Ectoparasite assemblage of the four-striped mouse, Rhabdomys pumilio: the effect of anthropogenic habitat transformation and temporal variation

by
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Declaration

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Acknowledgements

Dedication

I would like to dedicate this thesis with love to my parents, Luther and Muriel van der Mescht. They supported me through all the tough times and for that I can't thank them enough.

Abstract

Anthropogenic habitat transformation and subsequent fragmentation of natural vegetation is regarded as one of the largest threats to biodiversity in the world. The Cape Floristic Region (CFR) in the Western Cape Province of South Africa is classified as a biodiversity hotspot due to its high plant species diversity and endemism. Increasing growth in agricultural activities in this region has contributed to fragmentation of pristine natural vegetation. A diverse assemblage of small mammal species are found in this region, but very little is known with regard to their ectoparasite diversity. More importantly, no information is available on the effect of fragmentation on parasite burdens or species assemblages. The aims of the study were first to record relative density, average body size and body condition of an endemic rodent, *Rhabdomys pumilio*, trapped in two habitat types (pristine natural areas and remnant fragments). Secondly, compare diversity and species composition of ectoparasite species on this rodent in the two habitat types. In addition, body size measurements of the two most abundant flea species were recorded and compared for the two habitat types. Lastly, temporal variation in mean abundance of fleas, mites, ticks and the louse were recorded within a habitat fragment surrounded by vineyards. Three hundred and ten individuals of the Four-striped mouse, *R. pumilio*, were trapped and euthanized at 8 localities (4 remnant habitat fragments and 4 pristine natural areas) in the CFR. All ectoparasites were removed and identified. A total of 8361 ectoparasites that consisted of 6 flea, 1 louse, 8 mites and 11 tick species were recorded. Mites and fleas were found to be more abundant on mice during cool wet months, whereas ticks and the louse were more abundant during the hot dry months of the year. Rodent host body size was larger and they were in better body condition in remnant fragments compared to pristine natural localities. A positive body size relationship was found between the flea, *Listropsylla agrippinae*, and the host, with larger fleas recorded on rodents that occur in fragments. Mean abundance and prevalence of overall ectoparasites combined and separately for ticks, mites, louse and fleas were higher in fragments compared to natural localities. The study shows that *R. pumilio* is host to a large diversity of ectoparasite species in the CFR. Moreover, habitat fragments within agricultural landscapes can facilitate higher parasite burdens and prevalence in rodent populations. This can lead to an increase in disease risk given that several of the parasite species are important vectors of pathogens that can cause disease in domestic, wild animals and humans.

Opsomming

Menslike habitat transformasie en die daaropvolgende fragmentasie van natuurlike plantegroei word beskou as een van die grootste bedreigings vir biodiversiteit in die wêreld. Die Kaap Floristiese Streek (KFS) in die Wes-Kaap Provinsie van Suid-Afrika word geklassifiseer as 'n biodiversiteit 'hotspot' as gevolg van sy hoë plant spesies diversiteit en endemisme. Toenemende groei in landbou-aktiwiteite in hierdie streek het ook bygedra tot die fragmentasie van ongerepte natuurlike plantegroei. 'n Diverse versameling van die klein soogdier spesies word in hierdie streek aangetref, maar baie min is bekend met betrekking tot hul ektoparasiet diversiteit. Meer belangrik, geen inligting is beskikbaar oor die effek van fragmentasie op parasietladings of spesie samestelling nie. Die doel van die studie was eerstens om relatiewe digtheid, gemiddelde liggaams grootte en kondisie van *Rhabdomys pumilio* aan te teken vir twee habitat tipes (ongerepte natuurlike area en oorblyfsel fragment). Tweedens was die diversiteit en spesiesamestelling van ektoparasiete op *R. pumilio* vergelyk vir die twee habitat tipes. Daarna was die liggaams grootte metings van die twee mees volopste vlooi spesies aangeteken en vergelyk vir die twee habitat tipes. Laastens was die seisonale variasie van die gemiddelde hoeveelheid vlooie, myte, bosluise en die luis aangeteken binne 'n habitat fragment omring deur wingerde. Drie honderd en tien individue van die vier-gestreepte muis, *R. pumilio*, was gevang op 8 plekke (4 oorblyfsel habitat fragmente en 4 ongerepte natuurlike areas) in die KFS en daarna was die diere uitgesit. Alle ektoparasiete was verwyder en geïdentifiseer. 'n Totaal van 8361 ektoparasiete wat bestaan het uit 6 vlooie, 1 luis, 8 myte en 11 bosluis spesies was aangeteken. Myte en vlooie gevind was meer volop op muise tydens die koel nat maande, terwyl bosluise en die luis meer volop was gedurende die warm droë maande van die jaar. Knaagdier gasheer liggaam was groter en in 'n beter kondisie in die habitat fragmente in vergelyking met ongerepte natuurlike areas. 'n Positiewe liggaam grootte verwantskap was tussen die vlooi, *Listropsylla agrippinae*, en die gasheer gevind, met groter vlooie aangeteken op knaagdiere wat voorkom in fragmente. Gemiddelde hoeveelheid en voorkoms van die totale ektoparasiete gekombineer en afsonderlik vir bosluise, myte, die luis en vlooie was hoër in fragmente in vergelyking met natuurlike areas. Die studie toon dat *R. pumilio* gasheer is vir 'n groot verskeidenheid van ektoparasiet spesies in die KFS. Daarbenewens kan habitat fragmente binne landbou landskappe hoër parasietladings en voorkoms in knaagdier bevolkings fasiliteer. Dit kan

lei tot 'n toename in siekte risiko, gegee dat verskeie van die parasietspesies belangrike vektore is van patogene wat siektes kan veroorsaak in huishoudelike, wilde diere en die mens.

Thesis structure

Chapter 1 gives a general introduction to the topic of the thesis.

Chapter 2 describes the ectoparasite assemblages of *Rhabdomys pumilio* in the CFR. This chapter also discuss the temporal variation of ectoparasites in the CFR.

Chapter 3 focuses on the effect of habitat fragmentation on the ectoparasite abundance, prevalence and species composition of *R. pumilio* in the CFR. The body size relationship between host and parasite for the two most abundant flea species are included.

Chapter 4 is the general conclusion.

Chapters 2 and *3* follow the format of scientific manuscripts.

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Chapter 1

General introduction

1.1 Anthropogenic linked habitat transformation

Habitat transformation as a result of increase in human population and associated urban and agricultural development is a major threat to ecosystems. Habitat transformation and subsequent fragmentation are regarded as important contributors to the loss of plant and animal species diversity and ecosystem functioning (Saunders *et al*. 1991; Peterson *et al.* 1998; Martin and McComb 2002). In particular, habitat fragmentation negatively impacts on small mammal population dynamics and changes in the abundance of small mammals may alter ecosystem processes and lead to changes in productivity, sustainability and biodiversity (Peterson *et al.* 1998; Martin and McComb 2002). In addition, the intensification and extensification of agricultural activities have the potential to facilitate outbreaks in the remaining rodent populations due to the absence of natural predators and competitors in areas with abundant resources such as food and shelter (Wilcox and Gubler 2005).

The Cape Floristic Region (CFR) is regarded as one of the biodiversity hotspots of the world (Cowling *et al.* 2003). The region covers 87 892 km^2 of South Africa (SA) and is mainly situated in the south western part of the country (Rouget *et al.* 2003). It is renowned for its high plant diversity, endemism and a high number of critically endangered plant species (Goldblatt and Manning 2000; Cowling and Hilton-Taylor 1994). The climate of the region is Mediterranean and most of the rainfall is recorded in winter months with the summer months being relatively dry and hot (Tyson and Preston-Whyte 2000). Successful and expanding wine and crop farming has resulted in the fragmentation of pristine natural vegetation and places increased pressure on the plant and animal diversity of this region (Rouget *et al*. 2003). It is therefore not unexpected that studies indicate that fragmentation, caused mainly by agriculture, has an effect on amongst others the community structure of renosterveld shrublands (Kemper *et al.* 1999), on overall bird species diversity (Mangnall and Crowe 2003) and reptile diversity in the CFR (Mouton and Alblas 2002).

1.2 Fragmentation and the effect on host and parasite assemblages

Habitat fragments often vary with respect to level of isolation and biological characteristics. The absence of corridors between fragments and the subsequent restriction in host movement can have a negative impact on the genetic variability and demography of the fragmented vertebrate-host populations (Wolff *et al.* 1997; Ims and Andreassen 1999). This can consequently result in inbreeding, in the long-term, and an increase of homozygous individuals. Inbred populations may be more susceptible to parasites and disease because of their lower immunocompetence (Smith *et al.* 2009; Froeschke and Sommer 2005). Changes in space use and social relationships between individuals of the rodent host population may also take place due to habitat fragmentation (Ims and Andreassen 1999). Fragmentation will influence rodent host populations both directly and indirectly. Modification of habitat characteristics that include structure, size and resource availability will influence the rodent host population directly. In addition, the edge effect, decreasing of genetic diversity and increasing competition both inter- and intraspecifically, will have indirect influences on the rodent host population (Soulé 1991).

Generalist rodent species are able to adapt to these changing environments, utilizing the abundance of resources (shelter and food) more efficiently, and thus outcompetes specialist rodent host species (de la Penã *et al.* 2003; Krasnov *et al.* 2006b; Rodríguez and Peris 2007; Manor and Saltz 2008). For example, White-footed mice (*Peromyscus leucopus*) are habitat generalists and it was found that they are able to reach high densities in forest fragments as a result of abundant resources and a decrease in abundance of predators and competitors in the fragment (Allan *et al.* 2003). More specifically, the same trend was found in a recent study that looked at the impact of fragmentation on rodents in the CFR. Generalist species such as the Four-striped mouse, *Rhabdomys pumilio*, and the Pigmy mouse, *Mus minutoides*, were able to better adapt to transformed areas than more specialist species such as the Vlei-rat, *Otomys irroratus*, Verreaux's white-footed rat, *Myosorex verreauxii*, and the Cape gerbil, *Gerbilliscus afra* (Mugabe 2008). In addition, this study also looked at the potential negative effect that transformation has on *R. pumilio*, but found no difference in body condition index or body size between natural and transformed habitats. The author suggested that rodents tend to seek refuge and food within remnant fragments surrounded by agricultural activities (Mugabe 2008).

Studies on the effect of habitat transformation on small mammal assemblages in SA are scant (Lawes *et al.* 2000; Johnson *et al.* 2002; Wilson *et al.* 2010), especially in the CFR (Mugabe 2008). It is evident though that negative effects of fragmentations, on host populations, will be strongly influenced by the availability of resources. In particular, fragments in agricultural areas may provide food and shelter for small mammal species and can facilitate high population numbers. In addition, the absence of natural occurring predators and large herbivores in these fragments can further facilitate population growth (Allan *et al.* 2003; Wilcox and Gubler 2005; McCauley *et al.* 2008).

Although the effects of habitat transformation on rodents have been extensively studied in other parts of the world (Dickman and Doncaster 1987; Bowers *et al.* 1996; Ims and Andreassen 1999; Laakkonen *et al.* 2001) little is known with respect to the effects on the parasite assemblages of rodent hosts (Vaz *et al.* 2007; Püttker *et al.* 2008; Friggens and Beier 2010). A recent study by McCauley *et al.* (2008) looked at the effect of the removal of natural occurring large herbivores on the Pouched mouse (*Saccostomus mearnsi*) and their fleas in Kenya and found that the removal of large herbivores resulted in an increase in total number of fleas as a result of a near double increase in rodent density (McCauley *et al.* 2008). At present no information is available on the effect of habitat fragmentation on the natural ectoparasite assemblages of small mammals in the Western Cape Province (WCP) or SA.

Due to the intimate relationship between parasites and their hosts it is expected that changes in the host population dynamics and community structure will have knock-on effects on the parasite diversity and species composition. However, parasite life history will strongly influence the extent of the change.

1.3 Parasite life history

Parasite taxa differ with respect to life history and thus degree of host association, which will result in species-specific response to host- and environmental factors (Krasnov and Matthee 2010). Sucking lice (Anoplura, Phthiraptera) are permanent parasites, which live, feed, reproduce and die in the fur of the host animal from generation to generation until the host dies (Kim 2006). They rarely leave the host and are mainly transferred through direct contact (Marshall 1981). In general, fleas (Siphonaptera) spend part of their life in the burrow/nest (larvae and pupae) and the rest, to some extent, on the host (adults). Adult stages can further be divided into fur fleas (spend most of their time in the fur of the host) and nest fleas (spend most of their time in the host's burrow/nest) (Medvedev and Krasnov 2006). Mesostigmatid mites (Acari) are either permanent (on host throughout life cycle) or nidicolous (part of life cycle in nest/roost but is also found on host) parasites (Houck 1994). Ixodid ticks (Acari) mainly have a multi-host life cycle (two- and three host life cycles) with the different feeding stages feeding on different host individuals (Walker 1991; Walker *et al*. 2000). In general, rodents such as *R. pumilio* are predominantly infested by immature tick stages (larvae and nymphs), while all the life stages of lice and mites and only adult stages of fleas can occur on them (Marshall 1981; Walker 1991; Segerman 1995; Matthee *et al.* 2007).

1.4 Factors that shape parasite diversity and species assemblages

There are various factors that can influence parasite species composition, diversity and survival in fragmented landscapes. These factors can be grouped into environmental-, host- and parasite related factors (Krasnov and Matthee 2010). The local climate- and habitat variables (e.g. temperature, humidity, vegetation, soil composition) are important determinants of parasite species assemblage (Poulin 2007) and temporal variation in parasite abundance (Weil *et al.* 2006). Krasnov *et al.* (1998) found that the depth of the host burrow system influenced flea abundance and species composition to the extent that fur fleas were more abundant on hosts that use shallow burrows compared to deeper and more complex burrow systems. This pattern may be due to a higher tolerance level of fur fleas to external temperature and humidity. It was also

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found that the depth of the burrow depend on the soil structure of the habitat (Krasnov *et al*. 1998).

Parasite numbers vary between seasons on the host. The underlying causes of temporal variation can be attributed to seasonal changes in climate and in the physiology or behaviour of intermediate or definitive host species (Weil *et al.* 2006). In addition, individual parasite taxa are expected to differ seasonally in abundance according to their relationship with the host and their specific environmental needs both on and off the host. Fleas, mites, lice and ticks differ with respect to host association and will thus react differently to variation in climate. A number of studies have been done on temporal variation of various ectoparasite species on small mammals in SA (Horak *et al.* 1993; Louw *et al*. 1993, 1995; Braack *et al*. 1996; Anderson and Kok 2003). However, most of these studies have been on single taxa (e.g. ticks or fleas) and mostly in the summer rainfall regions of the country (Horak *et al.* 1993; Louw *et al*. 1993, 1995; Braack *et al*. 1996; Anderson and Kok 2003). More recently, a study was done on the full extent of ectoparasite species on *R. pumilio* in the WCP (Matthee *et al*. 2007). From this study it appears that fleas, lice and mites seem to increase in mean abundance during cooler wet months and ticks increase during hot dry months in the WCP (winter rainfall) on *R. pumilio* (Matthee *et al.* 2007).

As mentioned above vertebrate diversity is negatively affected by habitat transformation. Host species diversity, one of the factors that contribute to the biological characteristics of a fragment, is important due to a positive relationship between host species richness and parasite species richness (Krasnov *et al*. 2004; Poulin 2007). It is therefore more than likely that rodent species that are able to survive within remnant fragments will support a depauperate parasite assemblage compared to the same rodent species that co-occur with several other mammal species in extensive pristine natural areas (Rosenzweig 1995). On the other hand, it might be that the remaining generalist rodent species may in fact harbour high parasite diversity (Egoscue 1976; Matthee *et al*. 2007). More importantly, it is possible that a depauperate pattern will be masked if the fragments are close to peri-urban areas and frequently visited or used by domestic animals, which would facilitate host switching events and contribute to a change in the parasite species composition and richness of rodent species in these fragments (Shepherd and Leman 1983; Shepherd *et al*. 1983; McMichael 2004).

In addition to host species diversity, several other host-related factors such as host body size, body condition and density can also influence the parasite diversity and species composition. Rodent species that are able to adapt to and exploit fragments in agricultural landscapes benefit from additional shelter, food, water and protection against natural predators (Krasnov *et al.* 2006a; Friggens and Beier 2010). The availability of food will provide energy to host species for growth, reproduction and thermoregulation and may result in improved immunocompetence (Krasnov *et al.* 2006a). Host body size can influence parasite species richness, abundance and also parasite body size. Larger hosts tend to host a higher abundance of parasites because their body surface is larger and thus may provide more space and other resources (Moore and Wilson 2002; Poulin 2007). However, this pattern is not consistent for all taxa and thus the importance of host body size is said to be far from being universal (Krasnov *et al.* 2006a; Poulin 2007).

Parasite body size also appears to be positively correlated with host body size. Larger hosts provide more space and a greater supply of nutrients and it is therefore expected that selection would favour larger-bodied parasites (Poulin 2007). Contradicting results have been found for host and parasite body size relationships. Tick body size does not seem to correlate with host mass (Poulin 1998) whereas a correlation have been found between flea body size, host size and length of rodent host hair (Kirk 1991). In most animals there are a positive correlation between body size and fecundity, and this also seems true for some parasites (Peters 1983). However, the relationship between host and parasite body size is more complex as large body size may lead to a greater likelihood of dislodging from the host and thus selection may rather favour parasites with an intermediate size (Poulin 2007).

Availability of food can improve the condition of an animal and facilitate resistance to parasite infections (Oppliger *et al.* 1996; Brown *et al.* 2000; Jokela *et al.* 2005). Food availability for the host also influences parasite reproduction. For example, the survival of flea eggs and larvae depends heavily on the food availability to the host on which the parent flea fed (Krasnov *et al.* 2005b). In addition, the condition of a host individual can also vary during the year depending on hormone levels. Male hosts tend to have a higher parasite infestation than females, due to the suppressing effect of testosterone on immunocompetence (Zuk and McKean 1996). Host body

condition can therefore have a strong influence on the level of parasite infestation of the individual hosts (Hawlena *et al.* 2008).

Habitat fragmentation may also influence host density, which is one of the most important factors that can facilitate the spread and distribution of parasites among the host population (Krasnov *et al.* 2002). The reason for this is that host-acquired rate for parasites may be determined by the abundance of host individuals available for parasite colonization (Morand and Poulin 1998). A high abundance of host individuals will result in horizontal parasite transmission within and between host species, and this in turn can result in a higher abundance of parasites per individual host (Krasnov *et al.* 2006a). Removal of large herbivores has been shown to result in an increase in rodent host density and a subsequent increase in total flea abundance (McCauley *et al.* 2008). In addition, studies on both endoparasites (Haukisalmi and Hentonnen 1990) and ectoparasites (Zhonglai and Yaoxing 1997; Krasnov *et al.* 2002) have also shown a positive correlation between host density and parasite burden.

1.5 Fragmentation and the influence on vector borne diseases

Changes in host diversity and species composition will have a knock-on effect on parasite abundance, diversity and ultimately on the risk of disease. Many authors have supported the hypothesis that biological diversity can cause a dilution effect with regard to the transmission of pathogens. For example, the bacterium *Borrelia burgdorferi* (cause Lyme disease) are able to infest a variety of vertebrate host species (Ostfeld and Keesing 2000; LoGuidice *et al.* 2003). Studies have shown that the incidence of this disease seems to increase with a loss in vertebrate diversity in an area (Allan *et al.* 2003). Further, rodent dynamics are strongly influenced by predators (Ostfeld and Holt 2004). Low predator density within agricultural fragmented areas can thus lead to a trophic cascade resulting in increased transmission of rodent-borne disease to humans and other vertebrates in the area (Ostfeld and Holt 2004). A recent study by Friggens and Beier (2010) recorded an increase in flea infestation with increasing anthropogenic disturbance levels. More importantly flea infestation peaked at intermediate anthropogenic disturbance (agricultural sites). High flea infestation levels may lead to a higher probability of

infection with flea borne disease in the remaining vertebrate population (Friggens and Beier 2010).

1.6 Parasite diversity of small mammals in South Africa

Several studies have recorded parasite diversity of natural occurring small mammal species in SA (Fourie *et al.* 1992, 2002; Horak *et al.* 1999, 2002; 2005; Braack *et al.* 1996; Anderson and Kok 2003). These studies were mainly descriptive and with limited sample sizes per locality. The majority of studies were conducted in the central and northern parts of the country with only recent studies done in the southern parts of the WCP (Matthee *et al.* 2007, 2010). The study by Matthee *et al.* (2007, 2010) was the first to record a diverse assemblage of ectoparasites on *R. pumilio* in the CFR. The aim was to obtain adequate parasite species representation per locality through large sample sizes. Temporal variation in abundance was also recorded for the individual ectoparasite taxa. A total of 32 ectoparasite species were recorded from *R. pumilio* in natural and fragmented localities (Matthee *et al.* 2007) while 20 species were recorded on the same rodent at the De Hoop Nature Reserve (Matthee *et al.* 2010). In the latter study, several of the ectoparasites recorded on *R. pumilio* were shared with a co-occurring rodent, *O. irroratus*. Undescribed ectoparasite species were recorded in both of the studies. Based on this it is clear that the complete diversity of ectoparasites on *R. pumilio* is yet to be recorded. It is thus expected that future studies on this host in the WCP and SA will yield additional undescribed parasite species.

1.7 *Rhabdomys pumilio* as host

Rhabdomys pumilio (Sparrman 1784) is an endemic broad-niche rodent (Muridae) that occupies a vast range of habitats in South and southern Africa (Schradin and Pillay 2005; Skinner and Chimimba 2005). This rodent feeds on large quantities of green vegetation, but their primary food source has been described as seeds (Brooks 1974; Skinner and Chimimba 2005). *Rhabdomys pumilio* uses various nest types such as burrows and above-ground grass nests (Skinner and Chimimba 2005). They are opportunistic and often use burrows and nests of other

rodent species (Schradin 2006). Studies have shown that *R. pumilio* is socially plastic with solitary and territorial living in moist grasslands and a more communal social system in arid environments such as the Kalahari (Nel 1975), Namib (Krug 2002) and the succulent Karoo (Schradin and Pillay 2005). *Rhabdomys pumilio* is able to successfully adapt to urban and agricultural environments, which emphasize the economic importance of this rodent species (De Graaf 1981; Skinner and Chimimba 2005).

Rhabdomys pumilio has a diverse assemblage of ecto- and endoparasite species (Tipton 1960; Zumpt 1961; De Meillon *et al.* 1961; Till 1963; Ledger 1980; De Graaf 1981; Horak *et al.* 1986, 2005; Howell *et al.* 1989; Segerman 1995; Horak and Boomker 1998; Petney *et al.* 2004; Matthee *et al.* 2007, 2010; Froeschke *et al.* 2010) of which several ectoparasite species can act as vectors for *Anaplasma centrale, Anaplasma marginale, Babesia caballi, Babesia canis rossi, Yersinia pestis* and the virus that cause Crimean-Congo haemorrhagic fever (CCHF) (Walker 1991; Matthee *et al.* 2007, 2010). These ectoparasites are of major medical and veterinary importance and can cause disease in both domestic animals and humans (Walker 1991; Matthee *et al.* 2007, 2010).

Using *R. pumilio* as model the study aimed to address the current lack of information on the effect of agriculturally linked habitat fragmentation on the parasite diversity and species composition of a generalist small mammal species in the CFR of the WCP in SA. The study will confirm if fragmentation has a similar effect on the natural parasite diversity as is the case for plant and vertebrate species in the CFR (Kemper *et al.* 1999; Mouton and Alblas 2002; Mangnall and Crowe 2003). Given that several of the parasite species are known vectors for various pathogens it is important to elucidate any possible risks to humans and domestic animals that occur in close proximity to fragments.

The aims of the study were to:

1) Record the relative density, average body size and body condition of *R. pumilio* and to compare the data between two habitat types, extensive natural areas and remnant fragments surrounded by agricultural activities.

2) Compare the diversity and species composition of the ectoparasite species on *R. pumilio* populations that occur in the two habitat types.

3) Record the body size (vertical length, horizontal length, head length and product of vertical- and horizontal length) of the two most abundant flea species and to compare the body size measurements of the relevant flea species between the two habitat types.

4) Determine the effect of temporal variation on the mean abundance of fleas, mites, lice and ticks on *R. pumilio* individuals that occur in a habitat fragment, surrounded by vineyards, in the winter rainfall region of the CFR.

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Chapter 2

Species description and temporal variation of the ectoparasite species associated with *Rhabdomys pumilio* in the Cape Floristic Region, Western Cape Province

2.1 Abstract

The Cape Floristic Region (CFR) in the Western Cape Province is classified as a global biodiversity hotspot due to a high plant species richness and endemism. The region also host a diverse assemblage of small mammal species of which limited information is available on the ectoparasite diversity on them. Flea, louse, mite and tick species were recorded from 310 Four-striped mouse (*Rhabdomys pumilio*) individuals trapped at 8 localities in the CFR. The first aim was to quantify the species richness, mean abundance and prevalence of ectoparasite species of a broad niche rodent, *R. pumilio*, in the CFR. Secondly, to record the temporal variation in ectoparasite abundance on *R. pumilio* individuals that occurs in a remnant renosterveld fragment surrounded by vineyards. Mice were euthanized, examined under a stereoscopic microscope and all the ectoparasites were removed. A total of 8361 individuals that consisted of 6 flea, 1 louse, 9 mite and 11 tick species were recorded. Variable patterns in mean abundance were recorded for the individual ectoparasite taxa on *R. pumilio* during the year. Mites and fleas were found to be more abundant during the cooler wet months whereas ticks and the host specific louse were more abundant during the warmer dry months. Many of the ectoparasite species recorded on *R. pumilio* is of veterinary and medical importance.

2.2 Keywords: ectoparasites, small mammals, temporal variation, rodents

2.3 Introduction

The Cape floristic Region (CFR) in the Western Cape Province (WCP) is one of the global biodiversity hotspots of the world (Cowling *et al.* 2003) and cover 87 892 km^2 of South Africa's (SA) landscape (Rouget *et al.* 2003). The biodiversity status of the CFR is as a result of a high plant species richness and endemism in a relatively small area. The region also hosts a diverse assemblage of small mammal species (Skinner and Chimimba 2005). Small mammals and particularly rodents are characterised by rapid and maintained population growth, large population sizes and short generation times. Consequently, they play an important role in maintaining ecosystems (Morand *et al.* 2006). This is evident in the CFR where rodents perform important functional roles in plant ecology. For example, several rodent species are important pollinators (Namaqua rock rat, *Micaelomys namaquensis* and the Four-striped mouse, *Rhabdomys pumilio*) for endemic plant species such as members in the family Proteaceae. In addition, rodents such as *R. pumilio* and the Cape spiny mouse, *Acomys subspinosus* are known to predate on seeds of *Leucospermum* species (Rourke and Wiens 1992; Christian and Stanton 2004).

