vingerklip (CD), Vingerklip (HW), Outjo (CD) and Outjo (HW)). The two main clusters have a similarity distance of 0.3 (30%). The cluster comprising of Brandberg (HW), Vingerklip (CD), Vingerklip (HW), Outjo (CD) and Outjo (HW) is further divided into (a) Brandberg (HW), (b) Vingerklip HW and CD and (c) Outjo (HW and CD). ANOSIM revealed that small mammals' species composition did not differ significantly among the three sites during the two seasons (accept the null hypothesis). Similarly, the Shannon-Wiener species diversity (H') index of small mammal hosts did not differ significantly among sites during the hot wet and cold dry seasons. The null hypothesis that there is no significant difference in the species diversity of small mammals among the three sampling sites for the two seasons was accepted. However, the generalized linear model (GLM) showed a strong and positive relationship between species richness of small mammal hosts and altitude (i.e., an increase in species richness of the small mammal hosts was associated with an increase in altitude).

Nor *et al*. (2001) reported that the change in the physical environment primarily determines the patterns of species diversity of small mammals across a geographical gradient. Physical parameters such as temperature, precipitation, and atmospheric

pressure usually change drastically across elevations, shaping plants and animals' local diversity. Animal diversity tends to be more diverse in a floristically diverse habitat (Nor *et al*., 2001). Shuai *et al*. (2017) reported a distinct pattern in rodents' species richness on the two slopes of Mt. Taibai, China, with a monotonically decreasing pattern on one slope. A hump-shaped elevational pattern was evident on the second slope. The temperature was an important factor for the richness pattern on the 1st slope, and the mid-domain effect was used to explain the richness pattern on the 2nd slope (Shuai *et al*., 2017). Rai *et al*. (2014) reported a unimodal relationship between elevation and species richness of terricolous lichen species. The highest species richness was observed at the middle elevation sites. This was, however, not the case in the present study, as species richness was high at higher altitude sites as expected. The low elevation site had low species richness, and the high elevation site had high species richness.

Variation in topography, climate, and competition from vascular plant communities, combined with tolerance of specific growth forms to zoo-anthropogenic pressures, are factors that shaped the distribution of terricolous lichens in the Garhwal Himalaya, India (Rai *et al*., 2014). Nascimbene & Marini (2015) also found a positive relationship between species richness of epiphytic lichens and elevation. Temperature was also the main factor that influenced lichen diversity. McCain (2009) stated climate as the primary driver of bird elevational diversity combined with temperature and water availability. Mulungu *et al*. (2008) found that the species richness of rodents and shrews was high in the forest than in other areas such as tall grasses and moorland. They also noted that the species diversity of rodents and shrews was influenced by habitat complexity and heterogeneity. Species diversity also increased with altitude. Stanley & Hutterer (2007)

recorded a low species richness at 600 m a.s.l. and high at 2000 m a.s.l. This, however, could not be correlated with elevation. Rainfall was identified as the main factor affecting species richness. Rainfall figures were not recorded at the three sampling sites for this study, but one could observe that Outjo (1300 m a.s.l.) was wetter than Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l.). Martins *et al*. (2015) also noted a peak in species richness of bats at low elevations (500 - 1000 m a.s.l.), and there was a decrease in species richness of bats at high elevation. There was a significant difference in the species composition of bats along the elevational gradient.

Furthermore, Novillo & Ojeda (2014) noted topography as an essential factor in regulating biodiversity at local and regional scales. Topography has been reported to affect species richness patterns of the mammals of North American warm regions (Novillo & Ojeda, 2014). The high altitude site (Outjo) in the current study was dominated by short woody plants of less than 2.5 m. The middle (Vingerklip) and low (Brandberg) elevation sites were dominated mainly by tall woody plants of more than 4 m. The tall trees leave the ground open, thus exposing small mammals to predation and lack of food.

Hoffmann & Zeller (2005) noted that the quantity of cover is essential to the density and diversity of small mammals, but when the cover reaches threshold levels, the degree of plant species diversity becomes essential. Several studies have shown that small mammal's community structure is a function of plant architecture (Bond *et al*., 1980; Els & Kerley, 1980; Hoffmann & Zeller, 2005). They argued that microhabitat features such as vegetation structure, cover and height, relative humidity, litter depth, and foliage

height diversity are directly related to plant species' life form and growth pattern within a plant community; these factors are essential floristic variables affecting small mammal community structure. It has been shown that small mammal community structure is related to functional and general characteristics of vegetation structure such as height, density and that a change in vegetation structure induces changes in species composition and abundance of small mammals (Muck & Zeller, 2006). However, there was insufficient evidence in the current study to suggest that changes in the abundance of woody plants across the gradient influenced the abundance of small mammal hosts.

5.2. Abundance, species composition, richness and diversity of fleas recorded from small mammals

A total of 139 individual fleas were recorded from small mammal hosts sampled from the three sampling sites representing three flea species that included *X. cheopis*, *X. brasiliensis* and *L. dorripae*. All the flea species recorded in the present study have previously been recorded in Namibia at different localities (Shipanga 2007; Uusiku 2007; Shihepo *et al.* 2008; Mfune *et al*. 2013; Kapia 2018). The majority of fleas were recorded from small mammal hosts at Outjo (1300 m a.s.l.), accounting for 87.1%, followed by Vingerklip (1000 m a.s.l.) with 8.6% and then Brandberg (400 m a.s.l.) (4.3%). *Xenopsylla cheopis* and *X. brasiliensis* were mainly recorded from *M. natalensis*, *G. leucogaster*, *A. chrysophilus*, and *M. namaquensis* in Outjo (1300 m a.s.l.) and Vingerklip (1000 m a.s.l.) during the hot wet season**.** The abundance of fleas recorded from small mammals did not differ significantly among the sampling sites across the two seasons. Therefore H_0 was accepted. However, it can be observed that the

abundance of fleas recorded from small mammals was generally high in the high altitude site (Outjo) and lower in the low altitude site (Brandberg).

The HCA in the present study showed two main clusters of flea species composition that included: (a) Vingerklip (hot wet season), Outjo (cold dry season), and Outjo (hot wet season), and (b) a cluster that comprises Brandberg (hot wet season), Vingerklip (cold dry season), and Brandberg (cold dry season). The two clusters had a similarity distance of 0.3 (30% similarity). In cluster (a), species composition of fleas for Outjo during the hot wet and cold dry seasons were closely associated with a similarity distance of 0.8 (80%)**.** In cluster (b), flea species composition for Brandberg (400 m a.s.l.) during the hot wet season and Vingerklip during the cold dry season had a similarity distance of 0.6 (60%). The species composition of fleas of small mammals was not significantly different among the sampling sites across the two seasons.

The current study results show that most fleas were recorded from *M. natalensis* and *G. leucogaster*. Shihepo *et al*. (2008) also recorded a high number of fleas from *Mastomys* species. Stuart & Stuart (2015) highlighted that *Mastomys* species are subject to periodic population eruptions after good rains, resulting in abundant food. This could also be why many fleas were recorded from *M. natalensis* in the present study. A high abundance of fleas was recorded from *G. leucogaster* by Mfune *et al*. (2013). Maher & Timm (2014) did not find an association between species richness of fleas and elevation, but the diversity indices were higher at high elevation for fleas.