Rodents can be divided into generalist and specialist species according to their habitat requirements and environmental tolerance range (Morris 1996). Healthy ecosystems are normally characterised by high animal diversity that include both generalist and specialist species that compete for resources (de la Penã *et al.* 2003; Krasnov *et al.* 2006; Rodríguez and Peris 2007; Manor and Saltz 2008). However, in anthropogenic transformed environments, generalist rodent species tend to out-compete the specialist species, as they are able to adapt better to these conditions (Manor and Saltz 2008). Host characteristics such as habitat use, behaviour and body size can shape parasite species assemblages and diversity of individual small mammal species within an ecosystem (Krasnov *et al.* 1997, 1998, 2006; Matthee *et al.* 2010).

Little information is available on the ectoparasite species that are naturally associated with small mammals in SA. Most studies have focused on medical and veterinary important taxa and research are biased towards parasite control studies or studies only focusing on a single parasite taxon, e.g. ticks. More than 80 of the 650 ixodid tick species of the world are found in SA (Walker 1991). The majority of studies previously done on ticks in SA were conducted in the northern and central parts of the country, all of which are summer rainfall areas (see Braack *et al.* 1996; Horak *et al.* 1999, 2002b, 2005; Anderson and Kok 2003). In addition, most of the studies used the scrub method to remove ticks. The studies were mostly descriptive and aimed to highlight host preferences and temporal patterns in mean abundances (Fourie *et al.* 1992, 2002; Horak *et al.* 1993, 1999, 2002b, 2005; Braack *et al.* 1996).

Few of the studies done in SA to date recorded the abundance and prevalence of all the ectoparasite taxa that co-occur on a host species. One such study recorded the arthropod parasites of Yellow mongoose (*Cynictis penicillata*) and found 10 ixodid tick, 2 mite, 8 flea and 1 biting louse species (Horak *et al.* 1999). Recently completed studies by Matthee *et al.* (2007, 2010) recorded diverse assemblages of ectoparasite species on *R. pumilio* for several localities in the CFR and at De Hoop Nature Reserve, WCP. These studies highlight the importance of *R. pumilio* as a host for fleas, lice, mites and ticks. In total 32 ectoparasite species were recorded from *R. pumilio* in the CFR of which 4 species have never been found before (Matthee *et al.* 2007). The study was conducted in extensive pristine natural areas and fragments surrounded by wheat fields and vineyards. *Rhabdomys pumilio* individuals at De Hoop Nature Reserve harboured 20 ectoparasite species of which several were shared with a co-occurring rodent, the Vlei-rat, *Otomys irroratus* (Matthee *et al.* 2010). The high parasite diversity on *R. pumilio* is in accordance to our expectation as this rodent is locally abundant and regionally widespread and commonly occur in natural areas as well as urban and agricultural habitats in South and southern Africa (Schradin and Pillay 2005; Skinner and Chimimba 2005).

Parasite taxa differ in terms of life history and it is important to have an understanding of the respective life histories to predict and understand species-specific response to changes in

environmental conditions. In general lice are permanent parasites and never leave the host, while fleas and mites spend part of their life on the host and the rest in the nest of the host (Matthee and Krasnov 2009). Ticks sporadically attach to the host for blood meals and spend the rest of the time in the vegetation (Walker *et al.* 1991, 2000). Local environmental and habitat variables (e.g. temperature, humidity, vegetation, soil composition) are important determinants of parasite species assemblages in a host population (Poulin 2007). For example, Krasnov *et al.* (1998) found that the flea abundance and species composition were related to the depth of the host's burrow system. Hosts that made shallow burrows had a higher relative abundance of fur fleas whereas the hosts that made deeper burrows had a higher relative abundance of nest fleas. It was suggested that shallow burrows are subjected to higher external temperature and humidity (Krasnov *et al.* 1998). Replacement of one flea species by another on the same host species between two different habitats also illustrates the partial importance of abiotic factors (air temperature, relative humidity and substrate texture) for the development of preimaginal stages of certain flea species (Segerman 1995; Krasnov *et al.* 2001).

Individual parasite taxa are expected to differ seasonally in abundance and diversity according to their relationship with the host and their specific environmental needs both on and off the host. Seasonality in macroparasite abundance, prevalence and the severity of infections has been recorded by several studies (Nelson *et al.* 2002 cited in Morand *et al.* 2006; Wright *et al.* 2009). Temporal variation of ectoparasite abundances has been shown with a number of studies in the summer rainfall (Louw *et al.* 1995; Braack *et al.* 1996; Horak *et al.* 2002b) and winter rainfall (Louw *et al.* 1993) regions of SA, and more recently also in other parts of Africa (Makundi and Kilonzo 1994; Laudisoit *et al.* 2009). These studies in general found different patterns throughout seasons for individual parasite taxa. For example, flea abundance increased on rodent hosts during the cool wet months, when temperatures were between 22°C and 26°C, but declined during the months with the highest rainfall in north-eastern Tanzania (Makundi and Kilonzo 1994).

Most of the studies done on temporal variation of ectoparasites on small mammals in SA looked at scrub hares (Horak *et al.* 1993; Louw *et al.* 1993, 1995; Anderson and Kok 2003) although a study was also done on two rodents (Red veld rats, *Aethomys chrysophilus*, and Bushveld gerbils, *Gerbilliscus leucogaster*) in the north eastern parts of SA (Braack *et al.* 1996). More recently and specifically in the CFR, a winter rainfall region, the mean abundance of mites, fleas and lice seem to be higher on *R. pumilio* during the cold wet season. In contrast, ticks were found to have a higher mean abundance during the warm dry months. *Rhabdomys pumilio* individuals were trapped over 8 nights every 3 to 4 months at 2 localities (extensive natural vegetation while the other was a habitat fragment surrounded by wheat fields) in a slightly drier part of the CFR (Closest town is Wellington, 500 mm mean annual rainfall) (Midoko-Iponga 2004). The localities were in close proximity to one another and due to low rodent densities, during austral winter (June) and spring (September), it was decided to pool the data and to analyses the seasonal data as one locality (Matthee *et al.* 2007). Given the later it is uncertain how the temporal pattern will differ between extensive natural vegetation and fragmented habitats.

The aims of the study were two-fold:

1. Quantify species richness, mean abundance and prevalence of ectoparasite species of a broad niche rodent species in the CFR of the WCP.
2. Record temporal variation in mean abundance of fleas, lice, mites and ticks on *R. pumilio* within a remnant fynbos/renosterveld fragment, surrounded by vineyards, in the winter rainfall region of the WCP.

It is expected that the data will contribute information to existing ectoparasite species lists on rodents and specifically *R. pumilio* in the WCP. The temporal pattern recorded in the present study will also be compared with the study by Matthee *et al.* (2007) to see if variation in rainfall and differences in habitat use (wheat fields/natural vegetation versus vineyards) have an effect on the temporal variation of ectoparasite taxa. Knowledge regarding the temporal variation in parasite abundance on small mammals in the CFR will enable predictions with regard to the

seasonal pattern in disease risk for vector borne diseases such as tick bite fever in dogs, transmitted by the tick *Haemaphysalis elliptica*.

2.4 Materials and Methods

Host species

Rhabdomys pumilio is a small size diurnal murid rodent species (45.12 ± 1g) known to feed on large quantities of green vegetation, but their primary food source has been described as seeds (Brooks 1974; Skinner and Chimimba 2005). In addition, *R. pumilio* is able to successfully adapt to urban and agricultural environments, which emphasize the economic importance of this rodent species (De Graaf 1981; Skinner and Chimimba 2005). The social structure of *R. pumilio* has not been studied in the CFR; however the low shrub-like vegetation in the region is similar to the succulent Karoo (Mucina and Rutherford 2006) where the species form communal social systems. The group home range size is on average 1300 m^2 for males and females in the succulent Karoo (Schradin 2004, 2006). Males spend most of their day patrolling the territory and females spend more time on foraging (Schradin 2006).

The species breeds in spring, summer and autumn (September to April) in the CFR and there is a clear seasonal cycle. During the non-breeding winter months the population numbers decrease (David and Jarvis 1985). The CFR region has a high diversity of small mammal species (Skinner and Chimimba 2005) of which several species often co-occur with *R. pumilio* (Matthee unpublished data). For example, *O. irroratus* is often trapped at the same sites.

Study areas

For the study, *R. pumilio* individuals were trapped at 8 localities in the CFR, WCP during 2009 (Table 1). This region consists of a Mediterranean-type climate characterized by dry summers and wet winters (Midgley *et al.* 2003). The sample design included paired trapping at 4 natural sites and 4 habitat fragments that were surrounded by agricultural activities (vineyards or wheat fields). Two natural areas and 2 fragments that formed part of the previous study by Matthee *et al*. (2007) were resampled. The localities were all below 400 m above sea level and less than 200 km apart. The vegetation type mainly consisted of lowland fynbos/renosterveld (Mucina and Rutherford 2006). Habitat fragments consisted of remnant lowland fynbos/renosterveld fragments located within agricultural areas. A seasonal study was done on one of the fragments, Mulderbosch wine farm outside Stellenbosch. The mean monthly rainfall was 50 mm, with the wettest months being June to August and December to February the driest months. Mean annual rainfall recorded at Nietvoorbij, the closets weather station, was 856.36 mm (± 36.04) from 2005 to 2009. Climate data was provided by the weather service of Stellenbosch University and the Agricultural research council.

Rodent trapping

Rhabdomys pumilio individuals were trapped using Sherman-like live traps that were baited with a mixture of peanut butter and oats. The number of traps used per locality ranged from 100 to 200. Rodent trapping followed two designs where 22 to 30 *R. pumilio* individuals were trapped once at each of the 8 localities during austral spring and summer (October to December 2009) and secondly, 30 *R. pumilio* individuals were trapped every 3 months (February, May, August and November) in 2009 as part of a seasonal study at a single locality, Mulderbosch, in Stellenbosch (Table 1). Although it was initially the aim to catch 30 individuals at each site with each trapping period, this was not possible due to low rodent abundance at certain localities.

Only *R. pumilio* individuals were removed and all other rodents were identified and released at the specific site. The traps were checked twice daily. In an attempt to limit trap related deaths as a result of environmental exposure the traps were closed in the day during summer and again at night during winter. *Rhabdomys pumilio* individuals were euthanized with 2-4 ml Sodium Pentobarbitone (200 mg/kg) depending on individual weights. Each mouse was placed in a separate premarked plastic bag with a reference number. The rodents were frozen at -20°C and examined a few weeks later. The body weight (gram) and measurements (millimeter) of the hind foot, tail and total length of each rodent were recorded following parasite removal (see methods below). Trapping and handling of rodents were approved by the Ethical Committee of Stellenbosch University and the Western Cape Nature Conservation Board (Ethics nr: 2006B01007; Cape Nature permit nr: AAA004-00221-0035).

Table 1: Locality information and number of *Rhabdomys pumilio* (n = 310) examined in the Cape Floristic Region, Western Cape Province during 2009.

Locality	GPS	Size (km^2)	No. of sites	Sample size	Date Sampled
Natural areas					
Jonkershoek	33.98798 S, 18.95541 E	18.04	4	30	27-Oct
Elandskloof	34.08151 S, 18.55112 E	5.86	3	30	17-Nov
Wolwedans	33.55021 S, 18.46303 E	3.45	2	22	03-Dec
Voelvleidam	34.67125 S, 19.87806 E	8.13	3	30	06-Oct
Remnant fragments					
Zevenwacht	33.91749 S, 18.73224 E	1.1	3	29	03-Nov
Vergelegen	34.03580 S, 18.54208 E	0.21	4	23	29-Sep
Mulderbosch	33.53374 S, 18.48514 E	0.14	6	120* (34, 31, 27, 28)	Feb, May, Aug, Nov
Waterval Farm	32.59151 S, 19.01287 E	0.1	3	26	06-Oct

＊ Total number of individuals caught during February, May, August and November for the seasonal study at Mulderbosch.

Laboratory procedures

The frozen rodents were removed from the freezer the night before the animals were to be examined. Each animal was removed from the premarked plastic bag after which the bag was first systematically examined under a stereoscopic microscope. After this, the entire animal was

systematically examined under the stereoscopic microscope and all the fleas, lice, mites and ticks placed separately into specimen tubes, filled with 70 % ethanol and labeled with the relevant reference number. The ticks and mites were sent to expert taxonomists (Ivan Horak and Eddie Ueckermann) for identification, while the fleas and lice were kept for self identification. Fleas were mounted by the technique described in Segerman (1995). Lice were mounted in a polyvinyl alcohol solution (PVA). Lice were placed in the middle of a microscope slide and were firstly cleared with a drop of 85 % lactic acid over a flame till transparent. The specimen was then orientated dorso-ventrally in a drop of PVA and the cover slip was then slowly lowered onto the specimen. Identification of fleas and lice was done using a Leica DM 3000 light microscope and the morphological key of Segerman (1995) and Ledger (1980) and Johnson (1960), respectively. Following all the above, the carcasses were frozen for future reference.

Data analysis

Descriptive data analyses that included mean abundance, total counts, standard errors, standard deviations and total abundances were calculated in Microsoft Excel 2007. Species accumulation curves for each locality, trapped during spring/summer trap session, were drawn using abundance data calculated with the EstimateS 8.2 computer program (Colwell 2009) and by selecting one hundred randomizations with replacement (Gotelli and Colwell 2001). Temporal variaition data were analyzed in Statistica 9. A non-parametric Kruskal-Wallis test was used to calculate p values. Then, a post hoc test was run in which multiple comparisons of mean ranks for all groups were performed.

2.5 Results

Ectoparasite species accumulation curves for the combined data (all 8 localities) and for most of the individual localities, reached asymptotes (Figures 1, 2 and 3; Appendix 1: Figures 1 to 6). Ectoparasite species accumulation curves of the fragments (Figure 2) reached their asymptotes sooner than those of the natural (Figure 3) areas (also see Appendix 1: Figures 1 to 6). Jonkershoek Nature Reserve is an example of a locality that still showed a slight increase in the mean number of ectoparasite species found with increasing sampling effort (Figure 3).
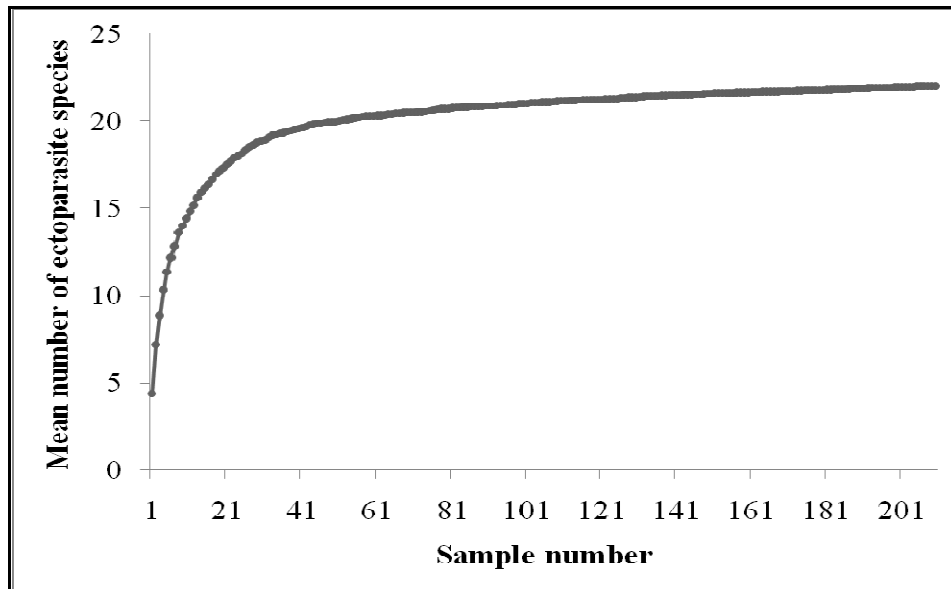
Figure 1: Species accumulation (mean ± S.E) (27.15 ± 2.29) curve of the ectoparasite species found on *Rhabdomys pumilio* (n = 217) sampled at 8 localities in the Cape Floristic Region, South Africa, October to December 2009. Resampling statistics using sample with replacement and 100 randomisations (Gotelli and Colwell 2001).
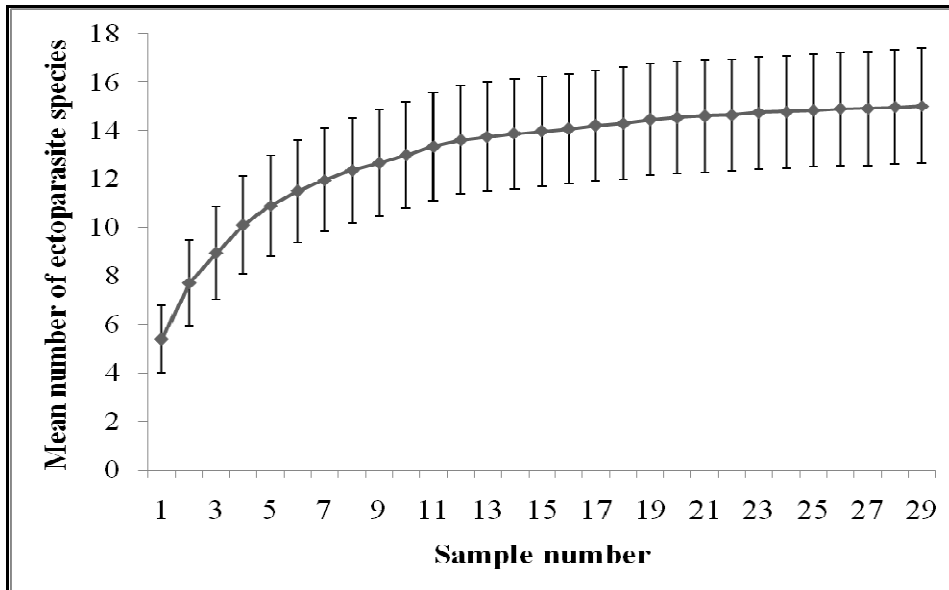
Figure 2: Species accumulation curve (mean ± S.E) (53.52 ± 12.61) of the ectoparasite species found on *Rhabdomys pumilio* (n = 29) sampled at Zevenwacht in the Cape Floristic Region, South Africa, October to December 2009. Resampling statistics using sample with replacement and 100 randomisations (Gotelli and Colwell 2001).
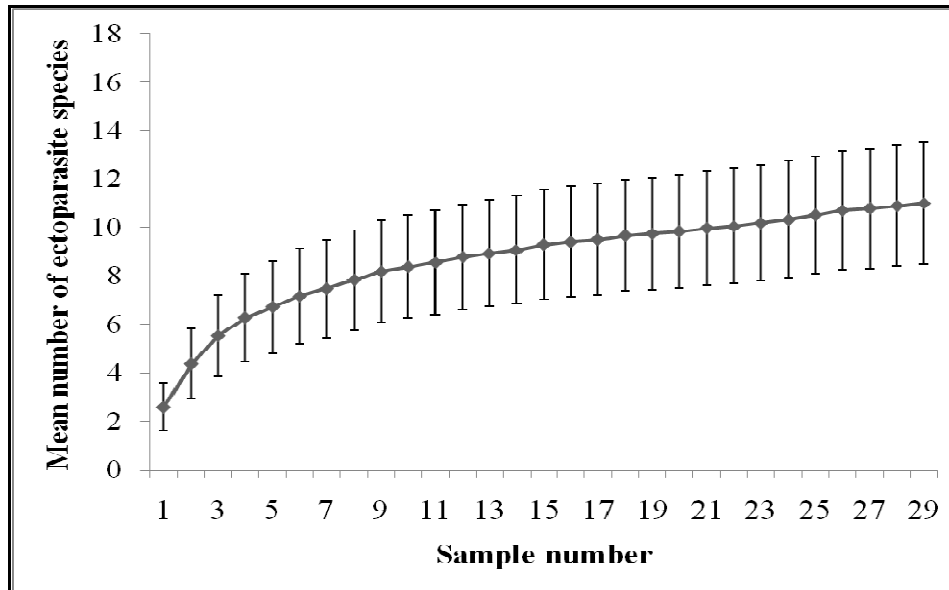
Figure 3: Species accumulation curve (mean ± S.E) (23.3 ± 4.77) of the ectoparasite species found on *Rhabdomys pumilio* (n = 30) sampled at Jonkershoek Nature Reserve in the Cape Floristic Region, South Africa, October to December 2009. Resampling statistics using sample with replacement and 100 randomisations (Gotelli and Colwell 2001).

A total of 310 mice were trapped of which 172 were males and 138 females. Seventy six percent (236) of the mice were reproductively active while the rest (74) were not reproductively active. Twenty six ectoparasite species (representing 13 genera) were recorded on *R. pumilio* (Table 2). Ectoparasites consisted of 11 tick, 9 mite, 6 flea and 1 louse species (Table 3). Total ectoparasite abundance was 8361 of which ticks represented 41.79 %, followed by lice (34.91 %), mites (15.06 %) and fleas (8.24 %). Ticks were the most prevalent and occurred on 77.1 % of the mice, followed by mites (73.23 %), fleas (64.52 %) and lice (56.13 %) (Table 3).

Table 2: Ectoparasite species recorded from *Rhabdomys pumilio* (n = 310) in the Cape Floristic Region in the Western Cape Province, South Africa, during 2009.

	Order	Suborder	Family/subfamily	Species
Fleas	Siphonaptera		Chimaeropsyllidae	
			Chiastopsyllinae	*Chiastopsylla rossi* (Waterson 1909)
			Chimaeropsyllinae	*Hypsopthalmus temporis* (De Meilon 1940)
			Ctenopthalmidae	
			Dinopsyllinae	*Dinopsyllus ellobius* (Rothschild 1905)
				D. tenax (Jordan 1930)
			Hystrichopsyllidae	
			Listropsyllinae	*Listropsylla agrippinae* (Rothschild 1904)
			Pulicidae	
			Xenopsyllinae	*Xenopsylla demeilloni* (Haesalbarth 1964)
Louse	Phthiraptera	Anoplura	Polyplacidae	*Polyplax arvicanthis* (Bedford 1919)
Mites	Parasitiformes	Mesostigmata	Laelaptidae	
			Laelaptinae	*Androlaelaps dasymys* (Radford 1939)
				A. fahrenholzi (Berlese 1911)
				A. rhabdomysi (Matthee and Ueckermann 2007)
				Laelaps sp.
				Laelaps giganteus (Berlese 1918)
			Macronyssidae	*Ornithonyssus bacoti* (Hirst 1913)
			Trombiculidae	Uncertain genus
		Astigmata	Atopomelidae	*Listrophoroides womersleyi* (Zumpt 1961)
Ticks	Parasitiformes	Ixodida	Ixodidae	
			Amblyomminae	
			Haemaphysalinae	*Haemaphysalis aciculifer* (Warburton 1913)
				H. elliptica (Koch 1844)
			Ixodinae	*Ixodes alluadi* (Neumann 1913)
				I. bakeri (Arthur and Clifford 1961)
				I. fynbosensis (Apanaskevich, Horak, Matthee and Matthee 2010)
				Ixodes sp.
			Rhipicephalinae	*Rhipicephalus capensis* (Koch 1844)
				R. follis (Dönitz 1910)
				R. gertrudae
				R. lounsburyi (Walker 1990)
				R. simus (Koch 1844)

Six flea species representing 5 genera were recorded on *R. pumilio* (Table 3). *Chiastopsylla rossi* was the most numerous, 1.10 (mean) (± 0.10 (se)) and prevalent (38.39 %) flea species followed by *Listropsylla agrippinae* with a mean abundance of 0.75 (± 0.08) and found on approximately a third of the mice (35.48 %). The lowest mean abundance was recorded for *Xenopsylla demeiloni* of which only a single specimen was found at 1 locality (Zevenwacht). Flea species in general consisted of mostly females and were prevalent on more than half (64.52 %) of the *R. pumilio* individuals. *Dinopsylla tenax* had almost double the amount of males to females while almost 4 times more *Hysopthalmus temporis* females were found than males (Table 3).

Only a single louse species, *Polyplax arvicanthis*, was recovered from *R. pumilio*. The mean abundance (9.42 ± 1.33) of the louse was the highest of all the ectoparasite species and it was present on more than half of the mice that were trapped (56.13 %). Only total counts were recorded for the louse.

Nine mite species belonging to at least 4 genera were recovered. An unknown *Trombiculidae* species was recorded on 50 % of *R. pumilio* individuals. The mite, *Androlaelaps fahrenholzi*, was the most abundant species (1.97 ± 0.14) and was present on approximately 50 % of the mice. *Laelaps giganteus* was the second most abundant mite (1.54 ± 0.19) and present on 38.39 % of the mice (Table 3). Both nymph and adult stages of the mites were recorded on *R. pumilio*. Three unknown *Laelaps* species were also found, consisting of mostly adult stages. *Laelaps* sp. 1 was found at Wolwedans, *Laelaps* sp. 2 at Voëlvleidam and *Laelaps* sp. 3 at Elandskloof, Voëlvleidam and Zevenwacht. Female biased-sex ratios were recorded for the adult mites (Table 3).

Eight tick species were recorded on *R. pumilio* (Table 3). The 3 genera were *Haemaphysalis*, *Ixodes* and *Rhipicephalus.* The ticks of the *Rhipicephalus gertrudae* group were the most prevalent (50.3 %) and had the highest mean (7.03 ± 1.51) and total abundances (2179) (Table 3). *Haemaphysalis elliptica* and *Ixodes fynbosensis* were the second and third most abundant tick

species with mean abundances of 1.58 (± 0.32) and 1.29 (± 0.28), respectively. Four specimens of an unknown *Ixodes* species were found at Voëlvleidam and Elandskloof. Most of the ticks that were collected were immature stages (larvae and nymphs). However, adult stages were recorded on *R. pumilio* for some species, *I. alluaudi, I. bakeri, H. elliptica* and *R. lounsburyi* (Table 3). Adult females were the predominant sex.

Table 3: Ectoparasite species proportions recovered from *Rhabdomys pumilio* (n = 310) in the Cape Floristic Region, South Africa, October to December 2009.

Ectoparasite species	Mean abundance (±SE)	Total abundance	Larvae (%)	Nymphs (%)	Adult (%)	Sex ratio (m:f)	Prevalence (%)
Fleas	**2.22 (±0.16)**	**689**			**100**	**1:1.15**	**64.52**
Chiastopsylla rossi	1.10 (±0.10)	290			100	1:1.67	38.39
Dinopsyllus ellobius	0.11 (±0.03)	33			100	1:1.06	7.10
Dinopsyllus tenax	0.17 (±0.04)	52			100	1:0.58	10.65
Hysopthalmus temporis	0.2 (±0.03)	61			100	1:3.36	12.90
Listropsylla agrippinae	0.75 (±0.08)	232			100	1:1.32	35.48
Xenopsylla demeilloni	0.003 (±0.003)	1			100	1:0	0.32
Louse	**9.42 (±1.33)**	**2919**					**56.13**
Polyplax arvicanthis	9.42 (±1.33)	2919					56.13
Mites	**4.06 (±0.28)**	**1259**		**8.18**	**91.82**	**1:15.28**	**73.23**
Androlaelaps fahrenholzi	1.97 (±0.14)	612		78.27	21.73	1:12.22	56.77
Androlaelaps dasymys	0.2 (±0.04)	63		44.44	55.56	1:6	13.55
Androlaelaps rhabdomysi	0.04 (±0.02)	11		33.33	66.67	1:7	1.61
Laelaps sp 1	0.04 (±0.02)	12		0	100	0:12	1.61
Laelaps sp 2	0.06 (±0.02)	19		5.26	94.74	0:18	3.87
Laelaps sp 3	0.11 (±0.03)	33		3.03	96.97	0:32	6.13
Laelaps giganteus	1.54 (±0.19)	478		0	100	1:22.9	38.39
Ornithonyssus bacoti	0.01 (±0.01)	3		0	100	0:3	0.97
Trombiculidae sp.			100				50.17
Ticks	**11.27 (±1.68)**	**3494**	**86.72**	**14**	**0.92**	**0:24**	**77.1**
Haemaphysalis aciculifer	0.19 (±0.05)	59	86.44	13.56	0	0	7.74
Haemaphysalis elliptica	1.58 (±0.32)	491	89.41	10.39	0.20	0:1	35.81
Ixodes fynbosensis	1.29 (±0.28)	401	74.31	25.69	0	0	21.61
Ixodes alluaudi	0.04 (±0.01)	11	18.18	9.09	72.73	0:8	3.55
Ixodes bakeri	1.05 (±0.16)	326	52.45	42.64	4.91	0:16	28.39
Ixodes sp	0.01(±0.01)	4	25	75	0	0	1.29
Rhipicephalus gertrudae group*	7.03 (±1.51)	2179	93.12	6.88	0	0	50.32
Rhipicephalus lounsburyi	0.09 (±0.04)	80	48.75	42.50	8.75	0:7	9.68

*Consists of immature stages of 5 different species which could not be distinguished, namely *R.gertrudae*, *R. follis*, *R. capensis*, *R. simus* and *R. lounsburyi*

Rank abundance graphs of the flea, mite and tick taxa show low evenness with two or three species dominating in each taxon (Figures 4 to 6). *Chiastopsylla rossi* and *L. agrippinae* dominated the flea community, *A. fahrenholzi* and *L. giganteus* dominated the mite community and the *R. gertrudae* group, *H. elliptica*, *I. fynbosensis* and *I. bakeri* dominated the tick community (Figures 4 to 6). The overall relative abundance of the louse was the highest followed by the ticks, *R. gertrudae* group and mite, *A. fahrenholzi* (Figure 7).
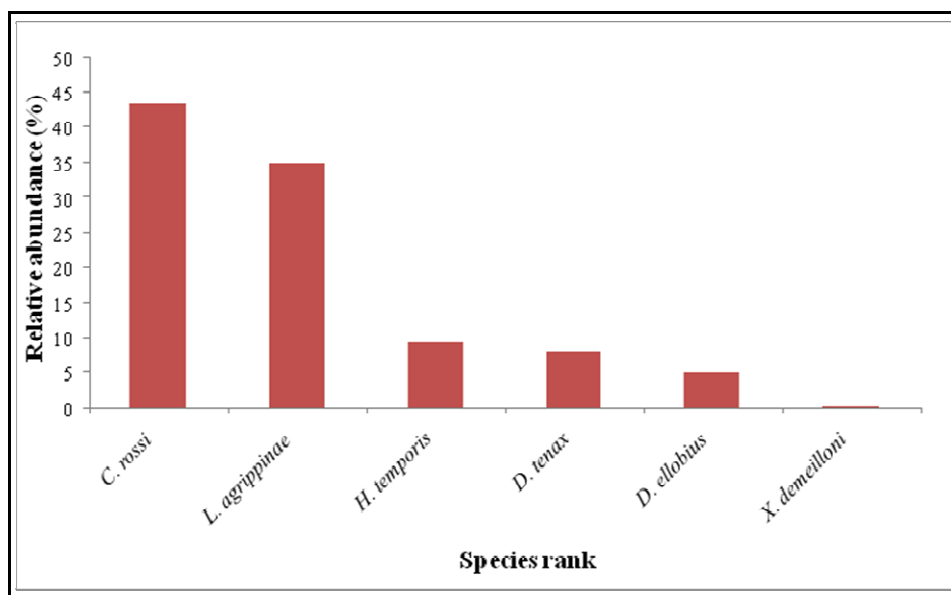
Figure 4: Rank abundance distribution of flea species recovered from *Rhabdomys pumilio* (n = 310) in the Cape Floristic Region in the Western Cape Province, South Africa, October to December 2009.
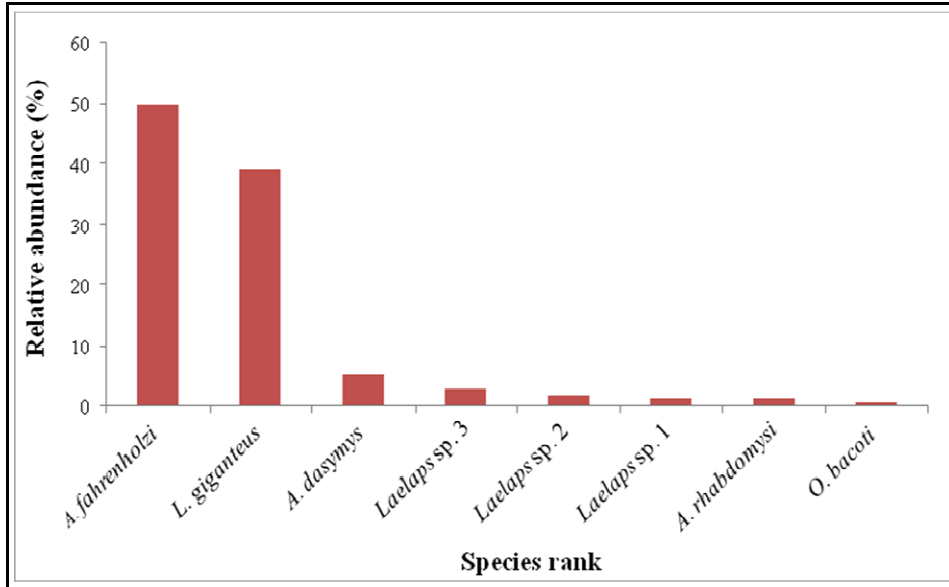
Figure 5: Rank abundance graph of mite species recovered from *Rhabdomys pumilio* (n = 310) in the Cape Floristic Region, South Africa, October to December 2009.
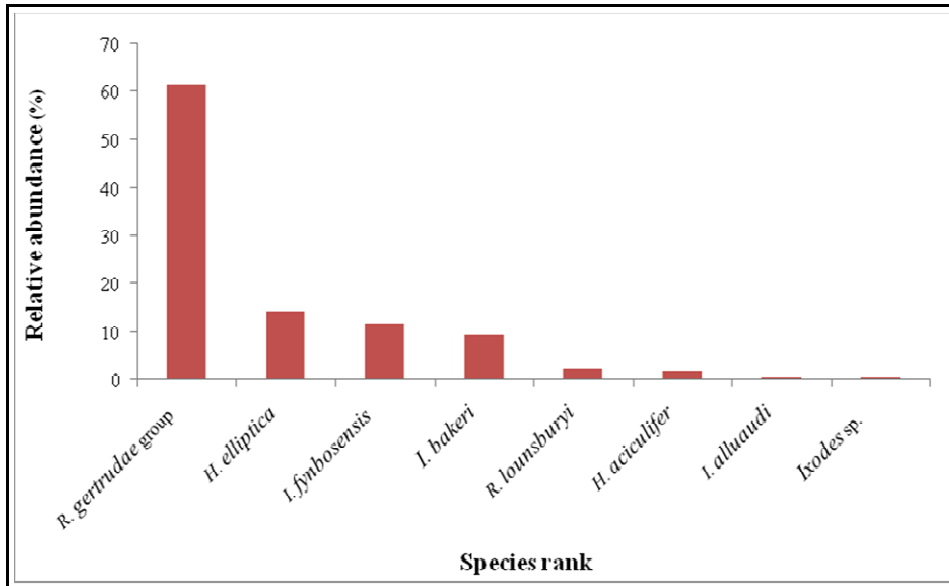
Figure 6: Rank abundance graph of tick species recovered from *Rhabdomys pumilio* (n = 310) in the Cape Floristic Region, South Africa, October to December 2009.
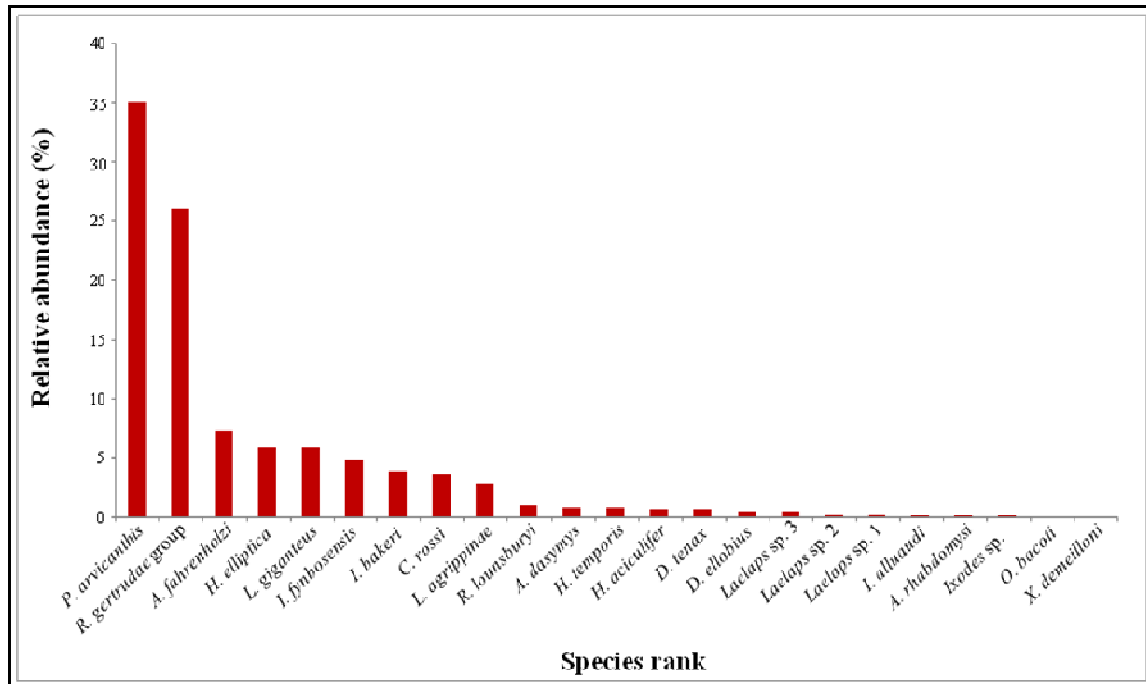
Figure 7: Rank abundance distribution of all ectoparasite species recovered from *Rhabdomys pumilio* (n = 310) in the Cape Floristic Region in the Western Cape Province, South Africa, October to December 2009.

Temporal variation

The CFR is situated in a winter rainfall region and the highest rainfall was recorded during the months of May, June and July (Figures 8). Mean abundances for the 4 ectoparasite taxa were variable on *R. pumilio* during the year. The level of infestation was the highest for ticks during the warmer and dryer summer months (February and November) (Figures 8 to 10). Significant differences were found between tick abundance of February and August ($p < 0.05$), February and November ($p < 0.01$), and May and November ($p < 0.01$). Mite infestations seem to increase during autumn (February and May) (Figures 8 to 10). Significant differences were found between mite abundance of February and May ($p < 0.01$), and between May and November ($p < 0.05$). Lice infestations peaked in spring (August and November) with significant differences between February and August ($p < 0.01$), February and November ($p < 0.01$), May and August ($p < 0.01$), and between May and November ($p < 0.01$). (Figures 8 to 10) No distinct seasonal pattern was observed for fleas, but significant differences in flea abundance were found for February and May ($p < 0.01$), and between May and August ($p < 0.01$) (Figures 8 to 10).
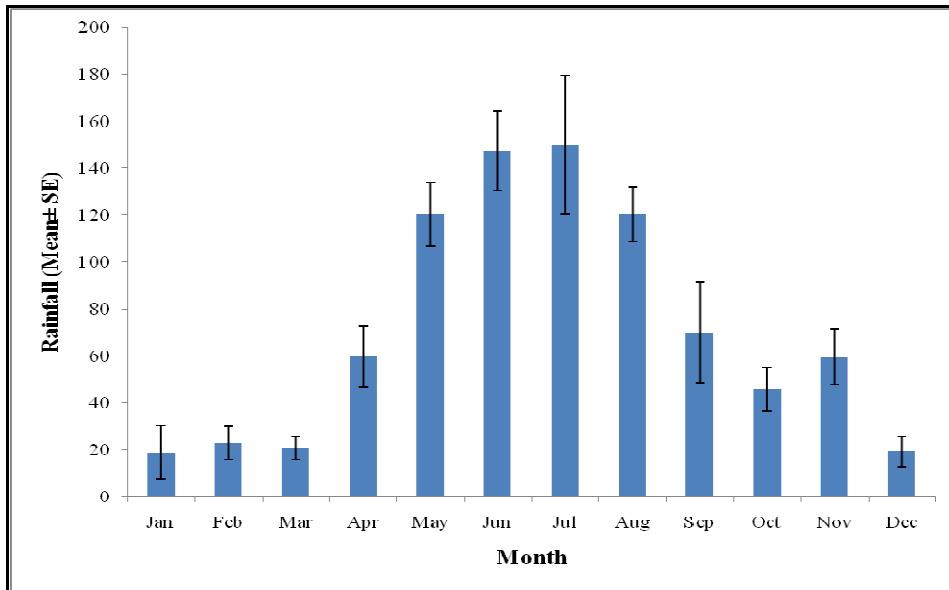
Figure 8: Mean monthly rainfall at Nietvoorbij Stellenbosch, Cape Floristic Region, South Africa for 2005 to 2009. Standard errors are included.
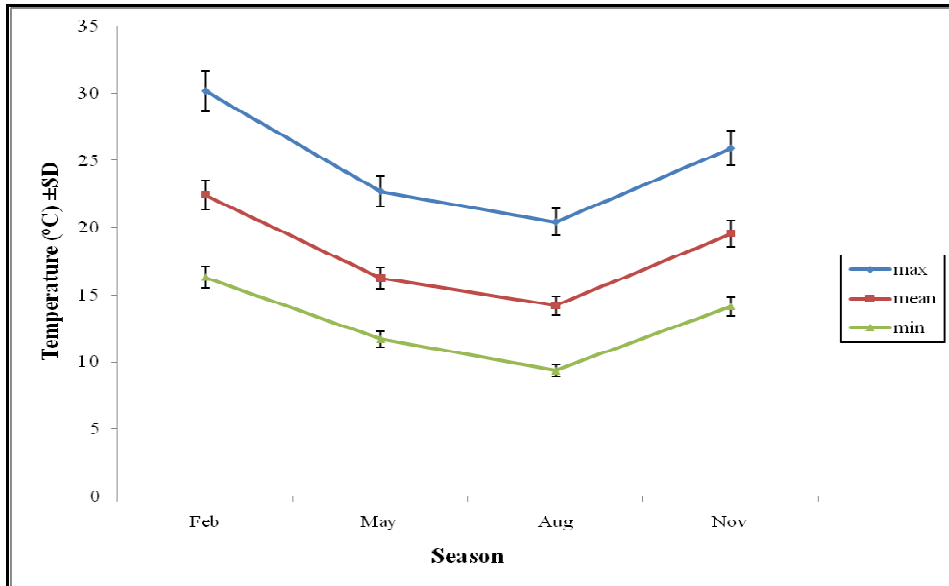
Figure 9: Temperatures (mean, max and min) over four sampling periods at Stellenbosch in the Cape Floristic Region, South Africa for the year 2009. Temperatures showed with 5 % standard deviation value error bars.
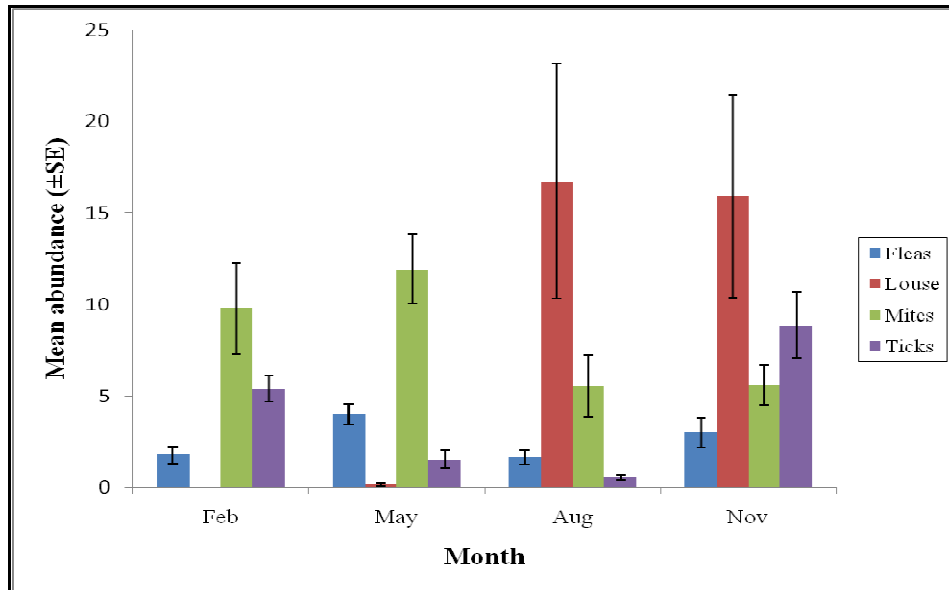
Figure 10: Temporal variation of fleas, louse, mites and ticks collected from *R. pumilio* (n = 120) at Stellenbosch, Cape Floristic Region, South Africa, in 2009. Mean abundance for each ectoparasite taxon is expressed as the total number of individuals of a particular taxon collected in a sampling month divided by the total number of mice recorded for the month. Standard errors are included.

The temporal patterns in mean abundance are more distinct when looking at the most abundant mite and flea species. The flea *C. rossi* and mite *A. fahrenholzi* showed a similar infestation pattern, with both species more common on *R. pumilio* during May (Figure 11a and c). *Chiastopsylla rossi* was significantly more abundant in May compared to February ($p < 0.01$), August ($p < 0.01$) and November ($p < 0.01$). *Androlaelaps fahrenholzi* was significantly more abundant in May compared to February ($p < 0.01$), but more abundant than in August and November, although not significant (Figure 11a and c). The tick, *H. elliptica*, was the most abundant during February and November which was the warmer, dryer months of the year (Figure 11 d). *Haemaphysalis elliptica* was significantly more abundant in February and November compred to the other two months ($p < 0.05$) (Figure 11 d). The counts for *H. elliptica* were high to extraordinary high (20, 31 and 95) on 3 of the female *R. pumilio* individuals that

were trapped in May at Mulderbosch. The counts were omitted from the temporal variation data analyses for the tick.
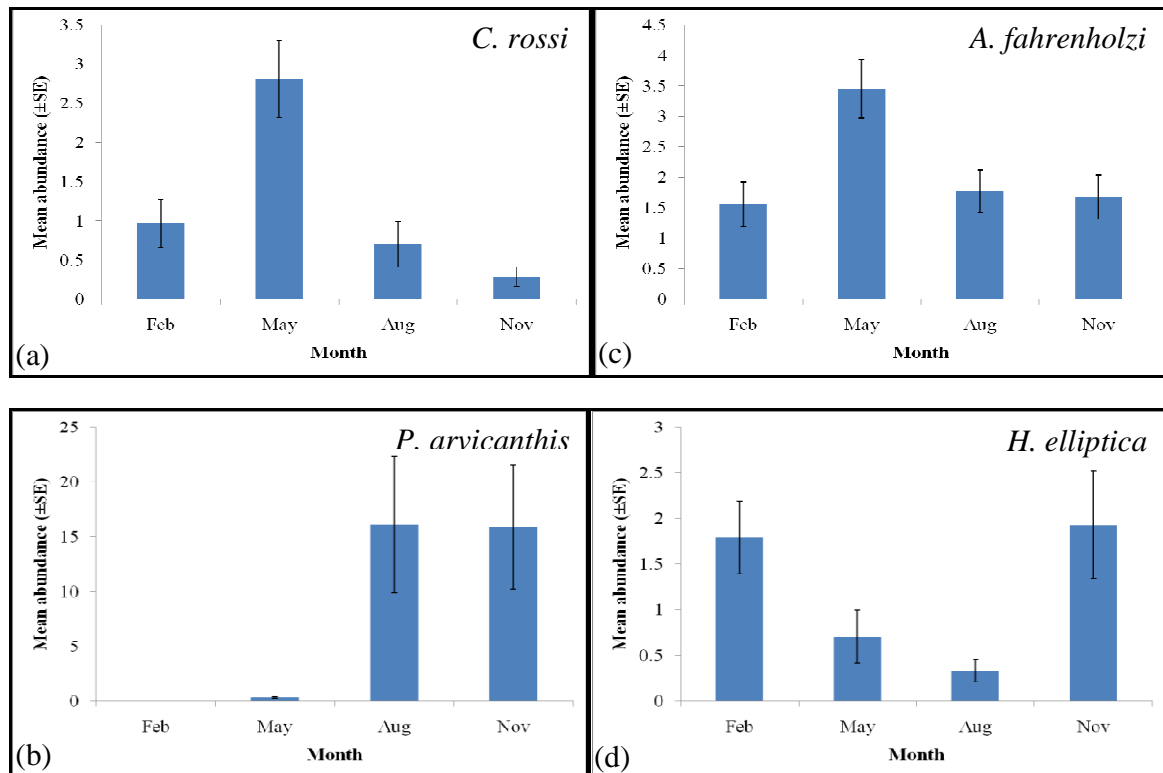
Figure 11: Temporal variation of the most abundant species within each of the four ectoparasite taxa recovered from *R. pumilio* (n = 120) at Stellenbosch, Cape Floristic Region, South Africa, in 2009. (a) flea, *Chiastopsylla rossi*, (b) louse, *Polyplax arvicanthis*, (c) mite, *Androlaelaps fahrenholzi* and (d) tick, *Haemaphysalis elliptica*. (*three outliers omitted from the analysis).

2.6 Discussion

The current study yielded a high ectoparasite species richness and diversity on a broad niche rodent species in the CFR of the WCP. Several new undescribed species and new locality records were recorded in the present study. This highlights the fact that the full extent of the ectoparasite diversity on *R.pumilio* in the CFR and SA is yet to be uncovered and that future studies in different habitat types might yield novel results. Based on limited and generally outdated host-parasite species lists it is suggested that future studies on generalist rodent species will also yield original data. This study also provided the first record of *X. demeilloni* on *R. pumilio* (Segerman 1995) albeit accidental. Novel data are provided on the prevalence of trombiculid (chigger) larvae on *R. pumilio* in the WCP and SA. This is also the first record where all the life stages of the tick *R. lounsburyi* occur on *R. pumilio* in the WCP and SA. Based on previous studies, *R. pumilio* can act as host for a large diversity of ectoparasite species (Matthee *et al.* 2007). A large sampling effort is therefore essential to record a representative number of parasite species. Species accumulation curves showed that sampling was adequate and largely representative for the region and the majority of individual localities. Most of the ectoparasites found on *R. pumilio* are important vectors for various pathogens and the current study provides an update to existing ectoparasite species lists of the CFR and the rest of SA.

Few studies have been done on the ectoparasite assemblages of small mammals in the WCP. The potential therefore exist to find new species, locality and host records with additional studies. This is evident from both the present study and the studies by Matthee *et al.* (2007, 2010). Studies in the WCP have focussed on flea and lice species of the scrub hare (*Lepus saxatilis*) at Bontebok National Park (Louw *et al.* 1993). Low ectoparasite species richness was found which may be attributed to the low host sample number (Louw *et al.* 1993). More recently a study recorded the ectoparasite diversity and temporal variation on *R. pumilio* at several inland localities in the CFR of the WCP (Matthee *et al.* 2007), while a second compared the ectoparasite diversity between *R. pumilio* and a co-occuring rodent species, *O. irroratus*, at one locality at the coast in the CFR (Matthee *et al.* 2010). Similar to the study by Matthee *et al.*

(2007, 2010) ticks were the most abundant and prevalent taxon on *R. pumilio* in the present study with the louse, *P. arvicanthis*, as the most abundant ectoparasite species.

Sex biased parasitism, on the host, is a common phenomenon for several parasite taxa (Cook and Beer 1955; Askew 1971; Marshall 1981). Previous studies on small mammals in South Africa also recorded on-host female bias sex ratios for fleas, lice, mites and some adult ticks (Horak and Fourie 1986; Louw *et al*. 1993, 1995; Matthee *et al.* 2007, 2010). The underlying reason for sex biased parasitism has been attributed to the difference in size, physiology and behaviour between male and female parasites (Marshall 1981; Krasnov *et al.* 2002, 2005). These factors change the way in which different sexes respond to different environmental variables and affects their distribution among habitats and hosts. Similar to previous studies the sex ratios of flea species found in the present study were female biased (Krasnov *et al.* 2005; Matthee *et al.* 2007). For example, *H. temporis* females were 4 times more abundant than males. Female bias for mites and ticks were also found in accordance with previous studies on *R. pumilio* (Matthee *et al.* 2007, 2010).

The flea taxon recorded in the present study was the most diverse in terms of the number of genera recorded on *R. pumilio*. Five flea genera that included 6 species were recorded. This is slightly fewer than the 8 species recorded previously on *R. pumilio* in the CFR (Matthee *et al*. 2007). All of the flea species found in the current study has the potential to act as vectors of *Yersinia pestis*, the plaque bacterium (De Meillon *et al.* 1961). *Yersinia pestis* has also been isolated from wild hosts, including *R. pumilio* (De Meillon *et al.* 1961; Sheperd 1983; Sheperd *et al*. 1983). Very little is known about the potential of South African flea species to act as intermediate hosts of cestodes and filarial worms (Matthee *et al.* 2007).