Krasnov *et al*. (2006) demonstrated that the species composition of flea assemblages in a given host and habitat is determined by the host and habitat identity. They further urged that host identity is an essential factor affecting flea species composition and found that flea populations varied less among populations of the same host species than among host species and habitats of the same type than among different habitats. Krasnov *et al*. (2010) further highlighted that host species composition play an important role in determining the composition and relative abundance of fleas. Host identity is crucial because it reflects a given flea's dependence on the host species (Krasnov *et al.,* 2006). A flea species can become adapted to particular host species' traits in highly host-specific parasites (Krasnov *et al*., 2010).

GLM done for this study showed a weak relationship between species richness of fleas recovered from small mammals and altitude. Furthermore, the Shannon-Wiener species diversity (H') index of fleas of small mammals hosts did not differ significantly among sites during the hot wet and cold dry seasons. Therefore, the present study results showed that fleas' abundance and species diversity on small mammal hosts were not affected by altitude as they did not differ significantly among the three altitudinal sites during the cold dry and hot wet seasons. The null hypothesis was accepted.

Maher & Timm (2014) did not find an association between species richness of small mammal fleas and elevation but the diversity indices were higher at higher elevations. They expected a change in species richness because of the harsh conditions at a higher elevation. There was a positive relationship between diversity indices and elevation, suggesting that stressful environmental conditions such as the high temperature at higher

elevation may strongly influence flea communities' structure. The evenness may be due to changes in the abundance of fleas within small mammal communities. A statistically non-significant relationship between species richness of fleas recovered from small mammals and elevation was observed in this study, suggesting that altitude did not affect fleas' species richness. Species richness of fleas collected from small mammal hosts was almost constant with an increase in altitude.

Acosta & Fernandez (2015) recorded high diversity values of fleas on rodents. They attributed this to the fact that fleas are more abundant and diverse in small and medium-sized mammals and because most fleas are generalists (i.e., they can parasitize more than one host species). Balaz *et al*. (2019) found that altitude affects flea distribution and diversity along an elevational gradient. However, the present study reported that an increase in flea species richness with increasing altitude was not statistically significant. Hence there was insufficient evidence to support the hypothesis that flea species richness was affected by altitude. The study on epifaunistic arthropod parasites of the four striped mouse, *Rhabdomys pumilio,* in the Western Cape Province, South Africa, was conducted by Matthee *et al*. (2007). They showed that the species richness of ectoparasites increased with the number of hosts examined. They attributed species richness to sampling effort and intensity. Habitat heterogeneity (Midgley *et al*., 2005) also contributes to species richness (Matthee *et al*., 2007). It is possible, therefore, that in this study, trapping small mammal hosts during the season when they are most abundant would have increased the abundance of trapped hosts and hence may have led to trapping more hosts that were infested with fleas. It is worth noting that it is a challenge to attribute changes in the diversity of fleas to altitude because these would

also have depended on whether the abundance and diversity of host small mammals are also affected by altitude, which in this study have not been strongly related (Matthee *et al*., 2007). This is compounded by the fact that different habitats have yielded different flea diversity and richness on small mammal hosts, even at the same altitude. For example, Mfune *et al*. (2013) did not find a statistically significant difference in flea species diversity on small mammal hosts among host species when they sampled small mammals in selected habitats, Windhoek, Namibia. However, Amutenya (2004) found a significant difference in flea species diversity on small mammals among different habitats in the same area.

Furthermore, Krasnov *et al*. (2004) correlated the mean number of host species exploited by a flea species with the mean and maximum flea species abundances per host in 16 regions out of 20 in the Holarctic Region. More fleas were recorded from the high altitude site, where many small mammal hosts were sampled. The current study results also showed that more fleas were sampled from small mammals at the high altitude site where many small mammal hosts were recorded. Krasnov *et al*. (2004) study results demonstrated positive correlations between the host range's breadth and fleas' local abundance in most studied regions.

Zimba *et al*. (2011) reported that the Percentage Incidence Index (PII) for *G. leucogaster* in relation to *X. brasiliensis* was significantly higher than the PII of *R. pumilio*, *M. natalensis* and *R. rattus*. *Gerbilliscus leucogaster* recorded the highest Specific Flea Index (SFI) while *R. pumilio* recorded the lowest indices. The PII and SFI of *X. brasiliensis* were highest during the cold dry season, followed by the hot wet season

(Zimba *et al*., 2011). The observed variation in flea indices on different rodent species was attributed to factors such as the immune status and grooming behaviour of the rodent host, the number of fleas lost over distances travelled by the rodent host species, and the type and degree of protection from external conditions offered by the shelter of the rodent host (Zimba *et al*., 2011).

Shihepo *et al*. (2008) recorded a high diversity of fleas in the Okawikenga Farm area, south-east of Otjiwarongo in north-central Namibia. They attributed this to specific local environmental conditions offering various suitable habitats to host species as ectoparasites are subjected to both the host species' internal and external environment. Stanko *et al*. (2002) identified host body size as the determinant for flea species richness on a host species. Hosts are considered islands that provide habitats for their parasites. Krasnov *et al*. (2004) found a positive correlation between flea and host species richness, suggesting that the ectoparasites' diversification responds to the host species' diversification. The diversification of hosts can increase the number of ectoparasites by either a higher probability of parasite co-diversification or introducing new parasite species.

5.3. Intensity of infestation of fleas on small mammals

The overall intensity of infestation of fleas on small mammal hosts did not differ significantly among the three altitudinal sampling sites during the cold dry, and hot wet seasons. The null hypothesis was accepted. This suggests that altitude did not affect the intensity of infestation of fleas. The intensity of infestation of fleas recorded from small

mammals did not differ significantly among the host species for Outjo (1300 m a.s.l.) and Vingerklip (1000 m a.s.l). Although the statistic revealed that there was no significant difference in the intensity of infestation of fleas, one could observe that the high altitude site (Outjo) had a high intensity of infestation of fleas than the middle (Vingerklip) and low altitude site (Brandberg). The results for Brandberg could not be computed because of the limited sample sizes for statistical analysis.

Litubezi (2013) investigated the intensity of infestation of fleas of small mammals but did not find a significant difference in the median intensity of infestation of fleas on *G. leucogaster* and *M. namaquensis* at different localities in Namibia. The localities were at different altitudes. These results are similar to those of the current study in that this study has shown that altitude did not affect the median intensity of infestation of fleas on small mammals sampled from the three altitudinal sampling sites. However, Tavassoli *et al*. (2010) found a statistically significant difference in the median intensity of infestation of fleas on dogs from different geographical regions. They attributed the difference to climate and seasonality. A study by Mfune *et al*. (2013) reported no statistically significant difference in the intensity of infestation of fleas on small mammals between *G. leucogaster* and *G. paeba* from selected sites in Windhoek. *Gerbilliscus leucogaster* and *G. paeba* were more susceptible to infection compared to *E. intufi* and *R. pumilio*. They suggested that the fleas found the two species to be favourable hosts.

The current study results showed that more fleas were sampled from *G. leucogaster, M. namaquensis* and *M. natalensis*. Uusiku (2007) showed no statistically significant

difference in the intensity of infestation of fleas among selected host species. The current study results showed that *M. namaquensis*, *A. chrysophilus*, *M. natalensis*, *G. leucogaster* and *S. campestris* were more susceptible to infestation given their high median flea numbers. *Thallomys nigricauda*, *T. paedulcus*, and *E. intufi* had the lowest median intensity of infestation of fleas. The low intensity of infestation of fleas on *Thallomys nigricauda*, *T. paedulcus*, and *E. intufi* may also be attributed to their (hosts) low sample sizes. Litubezi (2013) also found that *G. leucogaster* was more susceptible to infestation. *Gerbilliscus leucogaster* is a suitable/habitable host for fleas to survive and reproduce. The greater the variety of habitats, the greater the number of organisms that inhabit them; this corresponds to the number of niches available within that particular habitat (Rozenzweig, 1996). A higher number of fleas would be found on such hosts, thus higher intensity of infestation on that particular small mammal host. The low median intensity of infestation of fleas on *M. natalensis* may be due to the increased grooming activities that control the number of fleas on these hosts (Stanko *et al*., 2002).