In general the fleas in the present study were much more prevalent (64.52 %) on *R. pumilio* compared to the study by Matthee *et al.* (2007) where the flea prevalence was recorded as 46.70 %. It appears that this pattern is mainly driven by a higher prevalence for the two most abundant

fleas, *C. rossi* and *L. agrippinae*, while *D. ellobius* and *D. tenax* also displayed the same pattern. The most abundant flea in the present study, *C. rossi*, occurs throughout SA and share a large number of morphological features with a congeneric species, *C. numae* (Segerman 1995). Matthee *et al.* (2007) recorded both species on *R. pumilio* in the CFR. The two species differ with respect to the extent of host preference and geographical range. *Chiastopsylla rossi* has a much broader host preference and a wide geographical range compared to *C. numae*. For the former, the preferred host species are listed as the Highveld gerbil (*Gerbilliscus brantsii*), *O. irroratis* and *R. pumilio*. *Chaistopsylla rossi* has been experimentally tested to be able to transmit plaque (Ingram 1927).

Listropsylla agrippinae, the second most abundant flea in the current study and in the study by Matthee *et al.* (2007), also has a wide distribution throughout SA and it seems that the distribution of this species is not influenced by climatic factors (Segerman 1995). The principle hosts for *L. agrippinae* include *R. pumilio* and the Karoo rat (*Otomys unisulcatus*) (Segerman 1995). Both rodent species make above ground nests (Skinner and Chimimba 2005). This confirms previous observation that *L. agrippinae* is normally found on rodents with surface nests (Segerman 1995). The close association of this flea with the *R. pumilio* and *O. irroratus* was confirmed in a recent study conducted at De Hoop Nature Reserve in the WCP (Matthee *et al.* 2010). Interestingly, *L. agrippinae* seems to be replaced by a congeneric species, *L. dorripae*, on burrowing rodent species such as gerbils (*Gerbilliscus brantsii* and *G. leucogaster*) (Segerman 1995).

The genus *Dinopsyllus* was represented by two species, *D. tenax* and *D. ellobius*. *Dinopsyllus ellobius* is the most common and widespread species in the genus and it is found mainly in the moist grassland regions of SA and the coastal belt of the Western Cape (Segerman 1995). This flea is a common body and nest flea and has been recovered from a range of host species that include gerbils (*Gerbilliscus* spp.), *O. irroratus*, the Multimate mouse (*Praomys natalensis*) and *R. pumilio* (Segerman 1995). *Dinopsylla tenax* is less common compared to *D. ellobius* and is strictly found in the winter rainfall areas of the WCP (Segerman 1995). Both species were

recorded in the present study and by Matthee *et al.* (2007), but only *D. tenax* were recorded on *R. pumilio* at De Hoop Nature Reserve (Matthee *et al.* 2010). *Dinopsylla tenax* also has a range of rodent hosts namely, *O. unisulcatus*, *O. irroratus* and *R. pumilio* but it mainly occurs in their nests (Segerman 1995). *Dinopsylla ellobius* have been experimentally tested to transmit plaque (Ingram 1927).

Hypsophthalmus temporis appears to be fairly widespread throughout SA, although few records of the species exist (Segerman 1995). *Rhabdomys pumilio* and *O. irroratus* are the principle hosts of this flea species (Segerman 1995). Similar to the present study this flea was the third most abundant flea species on *R. pumilio* in the CFR and at De Hoop Nature Reserve (Matthee *et al.* 2007, 2010). The flea, *X. demeilloni*, has a restricted distribution with the only records along the west coast of SA (Segerman 1995). The main host species is the Hairy-footed gerbil, *Gerbillurus paeba*, which makes underground nests (Skinner and Chimimba 2005). In addition, the flea has also been recorded on another burrowing rodent, the Cape gerbil, *Gerbilliscus afra* (Segerman 1995). It seems that *X. demeilloni* has a preference for rodents that makes use of burrows and occurs on the western parts of southern Africa. This probably explains the low infestation (a single specimen) of this species on *R. pumlio*. The current study provides the first record of *X. demeilloni* on *R. pumilio* and the southern most locality record (Segerman 1995). Many species of the *Xenopsylla* genus are known to transmit plague, although no information exists on the potential of *X. demeilloni* (Segerman 1995).

The anoplurid louse *P. arvicanthis* was the most abundant and prevalent ectoparasite species on *R. pumilio* in the present study. A similar pattern was observed in the previous study on *R. pumilio* in the CFR (Matthee *et al.* 2007). This is supported by the fact that *R. pumilio* is listed as the only recognized and preferred host of *P. arvicanthis* (Ledger 1980). A recent study emphasized the importance of blood-sucking lice (Phthiraptera: Anoplura) as potential vectors of arthropod-borne pathogens and suggested that more studies are desperately needed on these lice (Hornok *et al.* 2010).

Studies that focus on the mesostigmatid mite diversity of natural occurring wildlife are limited in SA (Tipton 1960; Zumpt 1961; Till 1963; Louw *et al*. 1995; Horak *et al*. 1999; Anderson and Kok 2003; Matthee *et al*. 2007, 2010). Given the above it is not surprising that there may still be numerous undescribed mite species. In addition, variation exists between studies in the type of data that were recorded. For example, Horak *et al*. (1999) recorded species identities but no information was provided on species abundance, life stages or sex ratios. A total of nine mite species, from four different genera, were recorded in the present study. Three of the species (genus *Laelaps*) are new species that are currently undescribed. The study by Matthee *et al*. (2007) also yielded 3 separate undescribed mite (2 *Laelaps* and 1 *Androlaelaps* species) species on *R. pumilio* in the CFR (Matthee and Ueckermann 2008, 2009). At present, no information exists on the ecology and biology of most of these mite species. This is mainly because studies have mostly focussed on mite taxonomy and systematics.

Most of the mites (*A. dasymys, A. fahrenholzi, L. giganteus* and *O. bacoti*) found in this study occur on multiple rodent species and are widely distributed throughout Africa (Tipton 1960; Zumpt 1961; Till 1963). Distribution maps that are current and specific to SA and the WCP are lacking, and thus it is uncertain what the host- and geographic extent is of the various mite species in this region. Similar to the pattern found for fleas the prevalence of mites on *R. pumilio* was higher in the present study (73.23 %) compared to the previous study (68.20 %) by Matthee *et al*. (2007). Again this pattern was mainly driven by a higher prevalence of a few species such as *A. dasymys*, *A. fahrenholzi* and *O. bacoti*. The genus *Androlaelaps* consists of 26 species and occurs particularly on rodents or in their nests (Matthee and Ueckermann 2008). *Androlaelaps fahrenholzi* was the most numerous mite followed *by L. giganteus* in the current study. This is in accordance with the Matthee *et al*. (2007) study. A recently described mite, *A. rhabdomysi* (Matthee and Ueckermann 2008) was again recorded on *R. pumilio* in the present study. Fifteen species of *Laelaps* are found on small mammals, particularly rodents, in SA (Zumpt 1961; Matthee and Ueckermann 2009). Members in this genus are considered to be ectoparasites of a diverse group of small mammals and the medical importance of these mites are under speculation (Zumpt 1961; Matthee and Ueckermann 2009). *Laelaps giganteus* appears to be common on *R. pumilio* as it was the second most abundant and prevalent mite in the present

study and in Matthee *et al.* (2007). It was also the most abundant and prevalent mite on *R. pumilio* at De Hoop Nature Reserve (Matthee *et al.* 2010). This mite is a relative large mite (female length 1.274 ± 24.12 ɥm) compared to the rest of the mite species found on *R. pumilio* (Matthee *et al.* 2007). On the host, it is normally found at the base of the rodent's tale (Braack *et al.* 1996; Matthee *et al.* 2007). Zumpt (1961) list *L. giganteus* as a broad niche species that can occur on several rodents that include *O. irroratus* and *M. namaquensis*. However, the mite was absent from *O. irroratus* that was trapped together with *R. pumilio* at De Hoop Nature Reserve (Matthee *et al.* 2010). It is possible that the local host species range will differ spatially.

Three specimens of a tropical rat mite, *O. bacoti*, were found on *R. pumilio* in autumn at Mulderbosch. Information on the distribution of the mite is limited in most parts of the world (Baumstark *et al.* 2007). The study by Matthee *et al.* (2007) did record this mite species, although also in very low abundance and with a prevalence of 0.2 %. It was however absent from *R. pumilio* trapped at De Hoop Nature Reserve (Matthee *et al.* 2010). It is known to cause dermatitis in humans (Beck and Fölster-Holst 2009), it transmits a number of bacterial and viral infections under laboratory conditions and can act as an intermediate host for filarial worms, like *Litomosoides carinii* (Baker 1999). These bacterial and viral infections include *Rickettsia typhi* (murine typhus), *R. akari* (human rickettsial pox), *Coxiella burnetti* (Q fever), *Y. pestis* (plague), *Trypnosoma cruzi* (Chagas' disease) and coxsackie virus (Baker 1999).

Trombiculid larvae (Trombiculidae) were found on a large number (50.17 %) of the rodents that were trapped in the present study. The species identity and the number of species involved are uncertain at present. This is mainly due to a lack of taxonomic expertise in SA. The study by Matthee *et al.* (2007) also recorded Trombiculid mites on *R. pumilio*, but unfortunately, no information was recorded on the prevalence or abundance of the mites. The abundance, in the present study, ranged from very high (more than 50 % of body covered) to very low (only a few individuals present on a rodent). The parasitic stage of chigger mites (Trombiculidae) is the larvae and this stage is normally the only stage detected by entomologist and parasitologists, while other stages are found concealed within soil. The larvae are known to cause skin eruptions

and itching, also known as chigger dermatitis, in humans and other animals (Ewing 1944). Chigger dermatitis has been reported in SA on dogs and a child, but very few formal reports of this exist (Heyne *et al.* 2001). These mites are able to act as vectors for scrub typhus in some parts of the world (Traub and Wiseman 1974; Wenge *et al.* 2009).

Ticks are probably the best studied taxon of small mammal ectoparasites in SA. This is mainly due to the medical, veterinary and economic importance of several species. For example, *H. elliptica* is known to transmit *Babesia canis rossi* to dogs, *Rickettsia conori* and *C. burnetti* to humans (Walker 1991). Ixodid ticks that occur on *R. pumilio* (Matthee *et al.* 2007) and other small mammals mainly have a multi-host life cycle (two- and three host life cycles) with the different feeding stages feeding on different host individuals. Small mammals are very important hosts of mostly immature tick stages. This is evident from the fact that 76 % of ticks recognized by Horak *et al.* (2002a) have been found to parasitize small mammals (Durden 2006). The small mammals in any given region will mainly be parasitized by immature stages such as members of the genera *Amblyomma, Dermacentor, Haemaphysalis, Hyalomma, Ixodes* and/or *Rhipicephalus*. The immature stages drop from the host after a bloodmeal and develop into the next stage (Durden 2006). Adult tick stages will normally feed on larger mammals (Walker 1991).

Eleven tick species, representing a total of 3 genera, were found in the present study and larvae represented 87.72 % of the life stages. The tick species recorded in the present study were very similar to the species previously recorded on *R. pumilio* (Matthee *et al.* 2007, 2010). In the present study the *R. getrudae* group was the most abundant group of ticks. However, this group comprises several *Rhipicephalus* species (*R. gertrudae*, *R. follis*, *R. capensis*, *R. simus* and *R. lounsburyi*) which are difficult to distinguish at larval and nymph stage. All 5 species occur in the WCP and the immature stages prefer small mammals as hosts (Walker *et al.* 2000). The *R. gertrudae* group were more prevalent on *R. pumilio* (82.2 %) in the study by Matthee *et al.* (2007) compared to the current one (50.3 %). Adult *R. gertrudae* ticks are almost exclusively parasites of large herbivores, including humans and other primates (Horak *et al.* 2002b). Matthee and colleagues recorded 916 adult *R. gertrudae* ticks from the vegetation and human clothing at

different localities in the CFR in 2007 (Matthee *et al.* 2007). Heavy infestations of *R. gertrudae* have been linked with the death of young baboons in Namibia (Brain and Bohrman 1992). The distribution of this tick seems to be restricted to parts of SA and Namibia (Walker *et al.* 2000). In SA the distribution range comprises parts of the Northern, Western and Eastern Cape Provinces as well as the Free State Province (Walker 1991). The tick, *R. simus*, has been shown to experimentally transmit *Theileria parva parva*, *T. parva lawrencei*, *Anaplasma marginale* and *A. centrale* to cattle (Lounsbury 1906; Neitz 1962; Potgieter 1981; Potgieter and Van Rensburg 1987). This tick is also listed as a vector of *R. conori* to humans (Gear 1992).

Walker (1991) stated that *R. pumilio* is also the only known host for immature stages of *R. lounsburyi*. Subsequent studies did confirm the presence of the tick on *R. pumilio*, but in such low numbers that it could easily be interpreted as accidental infestations (Horak and Boomker 1998; Horak *et al.* 2005). More recently, nymph stages of the tick was recovered from *R. pumilio* individuals at several localities in the CFR and in larger numbers (Matthee *et al.* 2007). In the present study 80 individuals of *R. lounsburyi* were found. The life stages that were present included both of the immature stages and adult females. This study provides novel information in that this is the first record of all the life stages on *R. pumilio* in the WCP and SA. The present study therefore provides further evidence that *R. pumilio* can be considered as a preferred host of *R. lounsburyi*. The distribution of *R. capensis* is limited to the Western and Northern Cape Provinces in SA (Walker *et al.* 2000). Although little evidence exists, it seems that the immature stages prefer rodents as their hosts, while adult ticks prefer larger mammals like the Gemsbok (*Oryx gazella*) and Eland (*Taurotragus oryx*) as their wild hosts (Walker *et al.* 2000).

The preferred hosts for adult *H. elliptica* ticks are domestic dogs, and occasionally cattle, while the immature stages normally occur on rodents (Horak *et al.* 1986; Walker 1991). This was evident from the studies by Matthee *et al.* (2007, 2010) and the present one. *Haemaphysalis elliptica* is a vector for *B. canis rossi* which cause babesiosis in dogs and this tick is the only tick in its genus that is known to carry pathogens (Lewis *et al.* 1996; Apanaskevich *et al.* 2007). It is also a vector for *R. conori*, that causes human tick-bite fever, and *C. burnetti* which causes Q

fever in both humans and other animals (Walker 1991). Its distribution is discontinuously throughout SA where suitable hosts exist (Horak *et al.* 2005).

In the current study the genus *Ixodes* is represented by 4 species of which one is an undescribed species, *Ixodes* sp. *Ixodes* species differ from the other tick genera in that the adult stages are also often associated with rodents. *Ixodes fynbosensis* was the third most abundant tick species found in the present study. This tick was recently discovered on *R. pumilio* in the CFR (Matthee *et al.* 2007) and subsequently described (Apanaskevich *et al.* 2010). Not much information is currently available for this species but based on the results from the present study and the studies by Matthee *et al.* (2007, 2010) it does appear that *R. pumilio* is an important host for the larval and nymph stages and that the tick may be restricted to the higher rainfall regions of the CFR (Apanaskevich *et al.* 2010). Two adult females of this species were recovered from dogs at one of the localities included in the study by Matthee *et al.* (2007). Temporal data from the present study indicate that the immature stages are the most abundant during the warm, dry summer months. This pattern is supported by Matthee *et al.* (2007).

Both adult and immature stages of the ticks *I. alluadi* and *I. bakeri* prefer shrews as their hosts but they also parasitize various rodent species (Walker 1991). Although *I. alluadi* was one of the least abundant ticks of the current study, 72 % of the ticks that were found on *R. pumilio* were adults. This contrast results for *I. bakeri*, where a lower proportion of the ticks were adult stages (only 4.91 % were adults). For both tick species the larval stages represented approximately 50 % of the ticks. *Ixodes alluaudi* occurs throughout SA and Lesotho, but also extralimitally (Walker 1991). *Ixodes bakeri* has only been recorded in SA. Although disease risk associated with *Ixodes* species are poorly understood in general, we do know that adult females of one species *I. rubicundus* are responsible for paralysis in some domestic and wild animals in southern Africa (Walker 1991).

Seasonal fluctuations in macroparasite abundance can be attributed to seasonal changes in climate and in the physiology or behavior of host species (Weil *et al.* 2006). Fleas, lice, mites and ticks differ with respect to host association and will thus react differently to variation in climate. The climate of the CFR in the WCP is classified as a Mediterranean ecosystem with dry, hot summers and wet, cold winters (Midgley *et al.* 2003). It is therefore expected that given the distinct seasonal variation in climate that individual ectoparasite taxa will react accordingly different to this variation, depending on its association with the host. For example, it appears that flea abundance on the host may be determined by cool temperatures rather than rainfall as the abundance of the flea, *Ctenocephalides damarensis,* on *L. saxatilis*, in the summer rainfall region, increased during winter, peaked in abundance during late winter or spring and then decreased sharply (Louw *et al.* 1993; Louw *et al.* 1995). The same results were found for fleas on scrub hares in the WCP (winter rainfall area) in SA (Louw *et al.* 1993; Louw *et al.* 1995).

The present study differs from the study by Matthee *et al.* (2007) in that adequate sample sizes (27-30) were obtained during each of the 4 trap sessions. Moreover, the mice were trapped exclusively in a remnant renosterveld fragment surrounded by vineyards, i.e. the mice were confined to this specific habitat patch. The study by Matthee *et al.* (2007) was biased in that low rodent densities resulted in low sample numbers. As a result, data were combined for two vegetation types, remnant fragment and pristine natural vegetation, in one region. However, even after combining the data a low sample size (n = 17) was recorded for one of the trap sessions (September) (Matthee *et al.* 2007). Small sample size may be a confounding factor in studies that investigate temporal variation. This is mainly due to the fact that parasites have an aggregated distribution within the host population (Matthee and Krasnov 2009). In addition, natural variation in climatic factors from year to year may also affect the seasonal pattern in parasite abundance. It is therefore advisable that adequate samples sizes are obtained and that repeated sampling is conducted to confirm the observed pattern.

In the present study mean flea abundance was the highest on *R. pumilio* during late autumn or winter (May) with a mean daily rainfall of 2.7 mm and mean temperature of 15.5°C. This pattern

was also evident in the current study, although there was a higher abundance of *C. rossi* individuals during the summer months than found in Matthee *et al.* (2007) study. Matthee *et al.* (2007) found that the flea *C. rossi* were the most abundant during winter to early spring (June and September).

The host specific louse, *P. arvicanthis*, was absent from *R. pumilio* individuals that were trapped during late summer and autumn in Stellenbosch. The mean abundance and prevalence of the louse must have been very low and restricted to a few host individuals during these months. Increased temperatures associated with spring and summer resulted in peak abundances on *R. pumilio* individuals during spring (August) and early summer (November). This pattern is slightly different from a winter (June) and spring (September) abundance pattern recorded on *R. pumilio* previously in the CFR (Matthee *et al.* 2007). However, both studies support a pattern of low infestation levels during dry months (late summer and autumn) in the CFR. In general, the mean annual rainfall for Stellenbosch region (856.36 mm) is higher than for Elandsberg farm and nature reserve in Wellington (500 mm) (Midoko-Iponga 2004). It is therefore possible that higher rainfall during winter and relatively high rainfall during spring (September, October and November 2009) in the Stellenbosch region might explain the delay in seasonal abundance for *P. arvicanthis* in the present study.

Infestation by the louse *Eulinognathus denticulatus* on *L. saxatilis* at Kimberley in the Northern Cape Province of SA also followed a sharp increase in infestation from spring (September) to summer (December) (Anderson and Kok 2003). Rainfall patterns in the Kimberley area is characterized by a peak during the late summer months, with March the wettest month of the year (Anderson and Kok 2003). Various other studies done on lice of small mammals found contradicting results and concluded that there seems to be no clear seasonal trend in louse abundance (Louw *et al.* 1995; Braack *et al.* 1996; Monello and Gomper 2009). Interestingly, none of the lice found in the latter studies were host-specific. It is possible that the level of host-specificity may influence the general pattern of temporal variation observed on the host species.

Empirical studies on diversity and temporal patterns of mite species on natural occurring wildlife are limited in SA. This is especially true of data on the prevalence, intensities of infestation, interactions and the effects that mites have on their host animals (Braack *et al.* 1996). Anderson and Kok (2003) recently recorded the seasonal abundance of two mite species on *L. saxatilis* in the Northern Cape Province. The larval stages of the two mite species did show higher infestation rates during cool dry months, although the number of *L. saxatilis* sampled per month was low (n = 4 to 14). In the present study the mean abundance for the mite taxon and for the most abundant mite species, *A. fahrenholzi*, increased towards the end of summer (February) and reached a peak during autumn (May). High mite infestations during winter are also supported by Matthee *et al.* (2007) in the CFR. A study on the epifaunal arthropods of *A. chrysophilus* and *G. leucogaster* in the Kruger National Park (summer rainfall) did not show any clear seasonal patterns for mites, possibly because of a low host (*Gerbilliscus leucogaster* and *Aethomys chrysophilus*) sample number (n = 46 each) collected over 12 months (Braack *et al.* 1996).

Mean abundance for the combined tick species was high in February with a subsequent decrease during the cold and wet winter months. A peak in abundance was recorded during the onset of summer (November). A similar pattern was recorded for the most abundant tick, *H. elliptica*. A spring-summer peak is supported by Matthee *et al.* (2007). Temperature and rainfall are the main variables that can affect the hatching of tick eggs which will eventually influence the abundance of immature stages on rodents (Fourie and Horak 1987; ELGhali and Hassan 2010). A study done on *A. chrysophilus* and *G. leucogaster* in Kruger National Park (summer rainfall) recorded the highest abundance of *H. elliptica*/*spinulosa* larvae during September (spring) and nymphs during June-July (winter). The authors suggested that the small sample size prevented a clear pattern of the seasonal abundance of ticks (Braack *et al.* 1996).

It is evident from the current study that *R. pumilio* in the WCP is host to a diverse assemblage of ectoparasite species. In addition, this generalist rodent that is locally abundant and regionally widespread acts as an important host for several of the ectoparasite species. Mean abundances of the ectoparasite taxa on the host vary throughout the year in the CFR. The variation was taxon-

specific and largely ranged from a preference for cool wet conditions (fleas and mites) to warm and dry conditions (ticks and louse). Knowledge regarding the temporal variation in abundances is especially valuable for species that act as vectors. For example, the spring/summer peak of *H. elliptica* larvae and nymphs on broad niche small mammals such as *R. pumilio* precedes the summer peak for canine babesiosis that is transmitted by adult stages to dogs in the CFR.

2.7 References

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Chapter 3

The effect of anthropogenic habitat transformation on the ectoparasite abundance, prevalence, species richness and species composition of *Rhabdomys pumilio* in the CFR

3.1 Abstract

Habitat fragmentation due to human activities is still on the increase and has caused large losses of biodiversity in the world today. Although the effect of fragmentation has been studied for various small mammal species, very little is known about the effect on host-parasite systems as a whole. The aim was firstly, to record and compare relative density, average body size and body condition of Four-striped mice, *Rhabdomys pumilio,* individuals and compare host ectoparasite species abundance, prevalence and composition between pristine natural areas and remnant fragments. Lastly, the aim was to compare body size measurements of the two most abundant flea species for the two habitat types. *Rhabdomys pumilio*, were trapped with Sherman-like live traps at 4 pairs of remnant vegetation fragments surrounded by agriculture activities and continuous pristine natural areas in the Cape Floristic Region, Western Cape Province. Rodents were euthanized and all the parasites removed. Body measurements were recorded for each rodent individual. The findings show that *R. pumilio* individuals were in a significantly better body condition and were larger in fragments compared to pristine natural vegetation. In accordance, head and vertical length and product of horizontal length and width of female *Listropsylla agrippinae* fleas were also significantly larger in fragments. Mean abundance and prevalence of overall ectoparasites combined, ticks, mites, fleas and a host specific louse was higher on rodents in fragments compared to extensive natural localities. This was significantly so for overall combined ectoparasites and ticks, mites and fleas. Parasite species composition differed between the two habitat types although only a small percentage of the variation was explained by fragmentation. Several of the parasite species found in higher abundance on *R. pumilio* in the fragments are vectors of pathogens for humans and domestic animals.

3.2 Keywords: fragmentation, ectoparasites, rodents, body size, body condition, parasite abundance

3.3 Introduction

Anthropogenic transformation of natural habitats and subsequent habitat loss is considered to be the most important threat to biological diversity in the world (Sala *et al*. 2000). Transformation of natural habitats often leads to the fragmentation of natural vegetation with consequences for ecosystem health and stability (Saunders *et al.* 1991; Chapin *et al.* 2000). Fragmentation can directly or indirectly affect wildlife populations and especially rodents (Bolger *et al*. 1997; Wolff *et al.* 1997; Rodríguez and Peris 2007). Direct influences entail the modification of habitat characteristics that include structure, size and resource availability. Indirect influences include the edge effect, decreasing of genetic diversity and increasing competition both within species and between species (Soulé 1991). The consequence is a loss in diversity because generalist species normally out-compete specialists in transformed habitats (de la Penã *et al*. 2003; Krasnov *et al.* 2006; Rodríguez and Peris 2007; Manor and Saltz 2008). Parasites have an intimate relationship with their host and the surrounding environment. It is thus expected that changes in the host diversity, susceptibility and density in association with the external environment will have knock-on effects on the parasite species richness, abundance and species composition. These changes can have direct consequences on the spread of diseases within ecosystems (Daszak *et al.* 2001; Keesing *et al*. 2006).

Parasite assemblages of terrestrial mammals, and specifically rodents, are influenced by host factors (for example, body size, sex, reproductive state, density and diversity) (Krasnov *et al.* 1997, 1998, 2006; Matthee *et al.* 2010) and environmental factors (for example, precipitation, vegetation cover, soil texture and structure) (Krasnov *et al.* 1998; ELGhali and Hassan 2010; Froeschke *et al*. 2010; Friggens and Beier 2010). The latter is specifically important for parasite taxa that spend part of their life in the external environment such as host nests and the surrounding vegetation (Poulin 1998). On the other hand, host factors may be more important to more permanent parasite species as they are more dependent on the host than their habitat. Larger hosts provide larger surface areas, more space and other resources, which may facilitate higher species richness and abundance of parasites and also larger body size (Haukisalmi and Henttonen 1994; Arneberg *et al*. 1998; Haukisalmi *et al*. 1998; Arneberg 2002; Moore and Wilson 2002; Poulin 2007; Matthee *et al.* 2010). Body size, of several parasite taxa, seems to be

positively correlated with host body size. This is specifically true for permanent parasites such as lice (Phthiraptera) (Kim 1985; Harvey and Keymer 1991), although a similar pattern was also previously recorded for fleas (Kirk 1991). However, the strength of the relationship between host and parasite body size may be influenced by the length of time that a parasite spends on the host as no relationship has been found for ticks and various host species (Poulin 1998). The advantage for the parasite is that a larger body size seems to be related to increased fecundity and a longer life-span (Skorping *et al.* 1991; Poulin 2007). However, a larger body size poses a risk to parasites due to a higher frequency of dislodging through host activities such as grooming and allo-grooming (Mooring *et al.* 2004; Poulin 2007; Hawlena *et al.* 2007).

Studies on the relationship between host body size and parasite species richness have found contradicting results (Poulin 2007) and it seems that no apparent relationship exist between mammalian host body size and parasite species richness (Krasnov *et al.* 2006). However, a positive relationship does exist between small mammal host species richness and parasite species richness (Krasnov *et al.* 2004). Depauperate parasite assemblages are expected in areas with low small mammal host diversity (for example fragments) compared to areas where a higher diversity of small mammal host species co-occur (for example natural areas) (Rosenzweig 1995). In some instances it does seem that generalist rodent host species harbour higher parasite diversity that specialist species (Egoscue 1976; Matthee *et al.* 2007). Depauperate parasite assemblages can be masked by high incidences of contact with domestic animals. This may result in host switching events (McMichael 2004).

Host density is another host factor that is especially important with habitat fragmentation events. Fragments vary in terms of level of isolation and this will determine the movement that is possible for rodents between habitat fragments in a region. Prolonged and complete isolation will result in inbreeding of the rodent population, thus more homozygous individuals, and this will lower the immune competence of rodents in isolated fragments and result in a higher parasite infection probability (Froeschke and Sommer 2005). In addition, high rodent densities will result in competition between individuals for resources and this can induce stress (Martínez-Mota *et al.* 2007). Hormonal changes associated with food and reproductive stress can depress the immune systems of these rodents (Anderson and May 1979; Hughes and Randolph 2001). The combined

effect of high host densities and lower immune competence can facilitate higher parasite burdens and increased parasite transmission in fragmented populations (Eley *et al.* 1989; Mbora and McPeek 2009). A recent study by Friggens and Beier (2010) found that flea infestation increased with increasing disturbance levels and peaked at intermediate disturbance levels (e.g. agricultural areas). Remnant habitat fragments that are associated with farms may be a source of parasite and disease exchange because of the interface between wild-, peridomestic- and domestic mammals (Anderson and May 1979; Friggens and Beier 2010).

The Cape Floristic Region (CFR) in South Africa (SA) is a biodiversity hotspot due to high level of plant species richness and endemism (Cowling and Hilton-Taylor 1994; Goldblatt and Manning 2000). However, this region is also an important and successful wine producing region (Giliomee 2003). In addition, in recent years there has been increased growth in wild flower (Giliomee 2003) and rooibos tea farms in certain areas (Hansen 2006). Surveys have indicated that agriculture (including forestry plantations) is the major contributor to the transformation and fragmentation of natural habitats and already covers an estimated 22 725 km^2 (25.9 %) of the CFR (Rouget *et al.* 2003). The effect of habitat fragmentation is evident from recent studies on renosterveld shrublands (Kemper *et al.* 1999), overall bird species diversity (Magnall and Crowe 2003) and reptile diversity (Mouton and Albas 2002) in the CFR.

Agricultural fragments are normally associated with high abundance of food, water and shelter, which may benefit resident rodent populations through improved growth, reproduction and thermoregulation (Krasnov *et al.* 2006). Consequently, the availability of resources will counter the negative effects, such as food-related stress levels and reduced body condition, of fragmentation (Friggens and Beier 2010). In addition, rodents benefit further through a lower density of natural predators in these fragments (Wilcox and Gubler 2005). Various studies have been done on the biology, behaviour, systematics and distribution of rodent species in South and southern Africa. However, few studies have researched the effect of habitat transformation on small mammal diversity and species composition in this region (Lawes *et al.* 2000; Johnson *et al.* 2002; Mugabe 2008; Wilson *et al.* 2010). A single study done in the CFR suggested that small mammals tend to seek refuge and food within remnant fragments, situated between agricultural activities, especially when rodents are not able to feed on crops and pastures (Mugabe 2008).

The study also recorded that generalist rodents (Four-striped mouse, *Rhabdomys pumilio,* and African pygmy mouse, *Mus minutoides*) were able to better adapt to these transformed habitats than more specialist species such as the Vlei-rat (*Otomys irroratus*), Musk shrew (*Mysorex verreauxii*) and the Cape gerbil (*Gerbilliscus afra*) (Mugabe 2008). In addition, it appears that transformed habitats have no negative effect on body condition and body mass of rodents.

Globally very few if any studies have researched the effect of anthropogenic habitat fragmentation on ectoparasite burdens. However studies done on haemoparasites (Vaz *et al*. 2007; Cottontail *et al.* 2009) and gastrointestinal parasites (Püttker *et al.* 2008; Mbora and McPeek 2009; Wright *et al.* 2009) recorded resulting effects on these burdens. A recent study looked at the impact of anthropogenic habitat transformation on flea-borne disease. It was found that anthropogenic transformation has the potential to increase the risk of disease through the alteration of flea-host infection patterns (Friggens and Beier 2010). In most instances it seems generalist ectoparasite species abundance and prevalence increase as a result of fragmentation, but the peak in abundance and/or prevalence is ultimately determined by local environmental factors.

At present there is no information available on the effect of habitat fragmentation on parasite diversity, abundance or species assemblages of terrestrial animals in SA. *Rhabdomys pumilio* is an endemic generalist rodent species that successfully adapts to transformed habitats. Using this rodent as model the study aims to address the current lack of information in the Western Cape Province (WCP) and SA.

The following predictions are made based on the current literature:

1. Rodent body size (total length, body length and tail length) will be larger and body condition better in habitat fragments compared to extensive natural localities.
2. Flea body size will be larger in fragments compared to extensive natural localities.
3. Mean abundance and prevalence for the ectoparasites combined and the individual ectoparasite taxa will be higher on *R. pumilio* trapped in fragments compared to extensive natural localities.

The aims of the study are therefore set out to:

1. Record the relative density, average body size and body condition of *R. pumilio* and to compare this between extensive pristine natural localities and remnant fragments surrounded by agricultural activities.
2. Record the body size (head length, vertical length, horizontal length and product of vertical- and horizontal length) of the most abundant flea species on *R. pumilio* and to compare the mean and maximum body size of the individual flea species between natural and fragmented localities.
3. Compare the ectoparasite species abundance, prevalence and composition on *R. pumilio* populations that occur in natural and fragmented localities.

3.4 Materials and methods

Study areas

The study was conducted in the CFR of the WCP (Table 4; Figure 12). This region has a Mediterranean-type climate, characterized by warm dry summers and cold wet winters (Midgley *et al.* 2003). Sampling of *R. pumilio* included paired trapping at 4 large and continuous pristine natural areas and 4 habitat fragments within a matrix of agricultural activities (vineyards or crop fields). Two continuous natural areas and 2 fragments that formed part of the previous study by Matthee *et al*. (2007) were resampled. Localities were all below 400 m above sea level and less than 200 km apart. Vegetation type mainly consisted of lowland fynbos/renosterveld. Habitat fragments consisted of relatively small remnant lowland fynbos/renosterveld vegetation (Table 4; Figure 12). Locality sizes were estimated in Google Earth Pro 5.2.1 by drawing a polygon over the area. The aim was to use proclaimed Nature Reserves as "control" groups to test the effect of fragmentation. However, this was not possible in all cases mainly due to preceding fires in Stellenbosch, Paarl and Somerset West areas. As a result two smaller, but still relatively large areas with pristine natural vegetation were included as part of the control groups (Table 4).
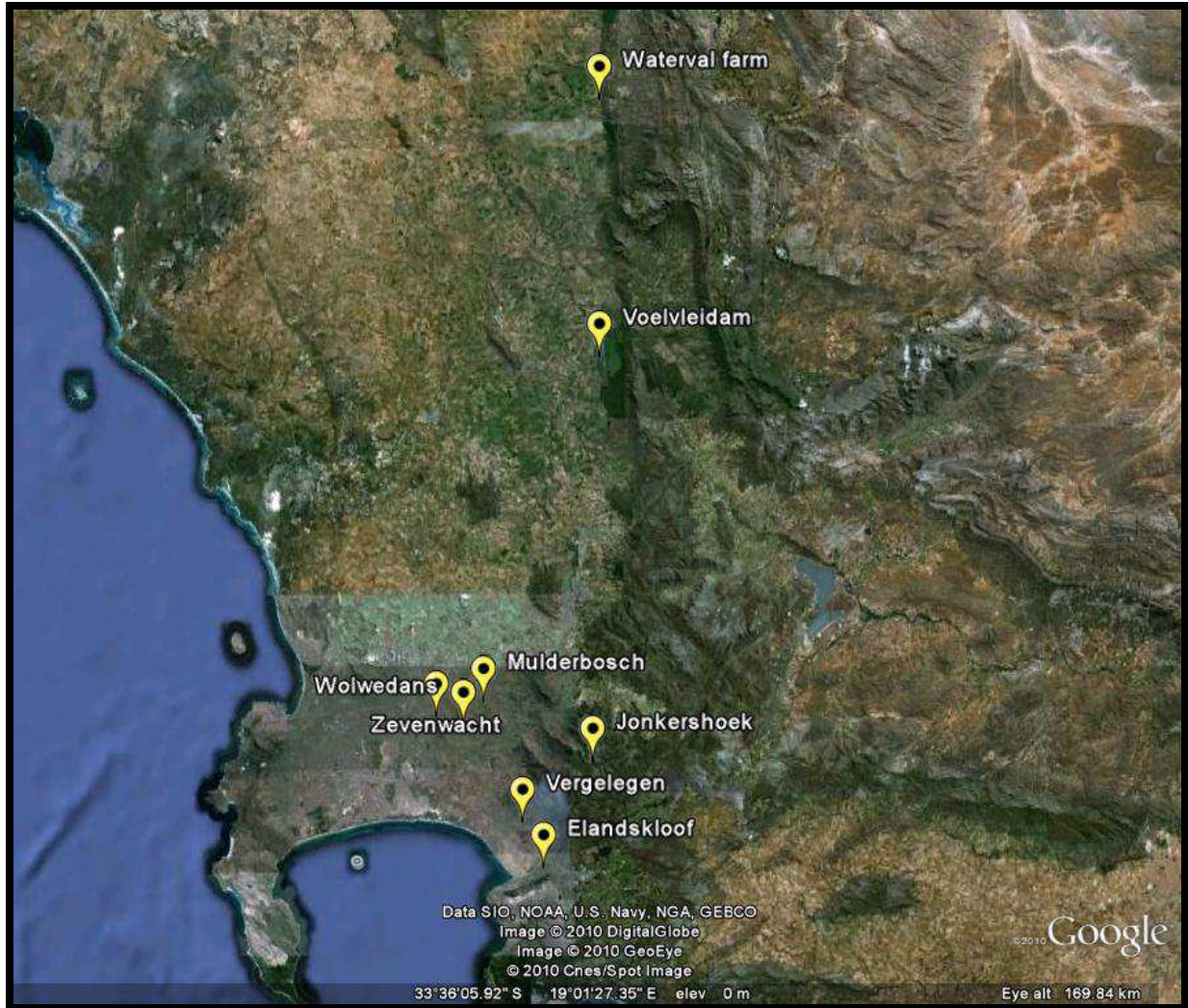
Figure 12: Map showing all 8 localities sampled in the Cape Floristic Region, Western Cape Province, South Africa, 2009. Map drawn in Google Earth Pro 5.2.1. Refer to Table 4 for estimated size of fragments and Nature Reserves.

Host species

Rhabdomys pumilio is an endemic rodent species (Muridae) that is regionally wide spread and locally abundant. It feeds on large quantities of green vegetation, but seeds are the primary food source. In addition, it is able to occupy a vast range of habitats (generalist) and is known to be able to successfully adapt to anthropogenic (urban and agricultural) environments. In a recent study done in the CFR only 2 species (*Rhabdomys pumilio* and *Mus minutoides*) were captured in transformed habitats whereas 6 species were captured in natural areas (Mugabe 2008). *Rhabdomys pumilio* was also present in high abundance at 9 localities in the CFR (Matthee *et al.* (2007) and along a rain fall gradient study from the WCP (Cape Town) to the northern part of Namibia (Caprivi). It is evident from previous studies that *R. pumilio* provides the ideal study species for assessing the ability of a generalist rodent to endure habitat disturbances (Schradin and Pillay 2005b; Mugabe 2008).

In general, *R. pumilio* breeds in spring, summer and autumn (September to April) in the CFR and there is a clear seasonal cycle. During the non-breeding winter months the population numbers decrease (David and Jarvis 1985; Krug 2002; Schradin and Pillay 2005a). The study by Mugabe (2008) partly confirmed the fact that *R. pumilio* breeds in the summer months, although the author suggested that breeding took place year-round in transformed habitats. The latter provides evidence that *R. pumilio* is able to take advantage of disturbed habitats.

Rhabdomys pumilio is socially plastic with social systems ranging from solitary territorial, in moist grasslands, to a communal social system in the succulent Karoo and desert (Nel 1975; Krug 2002; Schradin and Pillay 2005a and b). To date, no studies have been done on the level of sociality in the CFR or WCP, but from personal observation it seems that these rodents use a more communal social system. This is further supported by the fact that the vegetation in the CFR is more similar to the vegetation of the succulent Karoo compared to grassland of KwaZulu Natal (Mucina and Rutherford 2006).

Rodent trapping

Rhabdomys pumilio individuals were trapped using Sherman-like live traps that were baited with a mixture of peanut butter and oats. The number of traps used per locality ranged from 100 to 200. Rodent trapping followed a single design where 22 to 30 *R. pumilio* individuals were trapped over various trap nights at each of the 8 localities during austral spring and summer (October to December 2009) (Table 4). Although it was initially the aim to catch 30 individuals at each site with each trapping period, this was not possible due to low rodent abundance at certain localities. Only *R. pumilio* individuals were removed and all other rodents were identified and released at the specific site. The traps were checked twice daily. In an attempt to limit trap related deaths as a result of environmental exposure the traps were closed in the day during summer.

Rhabdomys pumilio individuals were euthanized with 2-4 ml Sodium Pentobarbitone (200 mg/kg) depending on individual weights. Each mouse was placed in a separate premarked plastic bag with a reference number. The rodents were frozen at -20°C and examined a few weeks later. The body weight (gram) and measurements (millimetre) of the hind foot, tail and total length of each rodent were recorded following parasite removal (see methods below). Trapping and handling of rodents were approved by the Ethical Committee of Stellenbosch University and the Western Cape Nature Conservation Board (Ethics nr: 2006B01007; Cape Nature permit nr: AAA004-00221-0035).

Table 4: Locality information, number of *Rhabdomys pumilio* examined and sex ratio at each of the localities (n = 8) in the Cape Floristic Region, Western Cape Province during 2009.

Locality	GPS	Size (km^2)	No. of sites	Sample size	Sex ratio (m:f)	Date sampled
Natural areas						
Jonkershoek	33.98798 S, 18.95541 E	18.04	4	30	2:1	27-Oct
Elandskloof	34.08151 S, 18.55112 E	5.86	3	30	1.31:1	17-Nov
Wolwedans	33.55021 S, 18.46303 E	3.45	2	22	1:1	03-Dec
Voëlvleidam	34.67125 S, 19.87806 E	8.13	3	30	1.5:1	06-Oct
Remnant fragments						
Zevenwacht	33.91749 S, 18.73224 E	1.10	3	29	2.22:1	03-Nov
Vergelegen	34.03580 S, 18.54208 E	0.21	4	23	1.3:1	29-Sep
Mulderbosch	33.53374 S, 18.48514 E	0.14	6	28	1:1	10-Nov
Waterval Farm	32.59151 S, 19.01287 E	0.10	3	26	1:1	06-Oct

Trapping density estimate

To obtain an estimate of rodent density at each locality the relative trap density (Rd) was calculated for each locality using two steps:

Step 1: Calculate the product of the number of traps (t) and trap nights* (n), divided by 100 to get a fraction of traps per hour (Th) in the field.

$$Th = \frac{(t)(n)}{100}$$

*One trap night equals 12 hours.

Step 2: Total number of mice trapped (m) at each locality divided by the fraction of traps per hour (Th) in the field form step 1.

$$Rd = m/Th$$

The answer to this equation then resulted in an estimate of the number of mice at each locality per trapping hour in the field.

Parasite removal and identification

The frozen rodents were removed from the freezer the night before the animals were examined in the laboratory. The animals were taken out of the premarked plastic bag after which the bag was first systematically examined under a stereoscopic microscope. After this, the entire animal was systematically examined under the stereoscopic microscope and all the fleas, lice, mites and ticks placed separately into specimen tubes filled with 70 % ethanol and labelled with the relevant reference number. Ticks and mites were sent to expert taxonomists for identification (Ivan Horak and Eddie Ueckermann), while fleas and lice were kept for self identification. Fleas were mounted by the technique described in Segerman (1995). Lice were mounted in a polyvinyl alcohol solution (PVA). Lice were placed in the middle of a microscope slide and were firstly cleared with a drop of 85 % lactic acid over a flame till transparent. The specimen was then

orientated dorso-ventrally in a drop of PVA and the cover slip was then slowly lowered onto the specimen. Identification of fleas and lice was done using a Leica compound microscope and the morphological key of Segerman (1995) and Ledger (1980) and Johnson (1960), respectively. Following all the above, the rest of the carcass was frozen for future reference.

Body condition index calculation

The body condition index was calculated as a residual from the regression of the body mass on the body size (total length) of *R. pumilio* individuals (Díaz and Alonso 2003; Schulte-Hostedde *et al.* 2004; Püttker *et al.* 2008). Pregnant females and individuals with cut tails were removed from the regression because of their different body proportions and resulting body condition index.

Preparation and measuring of fleas

Fleas were mounted by the technique described in Segerman (1995). Care was taken not to put pressure on the cover glass with the mounting of the fleas. A cover glass with a diameter of 10 mm and Labstar 1000 microscope slides, frosted with ground edges, were used. Three different measurements (total horizontal length, total vertical length of the whole body and total head length) were recorded for the two most abundant flea species on *R. pumilio*, namely *Listropsylla agrippinae* and *Chiastopsylla rossi* (Figure 13). Measurement parameters were determined through a study trial and discussion with experts in the field. Product of length was calculated by the product of horizontal and vertical length. Measurements of *L. agrippinae* were done on a Leica stereoscopic microscope and for. *C. rossi* it was done on a Leica compound microscope. The reason for this is the fact that *L. agrippinae* were too large to measure with the Leica compound microscope. Both the microscopes had cameras mounted on them and Leica software V 3.1.0 was used on a computer to measure individual fleas. All male and female *C. rossi* and *L. agrippinae* fleas recovered in the study were measured.
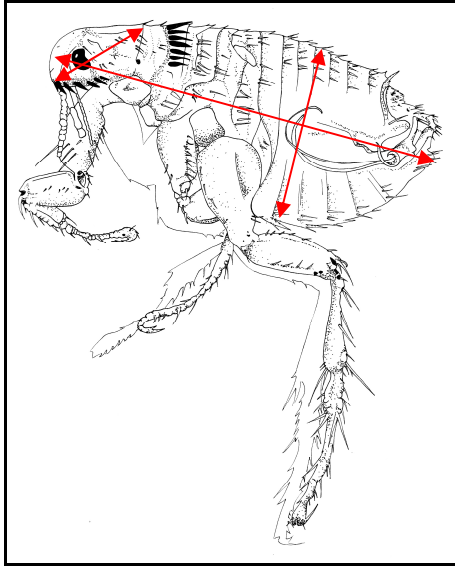
Figure 13: Illustration of the flea body measurements (head length, horizontal length and vertical length) taken of *Chiastopsylla rossi* and *Listropsylla agrippinae*. Image drawn by Pienette Loubser, 2010.

Data analysis

Descriptive statistics, which included mean abundance, total counts, standard errors, standard deviations, rank-abundances and total abundances, were calculated in Microsoft Excel 2007. Poisson and normal log transformed Generalized Linear Models (GLZ) was performed on parasite abundance and rodent body measurement data respectively, in Statistica 9. Models were corrected for over-dispersion by Pearsons Chi^2 statistics. Type 3 LR tests were performed to calculate the Wald statistics and the predicted means were plotted. Significance of explanatory variables of a statistical model was tested by the Wald statistical test (Quinn and Keough 2002). The larger the value of the Wald statistic (> 0), the more significant the effect that the predictor (explanatory variable) has on the model. Percentage deviances explained by the model were calculated by dividing the deviance statistic of the model by the deviance statistic of the null model. The null model was calculated by running a GLZ without the effect of habitat type and rodent host body size. Percentage deviance explained is calculated to explain the deviance and significance of the model by contrasting it with the null model (Quinn and Keough 2002). Mean measurements of male and female fleas, respectively on the same *R. pumilio* individual, were

calculated in Microsoft Excel 2007 to prevent pseudoreplication. Factorial analyses of variances (ANOVA's) were performed on normally distributed flea body measurement data using Statistica 9.

A binomial GLZ was performed in R 2.9.1 to look at the relationship between parasite abundance and prevalence, while compensating for the effect of rodent body size, parasite species and habitat type (natural/fragment). A binomial log link GLZ model was ran with parasite abundance, parasite species, habitat type, locality and the average total length of mice at each site as the variables. The model was:

GLZ (binomial, log link) y = parasite abundance + parasite species + habitat type + locality + average total length of mice at each locality.

A significant ($p < 0.01$) positive relationship was found between ectoparasite abundance and prevalence for all localities. All individual ectoparasite species also showed positive relationships between abundance and prevalence, although some were not significant. The model explained 71.97 % of the deviance, but when parasite species identity and habitat type was taken out the model only explained 36.61 %. The same relationship between prevalence and abundance was found by Matthee and Krasnov (2009) and thus no further analysis was done on prevalence. The effect of fragmentation on parasite species composition was determined using non-metric dimensional scaling and analysis of similarity (ANOSIM) using the program R 2.9.1.

3.5 Results

Relative density

A total of 218 mice were trapped of which 125 were males and 93 females. Most of the mice (94.95 %) were reproductively active. At several localities more male *R. pumilio* individuals were trapped compared to female individuals (Table 4). Relative density of *R. pumilio* was higher in the remnant fragments for 2 of the 4 paired localities (Table 5). Highest relative density was found at the Mulderbosch fragment (6.22) and the lowest at Jonkershoek Nature Reserve (0.83) (Table 5). There was no clear pattern in terms of parasite species richness (Table 5) although the highest species richness was recorded at Zevenwacht fragment (16) and the lowest at Voëlvleidam Nature reserve (11).

Table 5: Relative density and the total number of ectoparasites species found on *Rhabdomys pumilio* sampled at 8 localities in the Cape Floristic Region, South Africa, October to December 2009.

Locality	# Trap nights	# Traps	# Mice	Relative density	# Ectoparasite species
Natural areas					
Jonkershoek	19	190	30	0.83	14
Elandskloof	13	150	30	1.54	14
Wolwedans	5	200	22	2.20	15
Voelvleidam	9	100	30	3.33	11
Remnant fragments					
Zevenwacht	4	129	29	5.62	16
Vergelegen	18	148	23	0.86	14
Mulderbosch	3	150	28	6.22	14
Waterval Farm	8	100	26	3.25	13

Rodent body measurements

Rhabdomys pumilio individuals were larger in the fragments compared to the natural localities. Mean total length, observed body mass and the calculated body condition index were all significantly higher ($p < 0.05$) for *R. pumilio* individuals in the fragments compared to the natural localities (Figure 14; Table 6; Appendix: Figure 7 and 8). The GLZ model explained

94.70 % of the deviance and the significance of the effect of habitat type (explanatory variable) was supported by the Wald statistic (10.38) (Table 6).
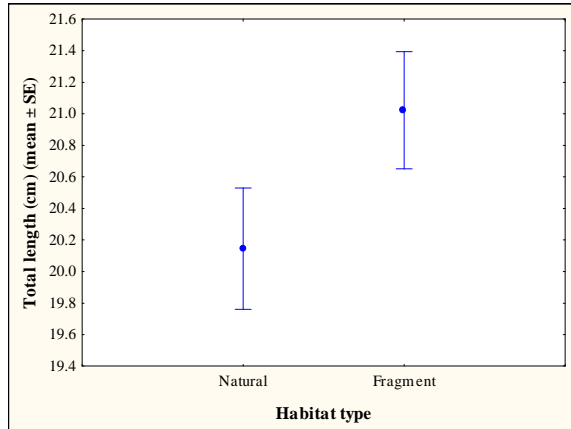
Figure 14: Mean predicted total length of *Rhabdomys pumilio* (n = 218) trapped in fragments and natural localities in the Cape Floristic Region, South Africa, 2009. (GLZ model (normal): y = habitat type).

Table 6: Breakdown of the GLZ model and analysis for mean total length of *Rhabdomys pumilio* in fragment and natural localities in the Cape Floristic Region, South Africa, 2009.

Model	% Deviance explained			
Model (normal): y = habitat type	94.70			
All effects				
Effect	**Degrees of freedom**	**Wald statistic**	**p-value**	
Intercept	1	208190.53	0*	
Habitat type	1	10.38	0.001*	
Parameter estimate				
Effect	**Level of effect**	**Estimate**	**Standard error**	**Wald statistic**	**p-value**
Intercept		3.02	0.01	208190.53	0*
Habitat type	natural	-0.02	0.01	10.38	0.001*
Scale		1.86	0.10	372	0

*indicates significant differences (p < 0.05)

Flea measurements

The two most abundant fleas on *R. pumilio* were *C. rossi* (n = 109) and *L. agrippinae* (n = 114). Head length of male, *L. agrippinae* fleas was significantly longer (p < 0.05) on mice trapped in fragments compared to natural localities (Figure 15a). Males of the second most abundant flea, *C. rossi*, did not show any significant difference (p > 0.5) in head size between the two habitat types (Figure 15b). All other body measurements were non-significant for males of both flea species.
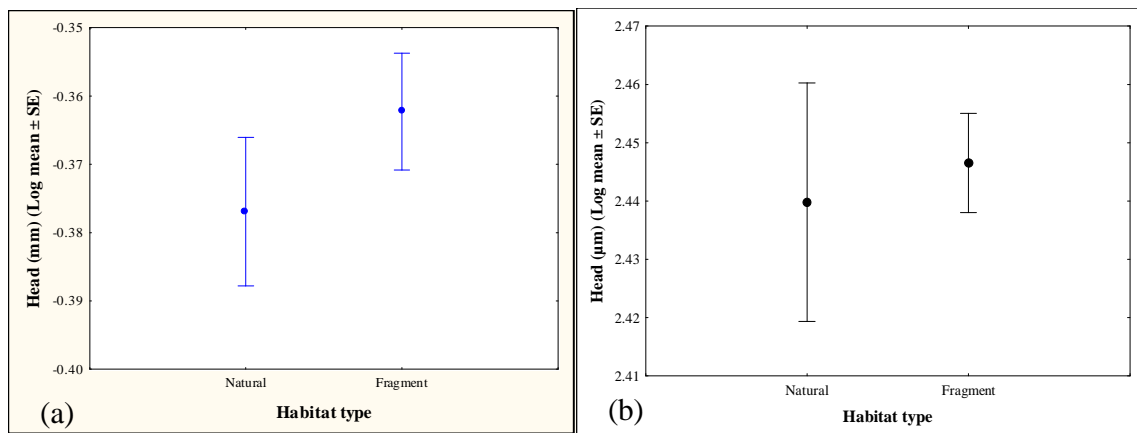
Figure 15: Mean head length of male (a) *Listropsylla agrippinae* and (b) *Chiastopsylla rossi* fleas recovered from *Rhabdomys pumilio* (n = 218) in the Cape Floristic Region, South Africa, 2009.