In the present study, no fleas were recorded from *E. intufi* and *C. hirta* during the two seasons (hot wet and cold dry seasons). Only three individuals of *E. intufi* were sampled, one during the hot wet season and two during the cold dry season, both from Vingerklip (1000 m a.s.l.). Failure to record fleas from *E. intufi* may be attributed to the smaller sample size. Mfune *et al*. (2013) suggested that *E. intufi* has a strong-smelling odour than other small mammals and may have contributed to the failure to attract fleas. Because of the strong smell of *E. intufi*, fleas will prefer to stay in the nest than on the body. *Gerbilliscus leucogaster* occupies abandoned burrows of other rodents in addition to their burrows (Mfune *et al*., 2013).

Canto *et al*. (2013) found a significant association between season and intensity of infestation of fleas. They found that more fleas were sampled during summer and autumn than during winter and spring (Canto *et al*., 2013). Young *et al*. (2015) found a significant negative effect of recent rainfall on the intensity of infestation of fleas, where drier sites had more fleas. This was unexpected, as more precipitation leads to higher relative humidity, which increases flea development and survival. However, this may be because flooding can kill developing fleas (especially in areas where drainage is poor, as in many of these sites), drier periods tend to be warmer, and fleas develop better in sites with warmer temperatures. Factors that may explain variation in the intensity of infestation of fleas among individual organisms in a population are body size, sex, and season (Young *et al*., 2015). A larger individual host is predicted to host a higher abundance of fleas because they present more extensive food resources for the ectoparasites. They also tend to live longer, thus representing a more predictable food source. Larger hosts may also provide better nutritional resources for fleas if they are in a better body condition (Young *et al*., 2015).

Factors such as the body size of the host and season may differ along an altitudinal gradient. This will, in turn, affect the intensity of infestation of fleas of small mammals. In this study, the high median intensity of infestation of fleas was anticipated at the high altitude site as it has a high mean abundance of woody plants, which provided enough food sources for the hosts than in low altitude sites where the mean abundance of woody plants was low. When the habitat supports a high number of small mammal hosts, the hosts will also support a high number of fleas. Hoffmann & Zeller (2005) suggested that

the total loss of ground vegetation cover leads to a reduced supply of food for small mammals. They further reported that disruption of habitat structure, cover and shelter leads to a high predation risk to the small mammals (Hoffmann & Zeller, 2005). Bushes represent areas of high food density and low predation risk.

5.4. Flea prevalence of infestation recorded from small mammals

The overall prevalence of infestation of fleas for the three altitudinal sampling sites was not significantly different during the hot wet season (accept the null hypothesis) but significantly different during the cold dry season (reject the null hypothesis). Several factors influence flea occurrence and the prevalence of infestation of fleas. Temperature and relative humidity are the two most important factors for the production, development and survival of fleas (Farkas *et al*., 2009). Furthermore, Farkas *et al*. (2009) reported that the prevalence of flea infestation in dogs and cats was statistically dependent on the season. However, the present study results show that flea prevalence of small mammals' infestation was high during the hot wet season and low during the cold dry season. The results also showed that flea prevalence of infestation on small mammals differed significantly between the altitudinal sampling sites during the cold dry season, being high at Outjo (high altitude site). Wall & Shearer (2001) reported that temperature range and humidity play a vital role in ectoparasites' life span and activity patterns. They further urged that seasonal changes in climatic conditions are suitable for causing fluctuations in ectoparasite populations' prevalence. Archer *et al*. (2014) found seasonal patterns in the prevalence and abundance of all ectoparasite species on the mole-rat, with higher prevalence during the cool wet winter. As a result, the species richness also varied with season. Ectoparasite burdens were most significant during the

wet summer in the highveld mole-rat, suggesting that humidity changes rather than temperature are responsible for the observed pattern (Archer *et al*., 2014).

The present study showed that flea prevalence was significantly higher in males than in females, a trend that was also recorded by Mfune *et al*. (2013). Males are more active than females and have more extensive home ranges. Males disperse further than females, increasing their chances of being infested by fleas (Mfune *et al*., 2013). Litubezi (2013) recorded a high flea prevalence in both males and females in Okahandja and low in Katima Mulilo, Namibia. Litubezi (2013) suggested that temperatures and vegetation cover in Okahandja were favourable, making hosts susceptible to infestation. However, Uusiku (2007) did not find a significant difference in flea prevalence of infestation between males and females, as did Camargo *et al*. (2016), who also did not find a significant difference in flea prevalence between sexes and between sites.

The middle and lower altitude sites' environmental conditions were not favourable for the flea species to enable their hosts' infestation (Camargo *et al*., 2016). Hoveka (2015) did not find a significant difference in the prevalence of infestation of fleas in *G. leucogaster* among their 3 study sites. The results for the present study showed that *G. leucogaster* had the highest flea prevalence of infestation in Vingerklip (middle altitude site), followed by Outjo (high altitude site) and then Brandberg (low altitude site). Hoveka (2015) also reported that host sex, mass, head-body length and reproductive state did not significantly influence the flea prevalence of small mammal hosts in the three regions studied. Many studies have found sex-biased differences in parasitism levels, with a tendency towards male-biased parasitism (Matthee *et al*., 2010). This may

be due to body size differences, with larger males providing more extensive food resources, but it has also been attributed to differences in immune function (caused by androgen immune suppression), grooming patterns, movement, and social contact patterns (Young *et al*., 2015).

5.5. Limitations of the study

The study sampled small mammal hosts at three selected habitats across an altitudinal gradient along the Ugab River, Namibia. The study also involved collecting ectoparasites (fleas) from small mammal hosts. Some limitations may have occurred during sampling of small mammal hosts and processing of fleas. It would have been ideal to trap the small mammal hosts at the three selected sampling sites (altitudes) simultaneously. This, however, could not be done due to the lack of manpower and resources. Sampling at the same time was necessary for uniformity. However, it was deemed sufficient to trap in three consecutive weeks to offset possible significant changes in the abundance of small mammals and associated fleas. The number of fleas collected from small mammals may be biased because the brush may not remove all ectoparasites (fleas) from the hosts. Some fleas may fly away from the host or the tray while the host is still being brushed. This may have affected the number of fleas collected per small mammal host. Weather conditions may have affected the number of small mammals captured, especially during the cold dry season. Low numbers of small mammals hosts and fleas were collected during the cold dry season especially at the low altitude site (Brandberg). This may have affected the results and statistical outcomes. An effort was made to trap small mammals where the Ugab River passes at the edge of the

desert, but no small mammals were trapped during a reconnaissance visit to the habitat in the desert. Hence the low altitude site of Brandberg (400 m a.s.l.) was selected.

CHAPTER 6

CONCLUSIONS AND RECOMMENDATIONS

6.1. Conclusions

The primary purpose of the study was to determine the abundance, species composition, richness and diversity of small mammals and the prevalence and intensity of infestation of the associated fleas across an altitudinal gradient along the Ugab River, Namibia. The main objectives of the study were to determine and compare (1) the abundance; (2) species richness; (3) species composition; and (4) diversity of small mammal hosts at the three selected sampling sites across an altitudinal gradient along Ugab River, and also to determine and compare: (5) abundance; (6) species richness; (7) species composition; (8) species diversity; (9) infestation prevalence; and (10) the intensity of flea infestation harboured by small mammal hosts at three selected habitats across an altitudinal gradient along the Ugab River, Namibia. Although the statistics revealed that the abundance of small mammals did not differ significantly across the three altitudinal sampling sites during the cold dry and hot wet seasons (accept the null hypothesis), it could be observed that small mammal abundance was high at the high altitude site (Outjo, 1300 m a.s.l.) and low at the low altitude site (400 m a.s.l.). Small mammal species diversity was not significantly different among the three sites, namely: Outjo (1300 m a.s.l), Vingerklip (1000 m a.s.l.) and Brandberg (400 m a.s.l) during hot wet and cold dry seasons. Species diversity was generally high at Outjo (high altitude site) than Vingerklip (middle altitude site) and Brandberg (low altitude site). The species composition of small mammal hosts did not differ significantly. It can, therefore, be

concluded that the species composition of small mammal hosts was not influenced by altitude. The abundance of small mammals' fleas did not differ significantly among the three sites for the two seasons. However, it could be observed that the abundance of small mammal fleas was high at Outjo (high altitude site) and generally low at Brandberg (400 m a.s.l.). According to the statistics, there was no significant difference in the diversity of fleas of small mammals among the three sampling sites across the two seasons. Species diversity of fleas was generally high at Outjo (high altitude site) and generally low at Brandberg (low altitude site). The species composition of fleas of small mammals did not differ significantly among the three sampling sites across the two seasons, as revealed by ANOSIM.

It can be concluded that altitude does not influence flea species composition. Several factors such as temperature, productivity, habitat heterogeneity and rainfall have been identified as the leading causes of the altitudinal gradients (Sanders, 2012). However, these factors did not affect the abundance, species composition, richness and diversity of small mammals and, in turn, the prevalence and intensity of infestation of fleas at the three altitudinal sites. The intensity of infestation was not affected by altitude as there was no significant difference in the intensity of infestation of fleas of small mammals among the three sampling sites across the two sampling seasons. The overall prevalence of infestation of small mammals' fleas differed significantly among the three sampling sites across the two seasons during the cold dry season. It can, therefore, be concluded that flea prevalence of infestation was influenced by altitude. However, this was not the case during the hot wet season as there was no significant difference in the prevalence of infestation of fleas of small mammals. Although this study showed that the mean

abundance of woody plants in the different height classes was significantly different among the three altitudinal sampling sites, it did not influence the diversity, richness and species composition of small mammals. Small sample sizes for small mammals and fleas, especially at Vingerklip (middle altitude site) and Brandberg (low altitude site) during the hot wet and cold dry season, may have caused sampling bias, which affected the statistics outcome. The study has filled the knowledge gap on the effects of altitude on the abundance, species richness, species composition, and diversity of small mammals in Namibia, although more studies are encouraged to address the limitations of this study.

6.2. Recommendations

This was the first study investigating the effects of altitudinal gradients on the species diversity of small mammals and the prevalence and intensity of infestation of their associated fleas in Namibia. It is recommended that more long-term comprehensive studies should be undertaken in Namibia to determine the influence of altitude on small mammal diversity, composition and richness, and the prevalence and intensity of infestation of associated fleas. This will increase the knowledge on the usage of different habitat types on the diversity and abundance of small mammals and their associated fleas. Small mammals are significant in maintaining natural ecosystems and also serve as indicator species. This information is, therefore, critical for their conservation efforts and biodiversity. It is recommended that further studies should include other small mammal ectoparasites such as mites, lice and ticks, as the present study only concentrated on the prevalence and intensity of flea infestation. Data must also be

collected at the same time at different altitudes for uniformity. It will also be essential to learn how altitudinal gradients influence the prevalence and intensity of the infestation of mites, ticks and lice.

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APPENDICES

Appendix A: Small mammal hosts trapped during the hot wet and cold dry seasons, 2018

Season	Site	Host ID.	Host species	Host sex	Host reproductive status	Infested (Yes/No)	Number of fleas collected
Hot wet	Outjo	OJ1A	*Micaelamys namaquensis*	M	DT	No	0
Hot wet	Outjo	OJ2A	*Micaelamys namaquensis*	M	DT	No	0
Hot wet	Outjo	OJ3A	*Micaelamys namaquensis*	F	CV	No	0
Hot wet	Outjo	OJ4A	*Mastomys natalensis*	M	AT	No	0
Hot wet	Outjo	OJ5A	*Mastomys natalensis*	M	DT	No	0
Hot wet	Outjo	OJ6A	*Mastomys natalensis*	M	DT	No	0
Hot wet	Outjo	OJ7A	*Mastomys natalensis*	F	CV	No	0
Hot wet	Outjo	OJ8A	*Mastomys natalensis*	M	AT	No	0
Hot wet	Outjo	OJ9A	*Mastomys natalensis*	F	CV	No	0
Hot wet	Outjo	OJ10A	*Aethomys chrysophilus*	M	DT	No	0
Hot wet	Outjo	OJ11A	*Aethomys chrysophilus*	M	AT	No	0
Hot wet	Outjo	OJ12A	*Mastomys natalensis*	M	AT	No	0
Hot wet	Outjo	OJ13A	*Aethomys chrysophilus*	F	CV	No	0
Hot wet	Outjo	OJ14A	*Crocidura hirta*	F	OV	No	0
Hot wet	Outjo	OJ15A	*Mastomys natalensis*	M	DT	No	0
Hot wet	Outjo	OJ16A	*Aethomys chrysophilus*	F	CV	No	0

Hot wet	Outjo	OJ17A	*Aethomys chrysophilus*	M	AT	No	0
Hot wet	Outjo	OJ18A	*Mastomys natalensis*	F	CV	No	0
Hot wet	Outjo	OJ19A	*Aethomys chrysophilus*	F	CV	Yes	1
Hot wet	Outjo	OJ20A	*Mastomys natalensis*	M	DT	No	0
Hot wet	Outjo	OJ21A	*Aethomys chrysophilus*	M	AT	No	0
Hot wet	Outjo	OJ22A	*Mastomys natalensis*	F	CV	Yes	1
Hot wet	Outjo	OJ23A	*Mastomys natalensis*	F	CV	No	0
Hot wet	Outjo	OJ24A	*Aethomys chrysophilus*	M	AT	No	0
Hot wet	Outjo	OJ25A	*Gerbilliscus leucogaster*	M	DT	No	0
Hot wet	Outjo	OJ26A	*Mastomys natalensis*	F	CV	Yes	1
Hot wet	Outjo	OJ27A	*Mastomys natalensis*	F	CV	No	0
Hot wet	Outjo	OJ28A	*Mastomys natalensis*	F	CV	Yes	1
Hot wet	Outjo	OJ29A	*Mastomys natalensis*	F	CV	No	0
Hot wet	Outjo	OJ30A	*Gerbilliscus leucogaster*	M	DT	Yes	1
Hot wet	Outjo	OJ31A	*Gerbilliscus leucogaster*	F	CV	Yes	7
Hot wet	Outjo	OJ32A	*Mastomys natalensis*	M	DT	Yes	1
Hot wet	Outjo	OJ33A	*Mastomys natalensis*	F	CV	Yes	1
Hot wet	Outjo	OJ34A	*Tatera leucogaster*	F	CV	Yes	4
Hot wet	Outjo	OJ35A	*Mastomys natalensis*	M	AT	Yes	1
Hot wet	Outjo	OJ36A	*Mastomys natalensis*	M	AT	Yes	1
Hot wet	Outjo	OJ37A	*Aethomys chrysophilus*	M	DT	Yes	1