Head length of female *L. agrippinae* fleas were also significantly longer (p < 0.05) on *R. pumilio* trapped in fragments compared to natural localities (Figure 16a). In addition, female *L. agrippinae* recorded significantly longer mean total vertical length (p < 0.05) and larger product of horizontal- and vertical length (p < 0.05) in fragments compared to natural localities (Figures 17a and 18a). In contrast, female *C. rossi* fleas showed no significant (p > 0.05) difference in head length (Figure 16b) and no significant differences in vertical length or product of length (Figures 17b and 18b).
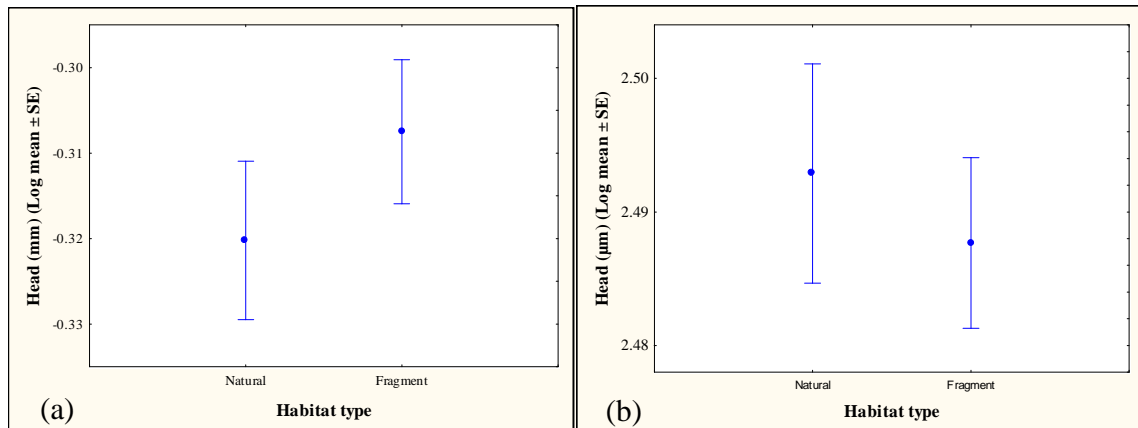
Figure 16: Mean head length of female (a) *Listropsylla agrippinae* and (b) *Chiastopsylla rossi* fleas recovered from *Rhabdomys pumilio* (n = 218) in the Cape Floristic Region, South Africa, 2009.
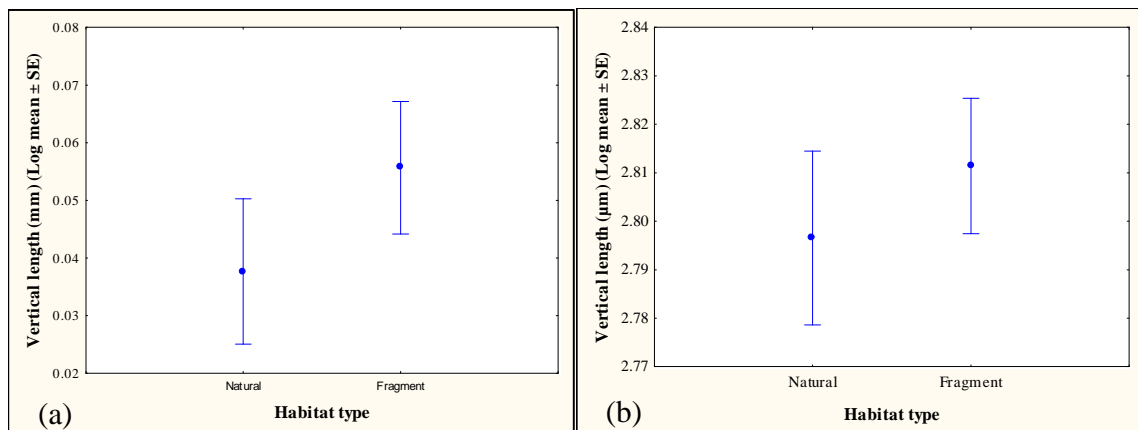
Figure 17: Mean vertical length of female (a) *Listropsylla agrippinae* and (b) *Chiastopsylla rossi* fleas recovered from *Rhabdomys pumilio* (n = 218) in the Cape Floristic Region, South Africa, 2009.
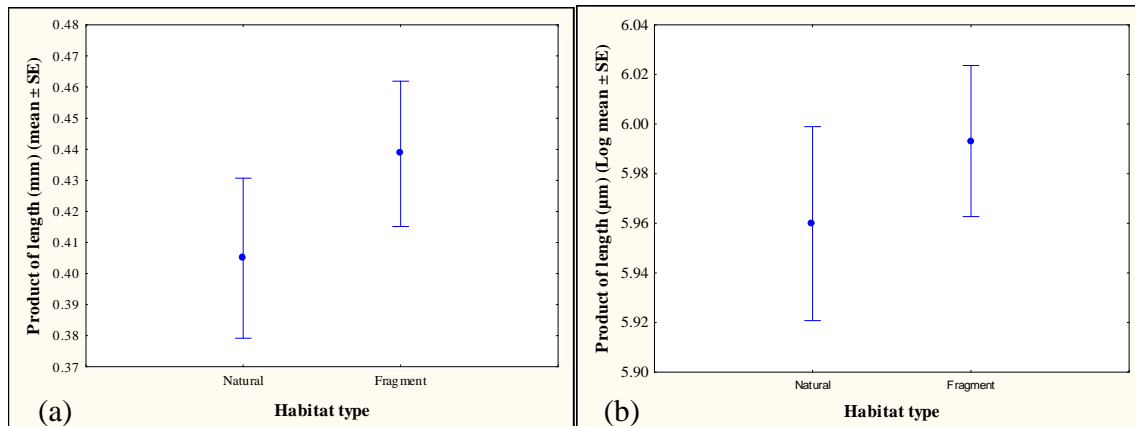
Figure 18: Mean product of horizontal- and vertical length of female (a) *Listropsylla agrippinae* and (b) *Chiastopsylla rossi* fleas recovered from *Rhabdomys pumilio* (n = 218) in the Cape Floristic Region, South Africa, 2009.

Ectoparasite abundance and prevalence

Ectoparasite species recorded on *R. pumilio* consisted of 11 tick, 8 mite, 6 flea and 1 louse species. All of these species were found in both habitat types, except for a new mite species (*Laelaps* sp 1) and a new tick species (*Ixodes* sp) that were only found in the natural localities. One specimen of the flea, *Xenopsylla demeilloni*, was recorded at one of the fragments (Zevenwacht). The total ectoparasite abundance for fragments was 3487 of which the louse represented 39.55 %, followed by ticks (35.36 %), mites (16.86 %) and fleas (8.23 %). Ticks were the most prevalent and occurred on 90.57 % of the mice in fragments, followed by mites (84.91 %), fleas (70.75 %) and the louse (70.75 %) (Table 7). Total ectoparasite abundance for natural localities was 4410 of which ticks represented 47.07 %, followed by the louse (24.94 %), mites (19.82 %) and fleas (8.16 %). Ticks were also the most prevalent in natural localities (77.68 %), followed by mites (72.32 %), the louse (66.07 %) and fleas (57.14 %) (Table 7).

Table 7: Mean abundance and prevalence of ectoparasite taxa and individual species recovered from *Rhabdomys pumilo* (n = 218) in fragments and natural localities in the Cape Floristic Region, South Africa, 2009.

Ectoparasite species	Mean abundance (±SE)		Prevalence (%)	
	Natural	**Fragment**	**Natural**	**Fragment**
Fleas	**1.61 (±0.20)**	**2.71 (±0.31)**	**57.14**	**70.75**
Chiastopsylla rossi	0.63 (±0.11)	0.94 (±0.16)	33.04	43.40
Dinopsyllus ellobius	0.12 (±0.04)	0.19 (±0.08)	9.82	10.38
Dinopsyllus tenax	0.03 (±0.02)	0.38 (±0.10)	2.68	20.75
Hysopthalmus temporis	0.17 (±0.05)	0.46 (±0.04)	11.61	7.55
Listropsylla agrippinae	0.66 (±0.11)	1.08 (±0.18)	33.04	40.57
Xenopsylla demeilloni	0	0.009 (±0.009)	0	0.94
Louse	**9.82 (±2.08)**	**13.01 (±2.70)**	**66.07**	**70.75**
Polyplax arvicanthis	9.82 (±2.08)	13.01 (2.70)	66.07	70.75
Mites	**3.83 (±0.54)**	**5.55 (±0.57)**	**72.32**	**84.91**
Androlaelaps fahrenholzi	1.57 (±0.20)	2.58 (±0.28)	52.68	68.87
Androlaelaps dasymys	0.26 (±0.06)	0.35 (±0.09)	16.96	20.75
Androlaelaps rhabdomysi	0.04 (±0.03)	0.07 (±0.04)	1.79	2.83
Laelaps sp 1	0.10 (±0.07)	0	3.57	0
Laelaps sp2	0.13 (±0.05)	0.04 (±0.02)	8.04	2.83
Laelaps sp3	0.07 (±0.04)	0.24 (±0.07)	3.57	14.15
Laelaps giganteus	1.66 (±0.42)	2.11 (±0.40)	27.68	46.23
Trombiculidae sp.			64.15	61.95
Ticks	**18.54 (±4.18)**	**12 (±1.87)**	**77.68**	**90.57**
Haemaphysalis aciculifer	0.23 (±0.08)	0.25 (±0.09)	8.93	9.43
Haemaphysalis elliptica	1.34 (±0.46)	2 (±0.80)	25.89	42.45
Ixodes fynbosensis	2.97 (±0.74)	0.64 (±0.17)	34.82	26.42
Ixodes alluaudi	0.027 (±0.015)	0.05 (±0.02)	2.68	4.72
Ixodes bakeri	1.67 (±0.35)	2.71 (±0.26)	42.86	37.74
Ixodes sp	0.018 (±0.013)	0	1.79	0
Rhipicephalus gertrudae group*	12.27 (±3.89)	6.53 (±1.48)	53.57	66.04
Rhipicephalus lounsburyi	0.009 (±0.009)	1.65 (±0.16)	0.89	16.04

*Consists of immature stages of 5 different species which could not be distinguished, namely *R. gertrudae*, *R. follis*, *R. capensis*, *R. simus* and *R. lounsburyi*

Mean predicted abundance for the combined ectoparasite taxa were not significantly different on the mice trapped in the fragments compared to the natural localities. (Figure 19; Table 8). The model explained 87.36 % of the deviance, but the significance of the effect of habitat type (explanatory variable) was not supported by the Wald statistic (Table 8).
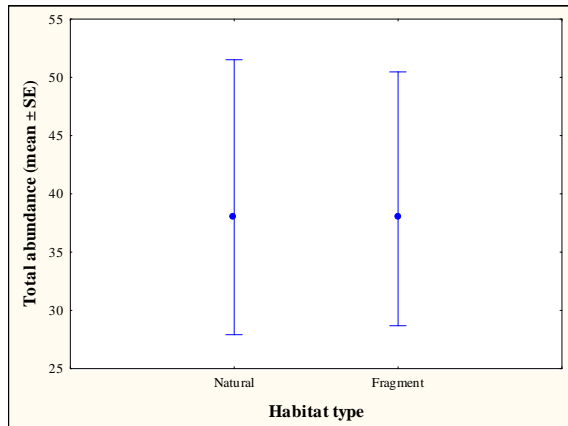
Figure 19: Mean predicted ectoparasite abundance on *Rhabdomys pumilio* (n = 218) in fragments and natural localities in the Cape Floristic Region, South Africa, 2009. (GLZ model (poisson, log link): y = habitat type + pair + sex + total length).

Table 8: Breakdown of the GLZ model and analysis for mean ectoparasite abundance on *Rhabdomys pumilio* in fragments and natural localities in the Cape Floristic Region, South Africa, 2009.

Model	Model p-value	% Deviance explained	Dispersion corrected		
Model(poisson, log link): y = habitat type + pair + sex code + total length	0*	87.36	Yes		
All effects					
Effect	**Degrees of freedom**	**Wald statistic**	**p-value**		
Intercept	1	1.00	0.32		
Habitat type	1	0.00	0.99		
Pair	3	5.99	0.11		
Sex code	1	3.34	0.07		
Total length	1	6.07	0.01*		
Parameter estimate					
Effect	**Level of effect**	**Estimate**	**Standard error**	**Wald statistic**	**p-value**
Intercept		1.07	1.07	1	0.32
Habitat type	natural	0	0.10	0	0.99
Pair	Somerset West	0.37	0.15	5.94	0.02*
Pair	Stellenbosch 1	-0.09	0.17	0.30	0.58
Pair	Porterville	-0.16	0.18	0.78	0.38
Sex code	0	0.20	0.11	3.34	0.07
Total length		0.12	0.05	6.07	0.01*
Scale		8.60	0		

* indicates significant differences (p < 0.05)

However when the data was re-analyzed without the data from two locality pairs (Elandskloof, Vergelegen, Mulderbosch and Wolwedans) mean predicted ectoparasite abundance was significantly higher (p < 0.05) on mice in fragments compared to natural localities (Figure 20; Table 9). In addition, the model explained 81.85 % of the deviance and the significance (p < 0.05) of the effect of habitat type (explanatory variable) was supported by the Wald statistic (4.59) (Table 9).

Figure 20: Mean predicted ectoparasite abundance on *Rhabdomys pumilio* (n = 115) in fragments and natural localities in the Cape Floristic Region, South Africa, 2009. Localities excluded: Elandskloof, Vergelegen, Mulderbosch and Wolwedans. (GLZ model (poisson, log link): y = habitat type + pair + sex + total length).

Table 9: Breakdown of the GLZ model and analysis for mean ectoparasite abundance on *Rhabdomys pumilio* in fragments and natural localities in the Cape Floristic Region, South Africa, 2009. Localities excluded: Elandskloof, Vergelegen, Mulderbosch and Wolwedans.

Model	Model p-value	% Deviance explained	Dispersion corrected		
Model(poisson, log link): y = habitat type + pair + sex code + total length	0*	81.85	Yes		
All effects					
Effect	Degrees of freedom	Wald statistic	p-value		
Intercept	1	1.68	0.20		
Habitat type	1	4.59	0.03*		
Pair	1	0.02	0.87		
Sex code	1	6.56	0.01*		
Total length	1	2.14	0.14		
Parameter estimate					
Effect	Level of effect	Estimate	Standard error	Wald statistic	p-value
Intercept		1.60	1.23	1.68	0.19
Habitat type	natural	-0.27	0.13	4.59	0.03*
Pair	Stellenbosch 1	-0.02	0.12	0.02	0.87
Sex code	0	0.42	0.16	6.56	0.01*
Total length		0.09	0.06	2.14	0.14
Scale		7.59	0		

*indicates significant differences (p < 0.05)

Fleas

Mean abundance of the flea taxon was significantly higher (p < 0.05) in fragments (2.71 (± 0.31)) compared to natural localities (1.61 (± 0.20)) (Table 7; Appendix: Figure 9, Table 1). Fleas in general were also more prevalent in fragments (70.75 %) than natural localities (57.14 %) (Table 7). The two most abundant flea species *L. agrippinae* and *C. rossi* were both more abundant in the fragments, but only *L. agrippinae* was significantly so (p < 0.05) (Figure 21; Table 10; Appendix: Figure 10; Table 2). The model explained 78.12 % of the deviance in mean abundance of *L.agrippinae* and the significance (p < 0.05) of the effect of habitat type (explanatory variable) was supported by the Wald statistic (4.59) (Table 10).

Figure 21: Mean predicted abundance of the flea, *Listropsylla agrippinae*, found on *Rhabdomys pumilio* (n = 218) in fragments and natural localities in the Cape Floristic Region, South Africa, 2009. (GLZ model (poisson, log link): y = habitat type + pair + sex + total length).

Table 10: Breakdown of the GLZ model and analysis of mean abundance for the flea, *Listropsylla agrippinae*, found on *Rhabdomys pumilio* in fragments and natural localities in the Cape Floristic Region, South Africa, 2009.

Model	Model p-value	% Deviance explained	Dispersion corrected		
Model(poisson, log link): y = habitat type + pair + sex code + total length	0*	78.12	yes		
All effects					
Effect	Degrees of freedom	Wald statistic	p-value		
Intercept	1	1.18	0.28		
Habitat type	1	4.97	0.03*		
Pair	3	14.08	0.003*		
Sex code	1	16.67	0*		
Total length	1	0.34	0.56		
Parameter estimate					
Effect	Level of effect	Estimate	Standard error	Wald statistic	p-value
Intercept		-1.34	1.24	1.18	0.28
Habitat type	natural	-0.26	0.12	4.97	0.03*
Pair	Somerset West	0.42	0.19	5.10	0.02*
Pair	Stellenbosch 1	-1.03	0.28	13.31	0*
Pair	Porterville	0.39	0.19	4.14	0.04*
Sex code	0	0.67	0.16	16.67	0*
Total length		0.03	0.06	0.34	0.56
Scale		1.46	0		

*indicates significant differences (p < 0.05)

The louse

Only a single louse species, *Polyplax arvicanthis*, were recovered in both habitat types (Table 7). Louse prevalence were higher in the fragments (70.75 %) compared to natural localities (66.07 %) (Table 7). Similarly, the mean abundance for the louse were higher, although not significant ($p > 0.05$) in fragments 13.01 ($\pm$ 2.70) compared to natural localities 9.82 ($\pm$ 2.08) (Table 7). The same trend was evident from mean predicted louse abundance (Figure 22). The model explained 92.64 % of the deviance and the non significance ($p > 0.05$) of the effect of habitat type (explanatory variable) was supported by the Wald statistic (0.49) (Table 11).
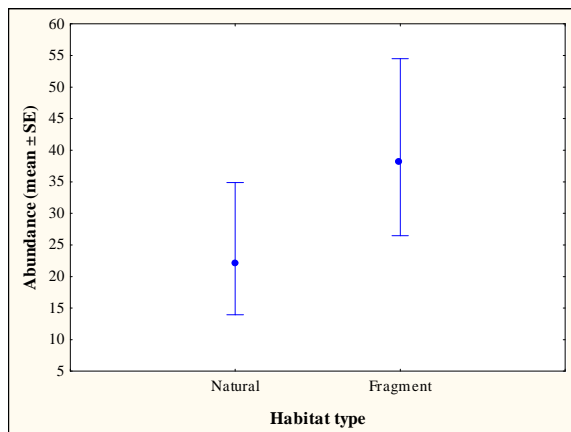

Figure 22: Mean predicted abundance of *Polyplax arvicanthis* on *Rhabdomys pumilio* (n = 218) in fragments and natural localities in the Cape Floristic Region, South Africa, 2009. (GLZ model (poisson, log link): y = habitat type + pair + sex + total length).

Table 11: Breakdown of the GLZ model and analysis for mean *Polyplax arvicanthis* abundance on *Rhabdomys pumilio* in fragments and natural localities in the Cape Floristic Region, South Africa, 2009.

Model	Model p-value	% Deviance explained	Dispersion corrected		
Model(poisson, log link): y = habitat type + pair + sex code + total length	0*	92.64	yes		
All effects					
Effect	Degrees of freedom	Wald statistic	p-value		
Intercept	1	0.42	0.52		
Habitat type	1	0.49	0.49		
Pair	3	2.24	0.52		
Sex code	1	3.71	0.05		
Total length	1	0.68	0.41		
Parameter estimate					
Effect	Level of effect	Estimate	Standard error	Wald statistic	p-value
Intercept		1.03	1.59	0.42	0.52
Habitat type	natural	-0.11	0.15	0.49	0.49
Pair	Somerset West	-0.30	0.30	1.03	0.31
Pair	Stellenbosch 1	0.04	0.25	0.02	0.88
Pair	Porterville	0.33	0.24	1.86	0.17
Sex code	0	0.36	0.19	3.71	0.05
Total length		0.06	0.08	0.68	0.41
Scale		7.29	0		

*indicates significant differences (p < 0.05)

Mites

Mean overall mite abundance on mice was significantly higher (p < 0.01) in fragments than natural localities (Appendix: Figure 11, Table 3). Mean abundance in fragments were 3.83 (± 0.54) and 5.55 (± 0.57) in natural localities (Table 7). Mites in general were also more prevalent in fragments (84.91 %) than natural localities (72.32 %) (Table 7). The two most abundant mite species in the two habitat types were *Laelaps giganteus* and *Androlaelaps fahrenholzi* (Table 7). Both these species were significantly (p < 0.05) more abundant in the fragments than in the natural localities (Table 7; Figure 23; Table 12; Appendix: Figure 12; Table 4). The model of mean predicted abundance of *L. giganteus* explained 74.93 % of the deviance and the significance (p < 0.01) of the effect of habitat type (explanatory variable) was supported by the Wald statistic (7.26) (Table 12).

Figure 23: Mean predicted abundance of the mite, *Laelaps giganteus*, found on *Rhabdomys pumilio* (n = 218) in fragments and natural localities in the Cape Floristic Region, South Africa, 2009. (GLZ model (poisson, log link): y = habitat type + pair + sex + total length).
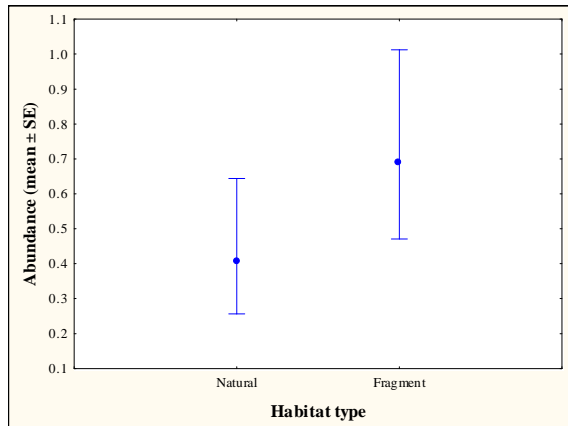
Table 12: Breakdown of the GLZ model and analysis for mean *Laelaps giganteus* abundance on *Rhabdomys pumilio* in fragments and natural localities in the Cape Floristic Region, South Africa, 2009.

Model	Model p-value	% Deviance explained	Dispersion corrected		
Model(poisson, log link): y = habitat type + pair + sex code + total length	0*	74.93	yes		
All effects					
Effect	Degrees of freedom	Wald statistic	p-value		
Intercept	1	6.41	0.01*		
Habitat type	1	7.26	0.01*		
Pair	3	22.83	0*		
Sex code	1	4.68	0.03*		
Total length	1	6.58	0.01*		
Parameter estimate					
Effect	Level of effect	Estimate	Standard error	Wald statistic	p-value
Intercept		-3.44	1.36	6.41	0.01*
Habitat type	natural	-0.39	0.15	7.26	0.01*
Pair	Somerset West	0.35	0.25	1.92	0.17
Pair	Stellenbosch 1	-0.51	0.30	2.86	0.09
Pair	Porterville	1.01	0.22	21.21	0*
Sex code	0	0.35	0.16	4.68	0.03*
Total length Scale		0.16 2.33	0.06 0	6.58	0.01*

*indicates significant differences (p < 0.05)

Ticks

In contract to fleas, the louse and mites the mean abundance for the combined tick taxon was significantly higher ($p < 0.01$) in natural areas (18.54 ± 4.18) than fragments (12 ± 1.87) (Figure 24a; Table 13). However, ticks were more prevalent on mice in fragments (90.57 %) than in natural localities (77.68 %) (Table 7). When the model was re-run but excluding Elandskloof, Vergelegen, Mulderbosch and Wolwedans the mean overall tick abundance were significantly ($p < 0.01$) higher in fragments than natural localities (Figure 24b; Table 14). The model for all sites (Table 13) explained 72.62 % of the deviance whereas the model without Elandskloof, Vergelegen, Mulderbosch and Wolwedans only explained 55.44 % (Table 14). The Wald statistic supported the significant effect of habitat type for both models (Table 13 and 14).

Figure 24: Mean predicted abundance of (a) ticks overall (all localities), and (b) ticks overall (without Elandskloof, Vergelegen, Mulderbosch and Wolwedans), found on *Rhabdomys pumilio* in fragments and natural localities in the Cape Floristic Region, South Africa, 2009. (GLZ model (poisson, log link): y = habitat type + pair + sex + total length).
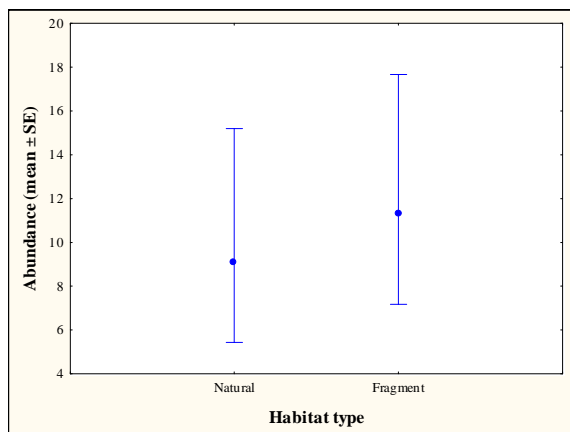
Table 13: Breakdown of the GLZ model and analysis for mean overall tick abundance on *Rhabdomys pumilio* in fragments and natural localities in the Cape Floristic Region, South Africa, 2009.