Hot wet	Outjo	OJ38A	*Mastomys natalensis*	F	CV	Yes	6
Hot wet	Outjo	OJ39A	*Mastomys natalensis*	M	DT	Yes	1
Hot wet	Outjo	OJ40A	*Micaelamys namaquensis*	F	CV	Yes	7
Hot wet	Outjo	OJ41A	*Mastomys natalensis*	F	CV	Yes	2
Hot wet	Outjo	OJ42A	*Micaelamys namaquensis*	M	DT	Yes	1
Hot wet	Outjo	OJ43A	*Gerbilliscus leucogaster*	M	DT	Yes	1
Hot wet	Outjo	OJ1B	*Mastomys natalensis*	M	AT	No	0
Hot wet	Outjo	OJ2B	*Mastomys natalensis*	F	CV	No	0
Hot wet	Outjo	OJ3B	*Mastomys natalensis*	F	CV	No	0
Hot wet	Outjo	OJ4B	*Mastomys natalensis*	F	CV	No	0
Hot wet	Outjo	OJ5B	*Mastomys natalensis*	M	AT	No	0
Hot wet	Outjo	OJ6B	*Mastomys natalensis*	F	CV	No	0
Hot wet	Outjo	OJ7B	*Aethomys chrysophilus*	F	CV	No	0
Hot wet	Outjo	OJ8B	*Mastomys natalensis*	F	CV	No	0
Hot wet	Outjo	OJ9B	*Mastomys natalensis*	M	DT	No	0
Hot wet	Outjo	OJ10B	*Mastomys natalensis*	M	DT	Yes	1
Hot wet	Outjo	OJ11B	*Aethomys chrysophilus*	F	CV	No	0
Hot wet	Outjo	OJ12B	*Mastomys natalensis*	M	AT	No	0
Hot wet	Outjo	OJ13B	*Mastomys natalensis*	F	CV	No	0
Hot wet	Outjo	OJ14B	*Aethomys chrysophilus*	M	AT	No	0
Hot wet	Outjo	OJ15B	*Aethomys chrysophilus*	F	CV	No	0

Hot wet	Outjo	OJ16B	*Mastomys natalensis*	M	DT	No	0
Hot wet	Outjo	OJ17B	*Aethomys chrysophilus*	M	DT	No	0
Hot wet	Outjo	OJ18B	*Mastomys natalensis*	M	DT	No	0
Hot wet	Outjo	OJ19B	*Mastomys natalensis*	F	CV	No	0
Hot wet	Outjo	OJ20B	*Mastomys natalensis*	F	OV	No	0
Hot wet	Outjo	OJ21B	*Mastomys natalensis*	M	DT	No	0
Hot wet	Outjo	OJ22B	*Mastomys natalensis*	F	OV	No	0
Hot wet	Outjo	OJ23B	*Mastomys natalensis*	M	DT	No	0
Hot wet	Outjo	OJ24B	*Mastomys natalensis*	F	CV	No	0
Hot wet	Outjo	OJ25B	*Mastomys natalensis*	F	CV	No	0
Hot wet	Outjo	OJ26B	*Mastomys natalensis*	M	AT	No	0
Hot wet	Outjo	OJ27B	*Micaelamys namaquensis*	F	OV	No	0
Hot wet	Outjo	OJ28B	*Micaelamys namaquensis*	M	DT	No	0
Hot wet	Outjo	OJ29B	*Micaelamys namaquensis*	M	DT	No	0
Hot wet	Outjo	OJ30B	*Mastomys natalensis*	F	CV	Yes	3
Hot wet	Outjo	OJ31B	*Mastomys natalensis*	F	CV	Yes	1
Hot wet	Outjo	OJ32B	*Mastomys natalensis*	F	CV	No	0
Hot wet	Outjo	OJ33B	*Mastomys natalensis*	M	DT	Yes	3
Hot wet	Outjo	0J34B	*Mastomys natalensis*	F	CV	No	0
Hot wet	Outjo	OJ35B	*Aethomys chrysophilus*	M	DT	Yes	4
Hot wet	Outjo	OJ36B	*Gerbilliscus leucogaster*	M	AT	Yes	2

Hot wet	Outjo	OJ37B	*Mastomys natalensis*	F	CV	Yes	1
Hot wet	Outjo	OJ38B	*Aethomys chrysophilus*	M	DT	Yes	3
Hot wet	Outjo	OJ39B	*Mastomys natalensis*	F	CV	Yes	2
Hot wet	Outjo	OJ40B	*Mastomys natalensis*	M	AT	Yes	3
Hot wet	Outjo	OJ41B	*Mastomys natalensis*	M	DT	No	0
Hot wet	Outjo	OJ42B	*Mastomys natalensis*	M	DT	Yes	1
Hot wet	Outjo	OJ43B	*Mastomys natalensis*	F	CV	Yes	1
Hot wet	Outjo	OJ44B	*Mastomys natalensis*	M	AT	Yes	1
Hot wet	Outjo	OJ45B	*Mastomys natalensis*	M	AT	No	0
Hot wet	Outjo	OJ46B	*Mastomys natalensis*	F	CV	No	0
Hot wet	Vingerklip	VK1A	*Gerbilliscus leucogaster*	M	DT	Yes	4
Hot wet	Vingerklip	VK2A	*Micaelamys namaquensis*	F	OV	No	0
Hot wet	Vingerklip	VK3A	*Thallomys nigricauda*	F	CV	Yes	1
Hot wet	Vingerklip	VK4A	*Micaelamys namaquensis*	F	CV	No	0
Hot wet	Vingerklip	VK5A	*Micaelamys namaquensis*	F	CV	No	0
Hot wet	Vingerklip	VK6A	*Micaelamys namaquensis*	F	OV	No	0
Hot wet	Vingerklip	VK7A	*Micaelamys namaquensis*	F	OV	No	0
Hot wet	Vingerklip	VK8A	*Micaelamys namaquensis*	M	DT	Yes	1
Hot wet	Vingerklip	VK1B	*Micaelamys namaquensis*	M	DT	No	0
Hot wet	Vingerklip	VK2B	*Micaelamys namaquensis*	F	CV	No	0
Hot wet	Vingerklip	VK3B	*Micaelamys namaquensis*	M	DT	No	0

Hot wet	Vingerklip	VK4B	*Elephantulus intufi*	F	OV	No	0
Hot wet	Vingerklip	VK5B	*Micaelamys namaquensis*	M	DT	No	0
Hot wet	Vingerklip	VK6B	*Micaelamys namaquensis*	F	CV	No	0
Hot wet	Vingerklip	VK7B	*Gerbilliscus leucogaster*	M	DT	Yes	5
Hot wet	Brandberg	BD1A	*Gerbilliscus leucogaster*	F	CV	Yes	1
Hot wet	Brandberg	BD2A	*Thallomys nigricauda*	F	OV	Yes	1
Hot wet	Brandberg	BD3A	*Thallomys nigricauda*	F	OV	No	0
Hot wet	Brandberg	BD4A	*Thallomys nigricauda*	M	AT	No	0
Hot wet	Brandberg	BD1B	*Thallomys paedulcus*	M	DT	No	0
Hot wet	Brandberg	BD2B	*Thallomys paedulcus*	F	CV	No	0
Hot wet	Brandberg	BD3B	*Saccostomus campestris*	F	CV	No	0
Cold dry	Outjo	OJ1A	*Micaelamys namaquensis*	F	CV	Yes	2
Cold dry	Outjo	OJ2A	*Micaelamys namaquensis*	F	CV	No	0
Cold dry	Outjo	OJ3A	*Aethomys chrysophilus*	M	DT	No	0
Cold dry	Outjo	OJ4A	*Saccostomus campestris*	F	CV	Yes	4
Cold dry	Outjo	OJ5A	*Micaelamys namaquensis*	F	CV	Yes	1
Cold dry	Outjo	OJ6A	*Aethomys chrysophilus*	F	CV	Yes	1
Cold dry	Outjo	OJ7A	*Micaelamys namaquensis*	M	DT	Yes	1
Cold dry	Outjo	OJ8A	*Mastomys natalensis*	M	DT	Yes	4
Cold dry	Outjo	OJ9A	*Micaelamys namaquensis*	M	AT	No	0
Cold dry	Outjo	OJ10A	*Aethomys chrysophilus*	M	AT	Yes	2

Cold dry	Outjo	OJ11A	*Micaelamys namaquensis*	F	OV	Yes	1
Cold dry	Outjo	OJ12A	*Mastomys natalensis*	M	DT	Yes	3
Cold dry	Outjo	OJ13A	*Micaelamys namaquensis*	F	CV	Yes	3
Cold dry	Outjo	OJ14A	*Micaelamys namaquensis*	F	CV	Yes	3
Cold dry	Outjo	OJ15A	*Aethomys chrysophilus*	M	AT	No	0
Cold dry	Outjo	OJ16A	*Aethomys chrysophilus*	F	OV	Yes	4
Cold dry	Outjo	OJ17A	*Micaelamys namaquensis*	M	AT	No	0
Cold dry	Outjo	OJ18A	*Mastomys natalensis*	F	CV	Yes	2
Cold dry	Outjo	OJ19A	*Aethomys chrysophilus*	M	AT	Yes	5
Cold dry	Outjo	OJ20A	*Aethomys chrysophilus*	F	OV	Yes	3
Cold dry	Outjo	OJ1B	*Aethomys chrysophilus*	M	AT	No	0
Cold dry	Outjo	OJ2B	*Mastomys natalensis*	F	CV	No	0
Cold dry	Outjo	OJ3B	*Aethomys chrysophilus*	M	AT	No	0
Cold dry	Outjo	OJ4B	*Micaelamys namaquensis*	M	AT	No	0
Cold dry	Outjo	OJ5B	*Micaelamys namaquensis*	M	AT	Yes	7
Cold dry	Outjo	OJ6B	*Gerbilliscus leucogaster*	F	CV	No	0
Cold dry	Outjo	OJ7B	*Aethomys chrysophilus*	F	CV	No	0
Cold dry	Outjo	OJ8B	*Aethomys chrysophilus*	F	CV	No	0
Cold dry	Outjo	OJ9B	*Mastomys natalensis*	M	AT	Yes	3
Cold dry	Outjo	OJ10B	*Gerbilliscus leucogaster*	F	CV	No	0
Cold dry	Outjo	OJ11B	*Aethomys chrysophilus*	F	OV	No	0

Cold dry	Outjo	OJ12B	*Micaelamys namaquensis*	M	AT	Yes	2
Cold dry	Outjo	OJ13	*Aethomys chrysophilus*	F	CV	Yes	1
Cold dry	Vingerklip	VK1A	*Gerbilliscus leucogaster*	F	CV	No	0
Cold dry	Vingerklip	VK2A	*Gerbilliscus leucogaster*	M	AT	No	0
Cold dry	Vingerklip	VK3A	*Micaelamys namaquensis*	F	CV	No	0
Cold dry	Vingerklip	VK4A	*Gerbilliscus leucogaster*	F	CV	No	0
Cold dry	Vingerklip	VK1B	*Micaelamys namaquensis*	F	OV	No	0
Cold dry	Vingerklip	VK2B	*Elephantulus intufi*	F	OV	No	0
Cold dry	Vingerklip	VK3B	*Gerbilliscus leucogaster*	F	CV	No	0
Cold dry	Vingerklip	VK4B	*Gerbilliscus leucogaster*	F	OV	Yes	1
Cold dry	Vingerklip	VK5B	*Elephantulus intufi*	F	OV	No	0
Cold dry	Brandberg	BB1A	*Thallomys paedulcus*	F	OV	No	0
Cold dry	Brandberg	BB2A	*Thallomys paedulcus*	M	AT	Yes	3
Cold dry	Brandberg	BB3A	*Micaelamys namaquensis*	F	CV	No	0
Cold dry	Brandberg	BB4A	*Micaelamys namaquensis*	F	CV	No	0
Cold dry	Brandberg	BB1B	*Thallomys paedulcus*	M	DT	Yes	1
Cold dry	Brandberg	BB2B	*Thallomys paedulcus*	F	CV	No	0
Cold dry	Brandberg	BB3B	*Saccostomus campestris*	F	CV	No	0

Appendix B: Flea species collected from small mammal hosts during the hot wet and cold dry seasons, 2018

Season	Host ID	Host species	Flea ID	Genus	Species	Flea Sex
Hot wet	OJ19A	*Aethomys chrysophilus*	OJ19AF1	*Xenopsylla*	*brasiliensis*	Female
Hot wet	OJ22A	*Mastomys natalensis*	OJ22AF1	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ26A	*Mastomys natalensis*	OJ26AF1	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ28A	*Mastomys natalensis*	OJ28AF1	*Xenopsylla*	*cheopis*	Female
Hot wet	OJ30A	*Gerbilliscus leucogaster*	OJ30AF1	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ31A	*Gerbilliscus leucogaster*	OJ31AF1	*Xenopsylla*	*cheopis*	Female
Hot wet	OJ31A	*Gerbilliscus leucogaster*	OJ31AF2	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ31A	*Gerbilliscus leucogaster*	OJ31AF3	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ31A	*Gerbilliscus leucogaster*	OJ31AF4	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ31A	*Gerbilliscus leucogaster*	OJ31AF5	*Xenopsylla*	*cheopis*	Female
Hot wet	OJ31A	*Gerbilliscus leucogaster*	OJ31AF6	*Xenopsylla*	*cheopis*	Female
Hot wet	OJ31A	*Gerbilliscus leucogaster*	OJ31AF7	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ32A	*Mastomys natalensis*	OJ32AF1	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ33A	*Mastomys natalensis*	OJ33AF1	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ34A	*Gerbilliscus leucogaster*	OJ34AF1	*Xenopsylla*	*cheopis*	Female
Hot wet	OJ34A	*Gerbilliscus leucogaster*	OJ34AF2	*Xenopsylla*	*cheopis*	Female
Hot wet	OJ34A	*Gerbilliscus leucogaster*	OJ34AF3	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ34A	*Gerbilliscus leucogaster*	OJ34AF4	*Xenopsylla*	*cheopis*	Male