Model	Model p-value	% Deviance explained	Dispersion corrected		
Model(poisson, log link): y = habitat type + pair + sex code + total length	0*	72.61	yes		
All effects					
Effect	**Degrees of freedom**	**Wald statistic**	**p-value**		
Intercept	1	0.54	0.46		
Habitat type	1	8.27	0.004*		
Pair	3	14.61	0.002*		
Sex code	1	0.18	0.68		
Total length	1	5.84	0.02*		
Parameter estimate					
Effect	**Level of effect**	**Estimate**	**Standard error**	**Wald statistic**	**p-value**
Intercept		-1.15	1.57	0.54	0.46
Habitat type	natural	0.41	0.14	8.27	0.004*
Pair	Somerset West	0.74	0.22	11.14	0.001*
Pair	Stellenbosch 1	-0.01	0.26	0	0.98
Pair	Porterville	-1.24	0.41	9.06	0.003*
Sex code	0	0.06	0.15	0.18	0.68
Total length		0.18	0.07	5.84	0.02*
Scale		7.55	0		

*indicates significant differences ($p < 0.05$)
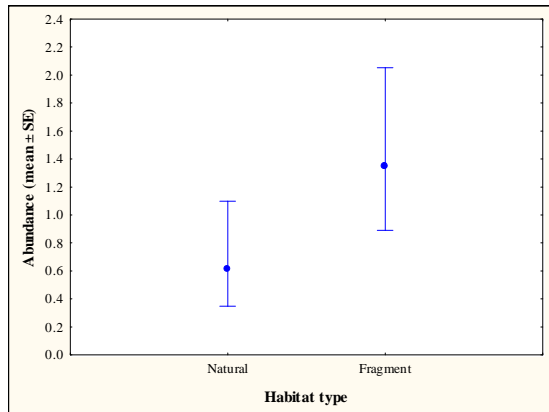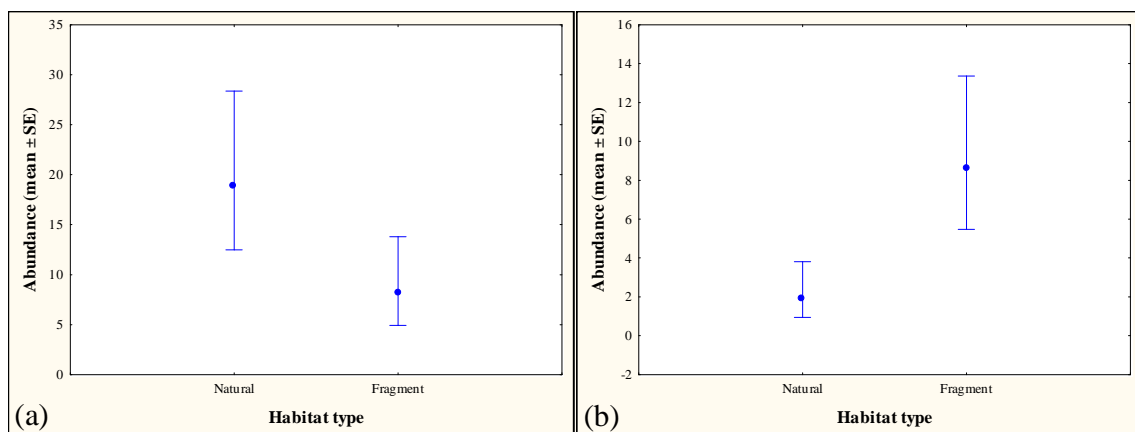
Table 14: Breakdown of the GLZ model and analysis for mean overall tick abundance on *Rhabdomys pumilio* in fragments and natural localities in the Cape Floristic Region, South Africa, 2009 without Elandskloof, Vergelegen, Mulderbosch and Wolwedans.

Model	Model p-value	% Deviance explained	Dispersion corrected		
Model(poisson, log link): y = habitat type + pair + sex code + total length	0*	55.44	yes		
All effects					
Effect	**Degrees of freedom**	**Wald statistic**	**p-value**		
Intercept	1	0.09	0.76		
Habitat type	1	19.83	0*		
Pair	1	9.30	0.002*		
Sex code	1	9.25	0.002*		
Total length	1	1.57	0.21		
Parameter estimate					
Effect	**Level of effect**	**Estimate**	**Standard error**	**Wald statistic**	**p-value**
Intercept		-0.45	1.51	0.09	0.76
Habitat type	natural	-0.76	0.17	19.83	0*
Pair	Stellenbosch 1	0.48	0.16	9.30	0.002*
Sex code	0	0.64	0.21	9.25	0.002*
Total length		0.09	0.07	1.57	0.21
Scale		3.95	0		

*indicates significant differences ($p < 0.05$)

Rhipicephalus gertrudae group and *H. elliptica* were the most abundant tick species on the mice in the study. When looking at fragments and natural localities separately it was found that *R. gertrudae* group was the most abundant tick species in both habitat types (Table 7). *Rhipicephalus gertrudae* group were significantly ($p < 0.01$) more abundant in the natural (12.27 ± 3.89) localities than the fragments (6.53 ± 1.48) (Figure 25a; Table 7, 15). In contrast, the prevalence of *R. gertrudae* group was more in the fragments (66.04 %) than in the natural (53.57 %) localities (Table 7). When the model was re-run without the data for Elandskloof, Vergelegen, Mulderbosch and Wolwedans, the mean abundance of *R. gertrudae* group were significantly ($p < 0.01$) more abundant in fragments than natural localities (Figure 25b). The model for all eight localities (Table 15) explained 78.93 % of the deviance whereas the model without Elandskloof, Vergelegen, Mulderbosch and Wolwedans only explained 56.42 % (Table 16). The Wald statistic supported the significant effect of habitat type for both models (Table 15 and 16).
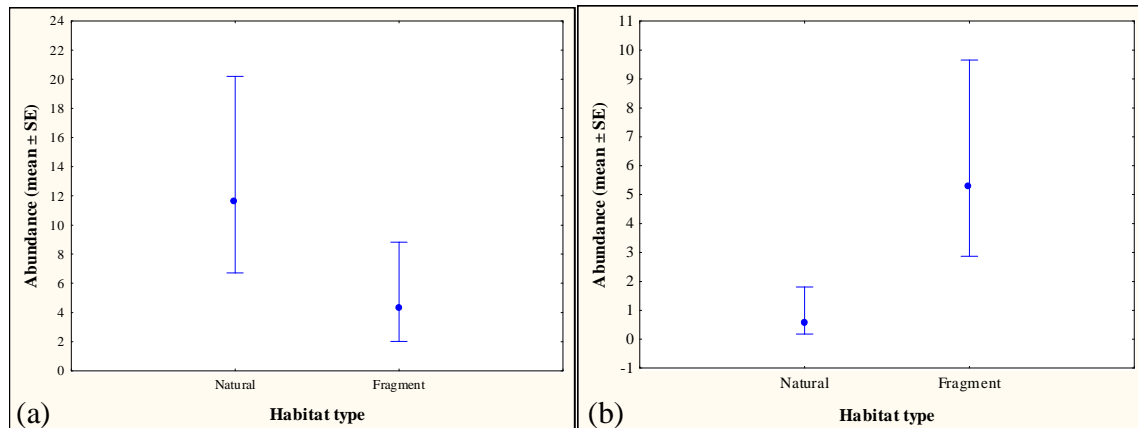
Figure 25: Mean predicted abundance of (a) *Rhipicephalus gertrudae* group (all localities) and (b) *Rhipicephalus gertrudae* group (without Elandskloof, Vergelegen, Mulderbosch and Wolwedans) found on *Rhabdomys pumilio* in fragments and natural localities in the Cape Floristic Region, South Africa, 2009. (GLZ model (poisson, log link): y = habitat type + pair + sex + total length).

Table 15: Breakdown of the GLZ model and analysis for mean abundance of *Rhipicephalus gertrudae* group on *Rhabdomys pumilio* in fragments and natural localities in the Cape Floristic Region, South Africa, 2009.

| Model	Model p-value	% Deviance explained	Dispersion corrected		
Model(poisson, log link): y = habitat type + pair + sex code + total length	0*	78.93	yes		
All effects					
Effect	Degrees of freedom	Wald statistic	p-value		
Intercept	1	1.90	0.17		
Habitat type	1	6.83	0.01*		
Pair	3	7.99	0.05*		
Sex code	1	0.07	0.79		
Total length	1	5.82	0.02*		
Parameter estimate					
Effect	Level of effect	Estimate	Standard error	Wald statistic	p-value
Intercept		-2.91	2.11	1.90	0.17
Habitat type	natural	0.51	0.19	6.83	0.01*
Pair	Somerset West	0.62	0.31	3.91	0.05*
Pair	Stellenbosch 1	0.07	0.35	0.04	0.85
Pair	Porterville	-1.42	0.60	5.71	0.02*
Sex code	0	-0.05	0.19	0.07	0.79
Total length		0.24	0.10	5.82	0.02*
Scale		7.87	0		

*indicates significant differences (p < 0.05)

Table 16: Breakdown of the GLZ model and analysis for mean abundance of *Rhipicephalus gertrudae* group on *Rhabdomys pumilio* in fragments and natural localities in the Cape Floristic Region, South Africa, 2009 without Elandskloof, Vergelegen, Mulderbosch and Wolwedans.

Model	Model p-value	% Deviance explained	Dispersion corrected		
Model(poisson, log link): y = habitat type + pair + sex code + total length	0*	56.42	yes		
All effects					
Effect	**Degrees of freedom**	**Wald statistic**	**p-value**		
Intercept	1	0.43	0.51		
Habitat type	1	15.91	0*		
Pair	1	7.81	0.01*		
Sex code	1	6.58	0.01*		
Total length	1	0.15	0.70		
Parameter estimate					
Effect	**Level of effect**	**Estimate**	**Standard error**	**Wald statistic**	**p-value**
Intercept		1.33	2.02	0.43	0.51
Habitat type	natural	-1.11	0.28	15.91	0*
Pair	Stellenbosch 1	0.62	0.22	7.81	0.01*
Sex code	0	0.73	0.28	6.58	0.01*
Total length		-0.04	0.10	0.15	0.70
Scale		4.00	0		

*indicates significant differences ($p < 0.05$)

Mean abundance of *H. elliptica* was higher, although not significantly so, in fragments (2 ± 0.80) than in natural localities (1.34 ± 0.46) (Figure 26a and b; Table 7, 17 and 18). Prevalence of *H. elliptica* in fragments was almost double that of natural localities (Table 7). When the model was re-run without the data for Elandskloof, Vergelegen, Mulderbosch and Wolwedans, the mean abundance of *H. elliptica* were still more abundant in fragments than natural localities but not significant not ($p > 0.05$) (Figure 26b). The model for all eight localities (Table 17) explained 94.87 % of the deviance whereas the model without Elandskloof, Vergelegen, Mulderbosch and Wolwedans only explained 66.43 % (Table 18). The Wald statistic supported the non-significant effect of habitat type for both models (Table 17 and 18).
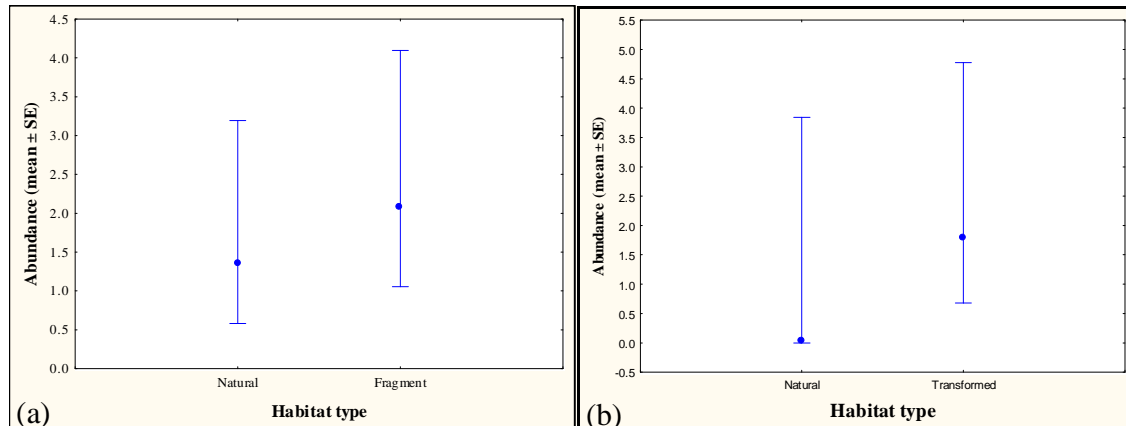
Figure 26: Mean predicted abundance of (a) *Haemaphysalis elliptica* (all localities) and (b) *Haemaphysalis elliptica* (without Elandskloof, Vergelegen, Mulderbosch and Wolwedans) found on *Rhabdomys pumilio* in fragments and natural localities in the Cape Floristic Region, South Africa, 2009. (GLZ model (poisson, log link): y = habitat type + pair + sex + total length).

Table 17: Breakdown of GLZ model and analysis for mean *Heamaphysalis elliptica* abundance on *Rhabdomys pumilio* in fragments and natural localities of the Cape Floristic Region, South Africa, 2009.

| Model	Model p-value	% Deviance explained	Dispersion corrected		
Model(poisson, log link): y = habitat type + pair + sex code + total length	0*	94.87	yes		
All effects					
Effect	Degrees of freedom	Wald statistic	p-value		
Intercept	1	0.77	0.38		
Habitat type	1	0.68	0.41		
Pair	3	0.59	0.90		
Sex code	1	0.59	0.44		
Total length	1	1.19	0.27		
Parameter estimate					
Effect	Level of effect	Estimate	Standard error	Wald statistic	p-value
Intercept		-2.44	2.78	0.77	0.38
Habitat type	natural	-0.21	0.26	0.68	0.41
Pair	Somerset West	0.22	0.40	0.30	0.58
Pair	Stellenbosch 1	-0.16	0.42	0.15	0.70
Pair	Porterville	-0.21	0.46	0.20	0.65
Sex code	0	0.22	0.28	0.59	0.44
Total length		0.14	0.13	1.19	0.27
Scale		4.72	0		

*indicates significant differences (p < 0.05)

Table 18: Breakdown of the GLZ model and analysis for mean abundance of *Haemaphysalis elliptica* on *Rhabdomys pumilio* in fragments and natural localities in the Cape Floristic Region, South Africa, 2009 without Elandskloof, Vergelegen, Mulderbosch and Wolwedans.

Model	Model p-value	% Deviance explained	Dispersion corrected		
Model(poisson, log link): y = habitat type + pair + sex code + total length	0*	66.43	yes		
All effects					
Effect	**Degrees of freedom**	**Wald statistic**	**p-value**		
Intercept	1	2.35	0.13		
Habitat type	1	2.87	0.09		
Pair	1	0.19	0.66		
Sex code	1	2.83	0.09		
Total length	1	1.51	0.22		
Parameter estimate					
Effect	**Level of effect**	**Estimate**	**Standard error**	**Wald statistic**	**p-value**
Intercept		-5.77	3.76	2.35	0.13
Habitat type	natural	-2.24	1.32	2.87	0.09
Pair	Stellenbosch 1	-0.13	0.29	0.19	0.66
Sex code	0	0.81	0.48	2.83	0.09
Total length		0.20	0.16	1.51	0.22
Scale		3.72	0		

*indicates significant differences (p < 0.05)

Ectoparasite species assemblage

Ectoparasite species assemblage differed significantly ($p < 0.001$) between fragments and natural localities. However only a small percentage of the variation was explained by transformation (Global R = 0.16) (Figure 27a and b). The ordination suggests that the species assemblages are more similar between fragmented localities (points closer to each other, Figure 27a), while the level of similarity is lower between pristine natural localities (points further apart, Figure 27a). When looking at specific regions (Figure 27b), there appears to be no clear separation between localities in terms of species assemblages.
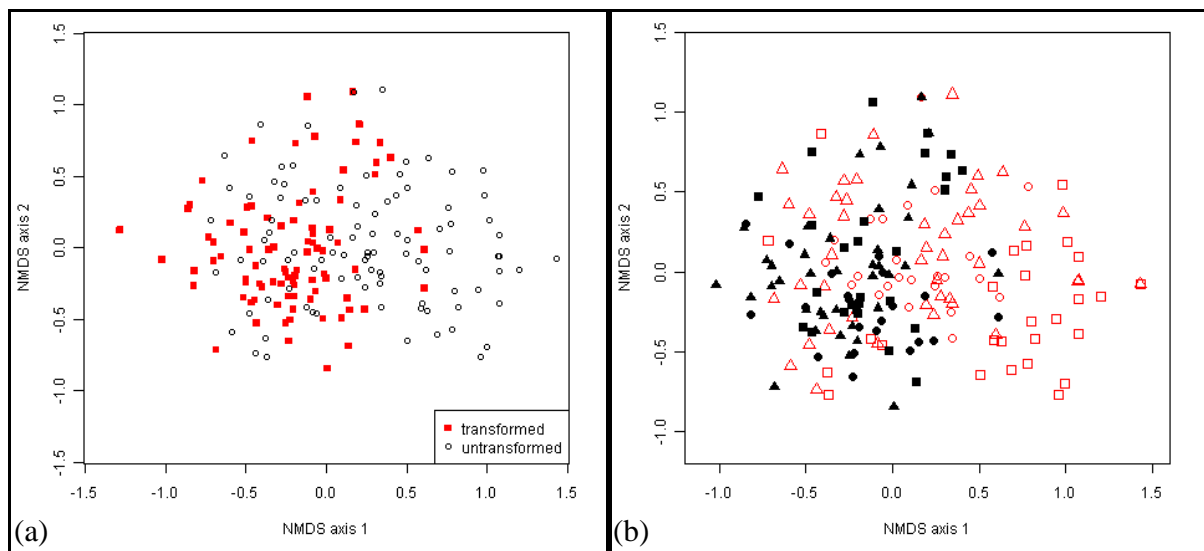
Figure 27: Non-metric multidimensional scaling of ectoparasite assemblage structure found on *Rhabdomys pumilio* (n = 218) at (a) fragments (transformed) and natural localities (untransformed) (b) three geographically different regions sampled (square = Porterville; circle = Somerset West; triangle = Stellenbosch) in the Cape Floristic Region, South Africa, 2009. (Global R = 0.16; $p < 0.001$; stress = 23.96).

3.6 Discussion

From the present study, it is evident that habitat transformation and subsequent fragmentation results in higher abundances and prevalence of ectoparasites on rodents. This pattern was most probably brought about by a combination of host factors such as higher host densities, larger host body size and improved body condition because of available resources in and around habitat fragments. Further, larger body size and improved condition of rodents in fragments enabled the most abundant flea in the study, *L. agrippinae* to take advantage and grow larger in transformed habitats.

Rhabdomys pumilio was the only rodent species that was recorded in high numbers and in all of the localities (pristine natural and remnant fragments) in the present study. This pattern is supported by previous studies in the CFR (Pretorius 1993; Matthee *et al.* 2007, 2010; Mugabe 2008) and a study done along a transect in the arid western part of SA and in Namibia (Froeschke *et al.* 2010). *Rhabdomys pumilio* is a generalist rodent species that is able to survive and thrive in natural and transformed habitats and it is therefore not surprising that it is able to out-compete more specialist species such as gerbils (*Gerbilliscus* sp) and elephant shrews (e.g. *Elephantulus edwardii*). This pattern confirms climate change predictions for SA taxa (Erasmus *et al.* 2002) and supports other studies that have shown that habitat transformation leads to an increase in generalist species and a loss in specialists (de la Penã *et al.* 2003; Krasnov *et al.* 2006; Rodríguez and Peris 2007; Manor and Saltz 2008).

The type of anthropogenic activities inside and outside fragments and the absence or low density of natural predators, and competing animal species can lead to uncontrolled population increases of generalist species (Díaz *et al.* 1999; Wilcox and Gubler 2005; Martínez-Mota *et al.* 2007; Mbora and McPeek 2009). High animal densities result in increased competition for food, which can result in increased stress levels (Martínez-Mota *et al.* 2007) and reduced immunocompetence (Anderson and May 1978). However, evident from the present study is the fact that the negative effects of fragmentation can be countered if resources (food, water and cover) are available in and around fragments (Wilcox and Gubler 2005; Friggens and Beier 2010). In the present study higher rodent densities were recorded in two of the four fragments, with a third showing no

difference between fragment and the paired natural locality. Habitat fragments included in the present study were characterized by the presence of water, food (in most cases, a seasonal cover crop such as wheat that grows amongst the vines) and cover (remnant renosterveld vegetation and also vegetation that was chopped and left and or timber logs that lay scattered in the fragments) (personal observation). The availability of resources might explain larger body size and better body condition of *R. pumilio* individuals in fragments compared to extensive natural areas. The fact that *R. pumilio*, a generalist, is able to take advantage of resources provided by transformed habitats in the CFR supports previous studies that generalist small mammal species are more able to survive habitat transformation (Erasmus *et al.* 2002; de la Peñã *et al.* 2003; Krasnov *et al.* 2006; Rodríguez and Peris 2007; Manor and Saltz 2008). A recent study done in a Brazilian secondary forest fragments within an agricultural matrix found that fragmentation had no negative effect on body condition and density of two generalist small mammal species (Montane grass mouse, *Akodon montensis* and Black-footed pygmy rice rat, *Oligoryzomys nigripes*) (Pűttker *et al.* 2008).

Animal body size tends to be positively related to longevity, a pattern repeatedly shown for mammals in particular (Peters 1983). The host animal is the main resource for parasites and larger host species would therefore be more predictable resources for their parasites (Peters 1983; Krasnov *et al.* 2006). In addition, larger hosts will provide parasites with a larger area and abundance of resources to utilize (Moore and Wilson 2002; Poulin 2007). This will result in more energy for the parasite to invest in body size, which in turn will result in increased fecundity (for females) and longer life-span for both sexes (Peters 1983; Poulin 2007). As mentioned above, *R. pumilio* trapped in the fragments were larger and in a better condition compared to natural localities. This may explain longer head length for male and female *L. agrippinae* fleas on mice trapped in fragments. Although *L. agrippinae* females also showed significantly longer vertical lengths and product, of horizontal length and width, in fragments the resulting difference may be biased because of the possibility that female fleas may be bearing eggs. Selection should favour high fecundity and thus larger female body size with abundant and high quality food resources (Poulin and Morand 1997). Controlled studies concur and have shown that fleas benefit from feeding on well-fed rodents through shorter development time and improved quality of offspring (Krasnov *et al.* 2005).

This pattern was not recorded for the second most abundant flea *C. rossi*. There are several possible reasons why no relationship was found for this flea. Firstly, *C. rossi* may be less tolerant of external environmental conditions (Segerman 1995). In addition, several burrowing rodent species such as Brants' whistling rat (*Parotomys brantsii*) and the common Highveld gerbil (*Gerbilliscus brantsii*) are listed as potential and preferred hosts respectively (Segerman 1995). Based on host preference and geographical descriptive information it therefore seems that *C. rossi* may be a nest flea. In contrast, *L. agrippinae* may be characterized as a fur flea as it seems to be more tolerant of variable climatic conditions and prefer rodents that make aboveground nests or stick nests (for example *R. pumilio* and the Bush karoo rat, *O. unisulcatus*) (Segerman 1995). It is therefore possible that the level of host association (i.e. time spent on the body of the host) may influence the degree to which the flea respond to host factors. Another factor may be the fact that *C. rossi* is one of the smaller flea species found on rodents in southern Africa (Segerman 1995) and was the smallest flea species on *R. pumilio* in the present study (mean female length 1.75 µm, range 1.6-1.9). Due to the small size it may be difficult to clearly distinguish between the morphological parts for measurements. In addition, although care was taken when fleas were removed from the pelage of the rodent, and mounted, it is possible that some individuals could have been damaged, which would bias the measurements.

Host-parasite size relationship has been tested by Kirk (1991) for a number of insects and their hosts. More specific, the author also looked at the relationship of flea body size and host body size. Surprisingly a significant positive regression was found for 42 flea species, even though fleas generally spend part of their life off the host. A positive relationship between parasite size and their host size has also been found for various other parasite taxa including chewing lice parasitizing rodents (Harvey and Keymer 1991; Morand *et al*. 2000), mites parasitic on flowers (Colwell 1986) and sucking lice parasitizing mammals (Kim 1985). Ticks, in contrast, did not show any body size relationship between host mass or environmental temperatures in the wild (Poulin 1998). The latter supports the above mentioned suggestion that the strength of the association between host and parasite body size may be related to the length of time that the parasite spend on the host.

Evident from the study is the fact that *R. pumilio* is host to a large number of ectoparasite species that can occur in high abundances and prevalence. High ecto- and endoparasite diversity and infestations have also previously been recorded for this common rodent in the WCP and other parts of SA (Matthee *et al.* 2007, 2010; Froeschke *et al.* 2010). This supports the patterns that habitat generalist hosts generally harbour high parasite diversity (Egoscue 1976; Matthee *et al.* 2007). Several of the parasite species that are found on *R. pumilio* are of importance in the etiology of zoonotic diseases in humans, and play an important role in the transmission of diseases of domestic and wild animals (Walker 1991; Norval and Horak 2004; Matthee *et al.* 2007). For example, all of the flea species found in the current study has the potential to act as vectors of *Yersinia pestis*, the plague bacterium (De Meillon *et al.* 1961). In addition *R. pumilio* is known to carry plague antibodies in certain parts of SA, especially the Eastern Cape Province (Sheperd and Leman 1983; Sheperd *et al.* 1983). In addition, the tick *H. elliptica* can transmit *Babesia canis rossi* to dogs and *Rickettsia conori* and *Coxiella burnetti* to humans. It is therefore evident that higher densities of *R. pumilio* in fragmented landscapes can pose a potential disease risk to humans and domestic animals that used these fragments.

Changes in rodent host diversity, density, susceptibility and behaviour will have knock-on effects on parasite assemblages and populations. Anthropogenic-linked diversity loss can favour generalist host species, which tend to harbour more parasite species and lead to higher parasite abundance (Egoscue 1976; Friggens and Beier 2010). In addition, higher rodent host densities can enhance transmission of parasites between and within species and a number of studies have shown that the prevalence of parasites is significantly associated with host density (Anderson and May 1979; Morand and Poulin 1998; Mbora and McPeek 2009). In addition, the extent of habitat transformation and characteristics of fragments vary greatly. Similarly the subsequent impact on parasite taxa may also be taxon-specific. Goodall (2008) studied the effect of fragmentation on bird lice and mites in Mexico and found that lice prevalence was highest in the least intensified agricultural system, whereas mite prevalence was highest in the most intensified. In addition, Friggens and Beier (2010) showed that flea abundance and prevalence increased with increasing disturbance and peaked at intermediate disturbances such as agricultural areas which supported the pattern found in this study. Further, nymphal and larval tick densities,

recorded using drag sampling, seem to be inversely correlated with area of forest fragments (Allan *et al*. 2003).