Hot wet	OJ35A	*Mastomys natalensis*	OJ35AF1	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ37A	*Aethomys chrysophilus*	OJ37AF1	*Xenopsylla*	*brasiliensis*	Female
Hot wet	OJ38A	*Mastomys natalensis*	OJ38AF1	*Xenopsylla*	*brasiliensis*	Male
Hot wet	OJ38A	*Mastomys natalensis*	OJ38AF2	*Xenopsylla*	*brasiliensis*	Male
Hot wet	OJ38A	*Mastomys natalensis*	OJ38AF3	*Xenopsylla*	*brasiliensis*	Male
Hot wet	OJ38A	*Mastomys natalensis*	OJ38AF4	*Xenopsylla*	*brasiliensis*	Male
Hot wet	OJ38A	*Mastomys natalensis*	OJ38AF5	*Xenopsylla*	*brasiliensis*	Male
Hot wet	OJ38A	*Mastomys natalensis*	OJ38AF6	*Xenopsylla*	*brasiliensis*	Female
Hot wet	OJ39A	*Mastomys natalensis*	OJ39AF1	*Xenopsylla*	*brasiliensis*	Female
Hot wet	OJ40A	*Micaelamys namaquensis*	OJ40AF1	*Xenopsylla*	*brasiliensis*	Female
Hot wet	OJ40A	*Micaelamys namaquensis*	OJ40AF2	*Xenopsylla*	*cheopis*	Female
Hot wet	OJ40A	*Micaelamys namaquensis*	OJ40AF3	*Xenopsylla*	*brasiliensis*	Male
Hot wet	OJ40A	*Micaelamys namaquensis*	OJ40AF4	*Xenopsylla*	*brasiliensis*	Female
Hot wet	OJ40A	*Micaelamys namaquensis*	OJ40AF5	*Xenopsylla*	*brasiliensis*	Male
Hot wet	OJ40A	*Micaelamys namaquensis*	OJ40AF6	*Xenopsylla*	*brasiliensis*	Male
Hot wet	OJ40A	*Micaelamys namaquensis*	OJ40AF7	*Xenopsylla*	*brasiliensis*	Male
Hot wet	OJ41A	*Mastomys natalensis*	OJ41AF1	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ41A	*Mastomys natalensis*	OJ41AF2	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ42A	*Micaelamys namaquensis*	OJ42AF1	*Xenopsylla*	*brasiliensis*	Female
Hot wet	OJ10B	*Mastomys natalensis*	OJ10BF1	*Xenopsylla*	*brasiliensis*	Female
Hot wet	OJ30B	*Mastomys natalensis*	OJ30BF1	*Xenopsylla*	*cheopis*	Male

Hot wet	OJ30B	*Mastomys natalensis*	OJ30BF2	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ30B	*Mastomys natalensis*	OJ30BF3	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ31B	*Mastomys natalensis*	OJ31BF1	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ33B	*Mastomys natalensis*	OJ33BF1	*Xenopsylla*	*brasiliensis*	Male
Hot wet	OJ33B	*Mastomys natalensis*	OJ33BF2	*Xenopsylla*	*brasiliensis*	Male
Hot wet	OJ33B	*Mastomys natalensis*	OJ33BF3	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ35B	*Aethomys chrysophilus*	OJ35BF1	*Xenopsylla*	*brasiliensis*	Female
Hot wet	OJ35B	*Aethomys chrysophilus*	OJ35BF2	*Xenopsylla*	*brasiliensis*	Male
Hot wet	OJ35B	*Aethomys chrysophilus*	OJ35BF3	*Xenopsylla*	*brasiliensis*	Female
Hot wet	OJ35B	*Aethomys chrysophilus*	OJ35BF4	*Xenopsylla*	*brasiliensis*	Male
Hot wet	OJ36B	*Gerbilliscus leucogaster*	OJ36BF1	*Xenopsylla*	*cheopis*	Female
Hot wet	OJ36B	*Gerbilliscus leucogaster*	OJ35BF2	*Xenopsylla*	*brasiliensis*	Male
Hot wet	OJ37B	*Mastomys natalensis*	OJ37BF1	*Xenopsylla*	*cheopis*	Female
Hot wet	OJ38B	*Aethomys chrysophilus*	OJ38BF1	*Xenopsylla*	*brasiliensis*	Male
Hot wet	OJ38B	*Aethomys chrysophilus*	OJ38BF2	*Xenopsylla*	*brasiliensis*	Female
Hot wet	OJ38B	*Aethomys chrysophilus*	OJ38BF3	*Xenopsylla*	*brasiliensis*	Male
Hot wet	OJ39B	*Mastomys natalensis*	OJ39BF1	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ39B	*Mastomys natalensis*	OJ39BF2	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ40B	*Mastomys natalensis*	OJ40BF1	*Xenopsylla*	*brasiliensis*	Male
Hot wet	OJ40B	*Mastomys natalensis*	OJ40BF2	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ40B	*Mastomys natalensis*	OJ40BF3	*Xenopsylla*	*brasiliensis*	Male

Hot wet	OJ42B	*Mastomys natalensis*	OJ42BF1	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ43B	*Mastomys natalensis*	OJ43BF1	*Xenopsylla*	*cheopis*	Male
Hot wet	OJ44B	*Mastomys natalensis*	OJ44BF1	*Xenopsylla*	*cheopis*	Female
Hot wet	VK1A	*Gerbilliscus leucogaster*	VK1AF1	*Xenopsylla*	*cheopis*	Male
Hot wet	VK1A	*Gerbilliscus leucogaster*	VK1AF2	*Xenopsylla*	*cheopis*	Male
Hot wet	VK1A	*Gerbilliscus leucogaster*	VK1AF3	*Xenopsylla*	*cheopis*	Female
Hot wet	VK1A	*Gerbilliscus leucogaster*	VK1AF4	*Xenopsylla*	*cheopis*	Female
Hot wet	VK3A	*Thallomys nigricauda*	VK3AF1	*Xenopsylla*	*brasiliensis*	Female
Hot wet	VK8A	*Micaelamys namaquensis*	VK8AF1	*Xenopsylla*	*brasiliensis*	Female
Hot wet	VK7B	*Gerbilliscus leucogaster*	VK7BF1	*Xenopsylla*	*cheopis*	Female
Hot wet	VK7B	*Gerbilliscus leucogaster*	VK7BF2	*Xenopsylla*	*cheopis*	Female
Hot wet	VK7B	*Gerbilliscus leucogaster*	VK7BF3	*Xenopsylla*	*cheopis*	Male
Hot wet	VK7B	*Gerbilliscus leucogaster*	VK7BF4	*Xenopsylla*	*cheopis*	Male
Hot wet	VK7B	*Gerbilliscus leucogaster*	VK7BF5	*Xenopsylla*	*cheopis*	Male
Hot wet	BB1A	*Gerbilliscus leucogaster*	BB1AF1	*Xenopsylla*	*cheopis*	Male
Hot wet	BB2A	*Thallomys nigricauda*	BB2AF1	*Xenopsylla*	*brasiliensis*	Male
Cold dry	OJ1A	*Micaelamys namaquensis*	OJ1AF1	*Xenopsylla*	*brasiliensis*	Female
Cold dry	OJ1A	*Micaelamys namaquensis*	OJ1AF2	*Xenopsylla*	*brasiliensis*	Female
Cold dry	OJ1A	*Micaelamys namaquensis*	OJ1AF3	*Xenopsylla*	*brasiliensis*	Female
Cold dry	OJ1A	*Micaelamys namaquensis*	OJ1AF4	*Xenopsylla*	*brasiliensis*	Female
Cold dry	OJ4A	*Saccostomus campestris*	OJ4AF1	*Xenopsylla*	*brasiliensis*	Male

Cold dry	OJ4A	*Saccostomus campestris*	OJ4AF2	*Xenopsylla*	*brasiliensis*	Female
Cold dry	OJ4A	*Saccostomus campestris*	OJ4AF3	*Xenopsylla*	*brasiliensis*	Female
Cold dry	OJ4A	*Saccostomus campestris*	OJ4AF4	*Xenopsylla*	*brasiliensis*	Female
Cold dry	OJ5A	*Micaelamys namaquensis*	OJ5AF1	*Xenopsylla*	*cheopis*	Female
Cold dry	OJ6A	*Aethomys chrysophilus*	OJ6AF1	*Xenopsylla*	*cheopis*	Male
Cold dry	OJ7A	*Micaelamys namaquensis*	OJ7AF1	*Xenopsylla*	*cheopis*	Male
Cold dry	OJ7A	*Micaelamys namaquensis*	OJ7AF2	*Xenopsylla*	*cheopis*	Male
Cold dry	OJ7A	*Micaelamys namaquensis*	OJ7AF3	*Xenopsylla*	*cheopis*	Male
Cold dry	OJ7A	*Micaelamys namaquensis*	OJ7AF4	*Xenopsylla*	*cheopis*	Male
Cold dry	OJ7A	*Micaelamys namaquensis*	OJ7AF5	*Xenopsylla*	*cheopis*	Male
Cold dry	OJ8A	*Mastomys natalensis*	OJ8AF1	*Xenopsylla*	*cheopis*	Female
Cold dry	OJ8A	*Mastomys natalensis*	OJ8AF2	*Xenopsylla*	*cheopis*	Male
Cold dry	OJ8A	*Mastomys natalensis*	OJ8AF3	*Xenopsylla*	*brasiliensis*	Male
Cold dry	OJ8A	*Mastomys natalensis*	OJ8AF4	*Xenopsylla*	*cheopis*	Female
Cold dry	OJ10A	*Aethomys chrysophilus*	OJ10AF1	*Xenopsylla*	*brasiliensis*	Female
Cold dry	OJ10A	*Aethomys chrysophilus*	OJ10AF2	*Xenopsylla*	*brasiliensis*	Male
Cold dry	OJ11A	*Micaelamys namaquensis*	OJ11AF1	*Xenopsylla*	*cheopis*	Male
Cold dry	OJ12A	*Mastomys natalensis*	OJ12AF1	*Xenopsylla*	*brasiliensis*	Female
Cold dry	OJ12A	*Mastomys natalensis*	OJ12AF2	*Xenopsylla*	*cheopis*	Male
Cold dry	OJ12A	*Mastomys natalensis*	OJ12AF3	*Xenopsylla*	*cheopis*	Male
Cold dry	OJ13A	*Micaelamys namaquensis*	OJ13AF1	*Xenopsylla*	*cheopis*	Female

Cold dry	OJ13A	*Micaelamys namaquensis*	OJ13AF2	*Xenopsylla*	*cheopis*	Female
Cold dry	OJ13A	*Micaelamys namaquensis*	OJ13AF3	*Xenopsylla*	*cheopis*	Male
Cold dry	OJ14A	*Micaelamys namaquensis*	OJ14AF1	Xenopsylla	*cheopis*	Male
Cold dry	OJ14A	*Micaelamys namaquensis*	OJ14AF2	*Xenopsylla*	*cheopis*	Male
Cold dry	OJ14A	*Micaelamys namaquensis*	OJ14AF3	*Xenopsylla*	*brasiliensis*	Male
Cold dry	OJ16A	*Aethomys chrysophilus*	OJ16AF1	*Xenopsylla*	*brasiliensis*	Male
Cold dry	OJ16A	*Aethomys chrysophilus*	OJ16AF2	*Xenopsylla*	*cheopis*	Female
Cold dry	OJ16A	*Aethomys chrysophilus*	OJ16AF3	*Listropsylla*	*dorripae*	Male
Cold dry	OJ16A	*Aethomys chrysophilus*	OJ16AF4	*Listropsylla*	*dorripae*	Male
Cold dry	OJ18A	*Mastomys natalensis*	OJ18AF1	*Xenopsylla*	*cheopis*	Female
Cold dry	OJ18A	*Mastomys natalensis*	OJ18AF2	*Xenopsylla*	*cheopis*	Female
Cold dry	OJ19A	*Aethomys chrysophilus*	OJ19AF1	*Xenopsylla*	*brasiliensis*	Male
Cold dry	OJ19A	*Aethomys chrysophilus*	OJ19AF2	*Xenopsylla*	*brasiliensis*	Male
Cold dry	OJ19A	*Aethomys chrysophilus*	OJ19AF3	*Xenopsylla*	*brasiliensis*	Male
Cold dry	OJ19A	*Aethomys chrysophilus*	OJ19AF4	*Xenopsylla*	*cheopis*	Female
Cold dry	OJ19A	*Aethomys chrysophilus*	OJ19AF5	*Listropsylla*	*dorripae*	Female
Cold dry	OJ20A	*Aethomys chrysophilus*	OJ20AF1	*Xenopsylla*	*brasiliensis*	Female
Cold dry	OJ20A	*Aethomys chrysophilus*	OJ20AF2	*Xenopsylla*	*brasiliensis*	Female
Cold dry	OJ20A	*Aethomys chrysophilus*	OJ20AF3	*Xenopsylla*	*brasiliensis*	Female
Cold dry	OJ5B	*Micaelamys namaquensis*	OJ5BF1	*Listropsylla*	*dorripae*	Male
Cold dry	OJ5B	*Micaelamys namaquensis*	OJ5BF2	*Listropsylla*	*dorripae*	Male

Cold dry	OJ5B	*Micaelamys namaquensis*	OJ5BF3	*Xenopsylla*	*cheopis*	Male
Cold dry	OJ5B	*Micaelamys namaquensis*	OJ5BF4	*Xenopsylla*	*brasiliensis*	Male
Cold dry	OJ5B	*Micaelamys namaquensis*	OJ5BF5	*Xenopsylla*	*brasiliensis*	Male
Cold dry	OJ5B	*Micaelamys namaquensis*	OJ5BF6	*Xenopsylla*	*brasiliensis*	Male
Cold dry	OJ5B	*Micaelamys namaquensis*	OJ5BF7	*Xenopsylla*	*brasiliensis*	Male
Cold dry	OJ9B	*Mastomys natalensis*	OJ9BF1	*Xenopsylla*	*brasiliensis*	Male
Cold dry	OJ9B	*Mastomys natalensis*	OJ9BF2	*Xenopsylla*	*cheopis*	Female
Cold dry	OJ9B	*Mastomys natalensis*	OJ9BF3	*Xenopsylla*	*cheopis*	Female
Cold dry	OJ12B	*Micaelamys namaquensis*	OJ12BF1	*Xenopsylla*	*cheopis*	Female
Cold dry	OJ12B	*Micaelamys namaquensis*	OJ12BF2	*Xenopsylla*	*cheopis*	Male
Cold dry	OJ13B	*Aethomys chrysophilus*	OJ13BF1	*Xenopsylla*	*brasiliensis*	Male
Cold dry	VK1B	*Gerbilliscus leucogaster*	VK4BF1	*Xenopsylla*	*cheopis*	Female
Cold dry	VK2B	*Thallomys paedulcus*	BB2AF1	*Xenopsylla*	*brasiliensis*	Female
Cold dry	VK3B	*Thallomys paedulcus*	BB2AF2	*Xenopsylla*	*brasiliensis*	Male
Cold dry	VK4B	*Thallomys paedulcus*	BB2AF3	*Xenopsylla*	*brasiliensis*	Male
Cold dry	VK5B	*Micaelamys namaquensis*	BB1BF1	*Xenopsylla*	*brasiliensis*	Male