In the present study mean abundances were higher for combined and also most of the individual flea, louse, tick and mite taxa on rodents in fragments compared to natural localities. The difference was significant for all the taxa combined and also for most of the individual taxa. Prevalence of fleas, the louse, mites and ticks were also higher in fragments compared to natural localities. Individual parasite species differ in terms of life history, and this is especially so for fleas (Marshall 1981; Krasnov *et al*. 1997). It is therefore essential to further explore individual species-specific patterns. Intraspecific analyses of the two most abundant flea (*L. aggripinae* and *C. rossi*) and mite (*L. giganteus* and *A. fahrenholzi*) species on *R. pumilio* confirmed the general flea and mite pattern. When looking at the individual tick species and specifically *R. gertrudae* group, a contrasting pattern was recorded for mean abundance; higher abundances were recorded on rodents in extensive natural localities compared to fragments. This is also in contrast to a higher prevalence for the tick taxon combined and for most of the abundant tick species. However, when two locality pairs were excluded from the analyses the abundance pattern changed to support the prediction. Two of the controlled natural localities, Elandskloof and Wolwedans, differed in certain habitat characteristics compared to the other two natural localities (Jonkershoek and Voëlvleidam). The latter two were large nature reserves (> 8 km^2); whereas Elandskloof and Wolwedans were relatively large continuous natural vegetation fragments (< 6 km^2) that were partly surrounded by vineyards and pastures.

The position of the trap lines, due to limited accessibility, and the relatively close proximity to peri-urban areas could have facilitated higher tick burdens in Elandskloof and Wolwedans. Although the aim was to use extensive pristine nature reserves this was not possible due to widespread seasonal fires in the Stellenbosch, Somerset West and Paarl regions of the CFR a few months prior to the start of the study. In addition, although no supporting data is available, it did seem that plant composition of Elandskloof and Wolwedans differed in general from Jonkershoek and Voëlvleidam (personal observation). Plant cover is an important factor for free-living tick stages as it influences the amount of shade available in the area, which can influence tick development and survival (ELGhali and Hassan 2010). Mean abundance and prevalence of

the tick *H. elliptica* however supported the prediction that larger burdens will be found on rodents in fragments compared to natural localities.

In conclusion, the current study show that habitat fragments surrounded by agricultural activities counter negative effects of fragmentation in that rodents have an improved body condition and are larger compared to natural localities. A combination of high quality hosts and plant cover, provided by remnant vegetation, did not only result in larger fleas but also facilitated an increase in the mean abundance and prevalence of generalist ectoparasite species such as fleas, mites and ticks in transformed areas. This could have major implications for disease transmission and risk in these areas. The current study is unique in that it's the first study to look at the effect of anthropogenic transformation on the complete ectoparasite burden of a host and it is also the first study on this topic to be done in the WCP and SA. Future studies on pathogen incidence will be valuable to confirm if there is a higher incidence of *B. canis rossi* in *H. elliptica* ticks in fragments.

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Chapter 4

General conclusion

The Cape Floristic Region (CFR) is classified as a biodiversity hotspot due to high plant diversity an endemism (Cowling and Hilton-Taylor 1994). Further, this region is also charactarized by a high diversity of small mammal species (Skinner and Chimimba 2005) and a diverse assemblage of insects (Giliomee 2003). However, at present not much is known with regard to parasite assemblages and diversity on terrestrial animals in this region. Recent studies have started to address this paucity of information by studying parasite diversity, species composition and temporal variation on *Rhabdomys pumilio*, a generalist rodent in the CFR (Matthee *et al*. 2007, 2010). The present study support earlier findings that *R. pumilio* in this region is an important host to a large number of ectoparasite species (Chapter 2). Many of the ectoparasites found are important vectors of pathogens and disease of domestic, wild animals and humans (Chapter 2). A clear temporal pattern was recorded for the different ectoparasites taxa that ranged from an on-host preference during cool wet months (mites and fleas) to high abundance during the hot dry months (ticks and a host-specific louse) (Chapter 2).

Anthropogenic habitat fragmentation is considered to be one of the largest threats to biodiversity loss in the world (Sala *et al*. 2000). To date most research efforts have focussed on the effect of fragmentation on plants and terrestrial animals. However, a growing body of literature stresses the important relationship between vertebrate hosts, parasites and disease risk (Platz *et al*. 2000; Daszak *et al.* 2001; Keesing *et al.* 2006). Against this backdrop, studies have recently been conducted on the effect of fragmentation on arthropod vectors and disease risk (Vaz *et al*. 2007; Püttker *et al*. 2008; Mbora and McPeek 2009; Cottontail *et al*. 2009; Wright *et al*. 2009; Friggens and Beier 2010). From this study, it is evident that fragments in agricultural landscapes provide ideal conditions for generalist rodent species, like *R. pumilio*, to grow larger, improve their body condition and to reach high densities (Chapter 3). Consequently, ectoparasites benefit from these conditions (increase in mean abundance and prevalence) (Chapter 3). In addition, certain host-dependent parasites, such as fur fleas, are able to physically adapt and benefit from feeding on a

better quality host (Chaper 3). This will have consequences on parasite fecundity, burden and disease risk in fragmented habitats.

The study highlights an additional adverse effect related to habitat fragmentation and emphasizes the importance of conserving connected and or extensive natural habitats within agricultural landscapes.

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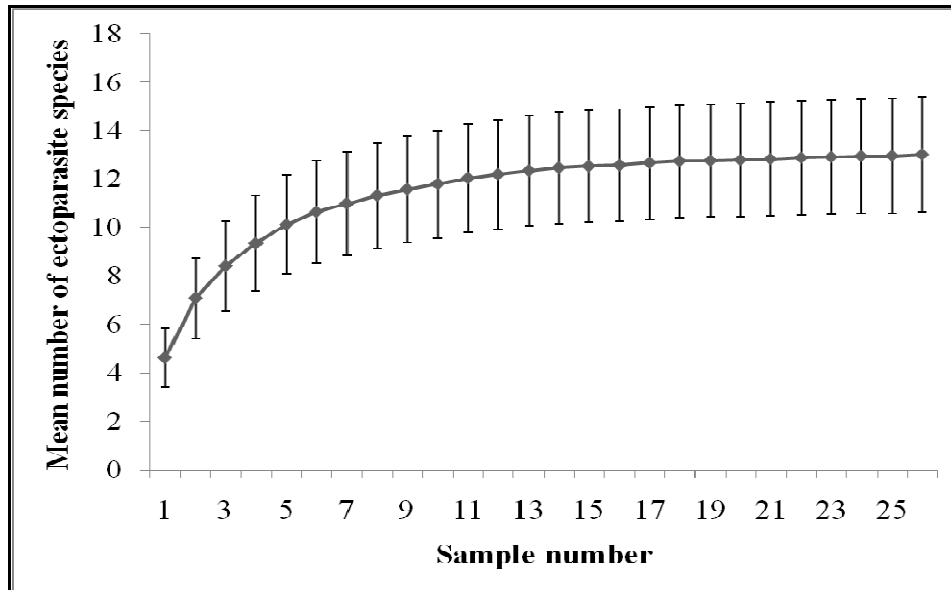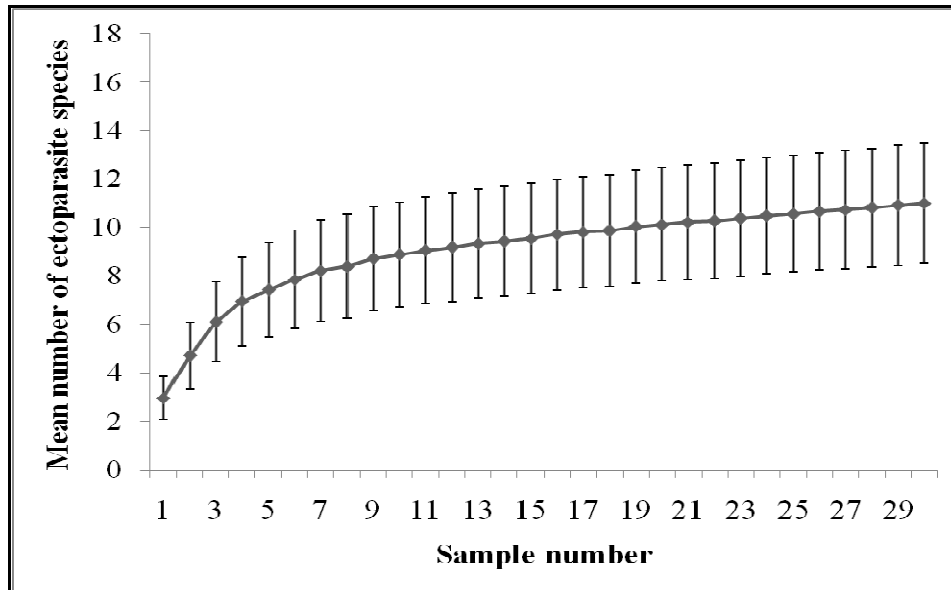
Appendix

Figures
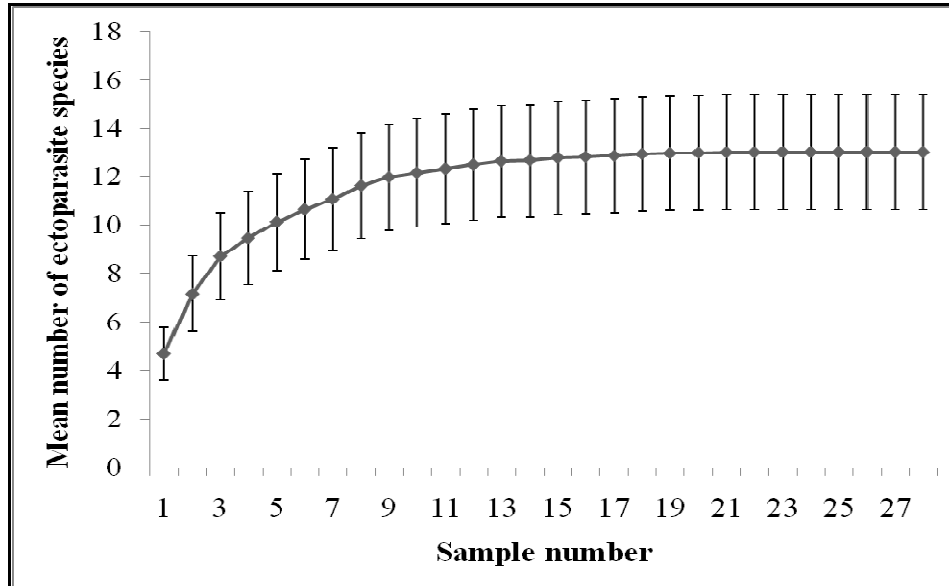
Figure 1: Species accumulation curve (mean ± SE) (31.64 ± 6.06) of the ectoparasite species found on 28 *Rhabdomys pumilio* sampled at Mulderbosch in the Cape Floristic Region, South Africa, October to December 2009. Resampling statistics using sample with replacement and 100 randomisations (Gotelli and Colwell 2001).
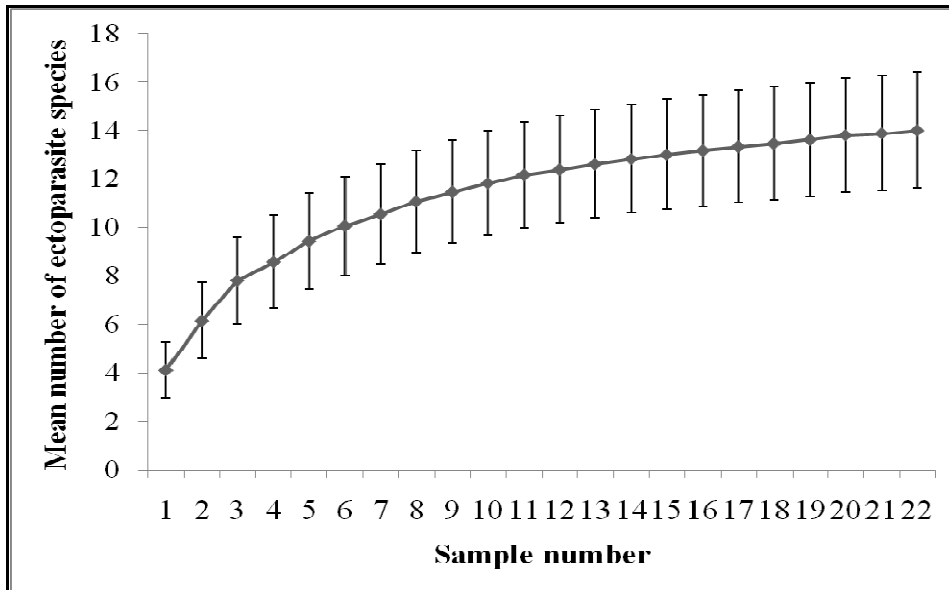
Figure 2: Species accumulation curve (mean ± SE) (37.91 ± 16.95) of the ectoparasite species found on 22 *Rhabdomys pumilio* sampled at Wolwedans in the Cape Floristic Region, South Africa, October to December 2009. Resampling statistics using sample with replacement and 100 randomisations (Gotelli and Colwell 2001).
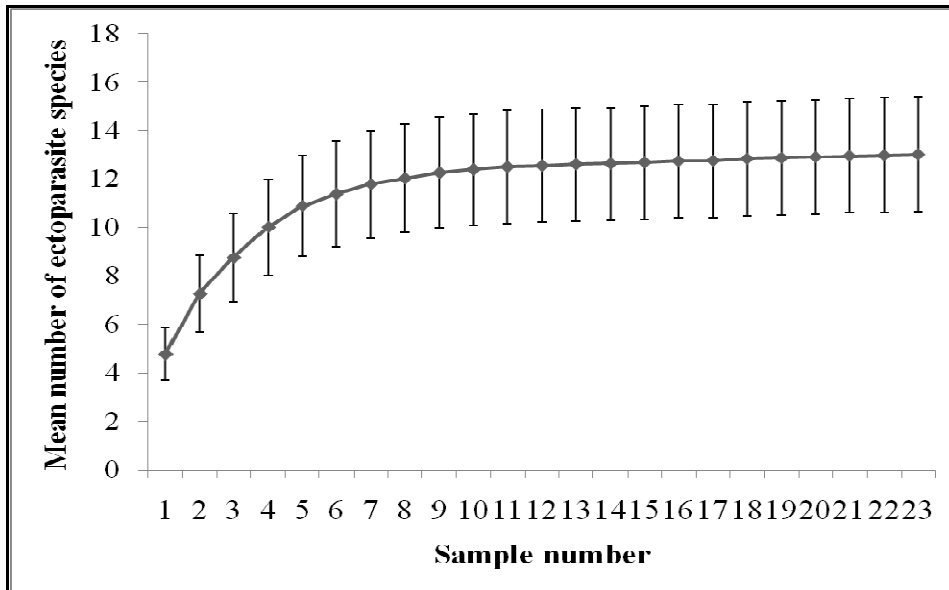
Figure 3: Species accumulation curve (mean ± SE) (40.12 ± 10.28) of the ectoparasite species found on 26 *Rhabdomys pumilio* sampled at Waterval farm in the Cape Floristic Region, South Africa, October to December 2009. Resampling statistics using sample with replacement and 100 randomisations (Gotelli and Colwell 2001).

Figure 4: Species accumulation curve (mean ± SE) (28.53 ± 7.67) of the ectoparasite species found on 30 *Rhabdomys pumilio* sampled at Voëlvleidam in the Cape Floristic Region, South Africa, October to December 2009. Resampling statistics using sample with replacement and 100 randomisations (Gotelli and Colwell 2001).
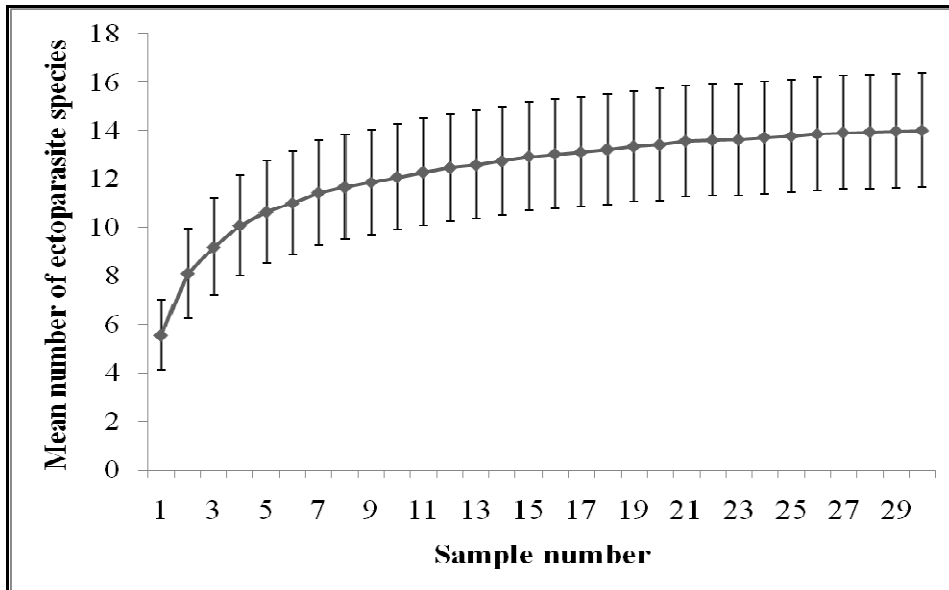
Figure 5: Species accumulation curve (mean ± SE) (46.48 ± 13.54) of the ectoparasite species found on 23 *Rhabdomys pumilio* sampled at Vergelegen in the Cape Floristic Region, South Africa, October to December 2009. Resampling statistics using sample with replacement and 100 randomisations (Gotelli and Colwell 2001).

Figure 6: Species accumulation curve (mean ± SE) (61.37 ± 9.65) of the ectoparasite species found on 30 *Rhabdomys pumilio* sampled at Elandskloof in the Cape Floristic Region, South Africa, October to December 2009. Resampling statistics using sample with replacement and 100 randomisations (Gotelli and Colwell 2001).
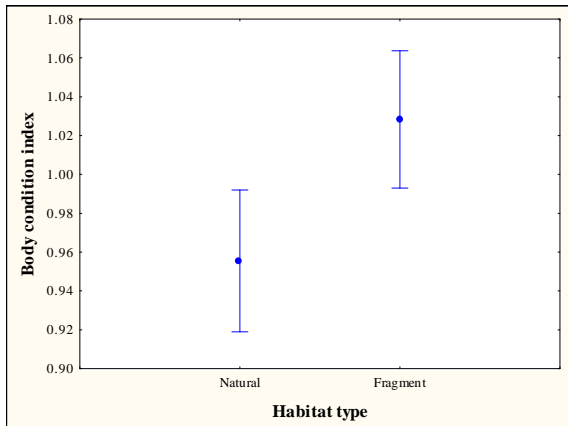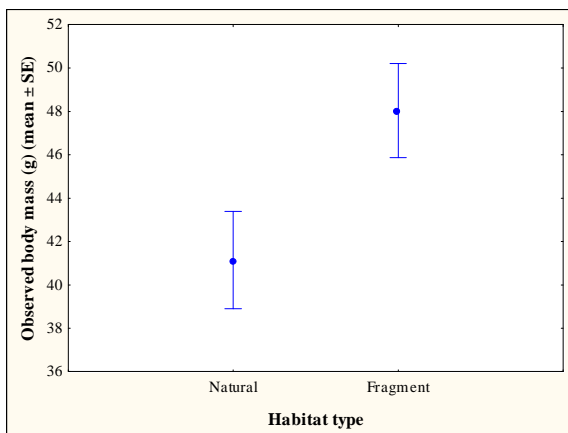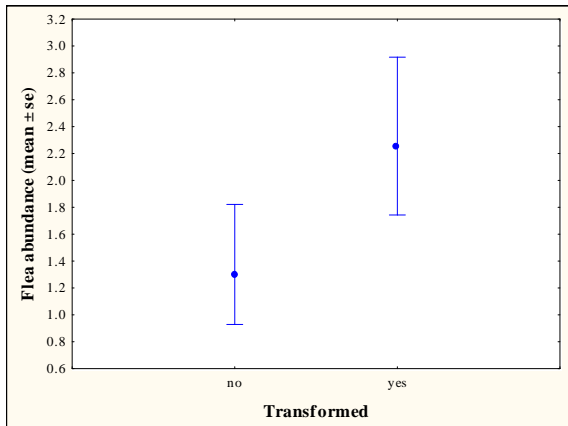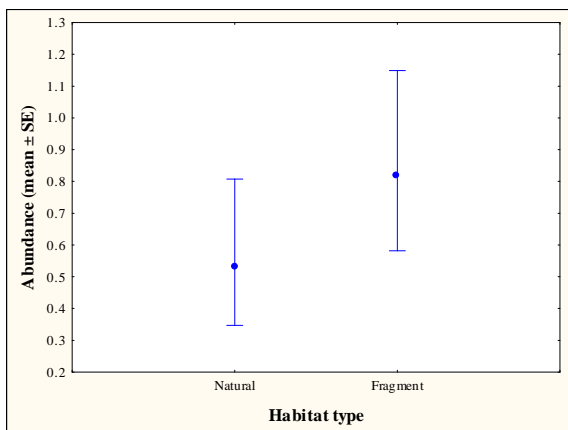
Figure 7: Body condition index of *Rhabdomys pumilio* (n = 218) in fragment and natural localities of the Cape Floristic Region, South Africa, 2009. (GLZ model (normal): y = habitat type).

Figure 8: Observed body mass of *Rhabdomys pumilio* (n = 218) in fragment and natural localities of the Cape Floristic Region, South Africa, 2009. (GLZ model (normal): y = habitat type).

Figure 9: Mean overall predicted abundance of fleas found on *Rhabdomys pumilio* (n = 218) in fragments and natural localities of the Cape Floristic Region, South Africa, 2009. (GLZ model (poisson, log link): y = habitat type + pair + sex + total length).

Figure 10: Mean predicted abundance of *Chiastopsylla rossi* found on *Rhabdomys pumilio* (n = 218) in natural and fragment localities of the Cape Floristic Region, South Africa, 2009. (GLZ model (poisson, log link): y = habitat type + pair + sex + total length).
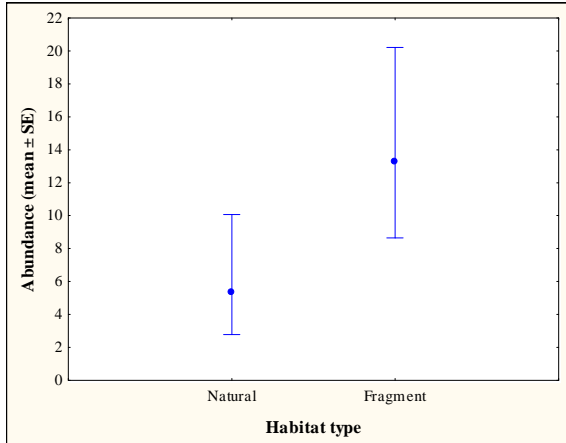
Figure 11: Mean overall predicted abundance of mites found on *Rhabdomys pumilio* (n = 218) in natural and fragment localities of the Cape Floristic Region, South Africa, 2009. (GLZ model (poisson, log link): y = habitat type + pair + sex + total length).
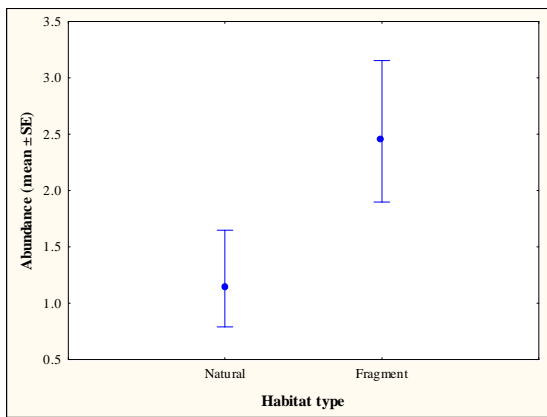
Figure 12: Mean overall predicted abundance of the mite, *Androlaelaps fahrenholzi*, found on *Rhabdomys pumilio* (n = 218) in natural and fragment localities of the Cape Floristic Region, South Africa, 2009. (GLZ model (poisson, log link): y = habitat type + pair + sex + total length).

Tables

Table 1: Breakdown of GLZ model and analysis for mean flea abundance on *Rhabdomys pumilio* in fragment and natural localities of the Cape Floristic Region, South Africa, 2009.

Model	Model p-value	% Deviance explained	Dispersion corrected		
Model(poisson, log link): y = habitat type + pair + sex code + total length	0*	81.88	yes		
All effects					
Effect	**Degrees of freedom**	**Wald statistic**	**p-value**		
Intercept	1	1.12	0.29		
Habitat type	1	8.25	0.004*		
Pair	3	9.65	0.02*		
Sex code	1	12.84	0*		
Total length	1	2.63	0.10		
Parameter estimate					
Effect	**Level of effect**	**Estimate**	**Standard error**	**Wald statistic**	**p-value**
Intercept		-1.06	1.01	1.12	0.29
Habitat type	natural	-0.27	0.10	8.25	0.004*
Pair	Somerset West	0.31	0.15	4.51	0.03*
Pair	Stellenbosch 1	-0.46	0.18	6.80	0.01*
Pair	Porterville	0.21	0.15	2.04	0.15
Sex code	0	0.40	0.11	12.84	0*
Total length		0.08	0.05	2.63	0.10
Scale		1.84	0		

*indicates significant differences ($p < 0.05$)

Table 2: Breakdown of GLZ model and analysis for mean *Chiastopsylla rossi* abundance on *Rhabdomys pumilio* in fragment and natural localities of the Cape Floristic Region, South Africa, 2009

Model	Model p-value	% Deviance explained	Dispersion corrected		
Model(poisson, log link): y = habitat type + pair + sex code + total length	0*	89.57	yes		
All effects					
Effect	**Degrees of freedom**	**Wald statistic**	**p-value**		
Intercept	1	1.09	0.30		
Habitat type	1	3.19	0.07*		
Pair	3	10.96	0.01*		
Sex code	1	2.88	0.09		
Total length	1	0.51	0.47		
Parameter estimate					
Effect	**Level of effect**	**Estimate**	**Standard error**	**Wald statistic**	**p-value**
Intercept		-1.30	1.25	1.09	0.30
Habitat type	natural	-0.22	0.12	3.19	0.07*
Pair	Somerset West	0.26	0.21	1.55	0.21
Pair	Stellenbosch 1	-0.12	0.22	0.29	0.59
Pair	Porterville	0.56	0.19	8.81	0.003*
Sex code	0	0.23	0.13	2.88	0.09
Total length		0.04	0.06	0.51	0.47
Scale		1.47	0		

*indicates significant differences ($p < 0.05$)

Table 3: Breakdown of GLZ model and analysis for mean overall mite abundance on *Rhabdomys pumilio* in fragment and natural localities of the Cape Floristic Region, South Africa, 2009.

Model	Model p-value	% Deviance explained	Dispersion corrected		
Model(poisson, log link): y = habitat type + pair + sex code + total length	0*	80.74	yes		
All effects					
Effect	**Degrees of freedom**	**Wald statistic**	**p-value**		
Intercept	1	0.19	0.66		
Habitat type	1	7.01	0.01*		
Pair	3	7.41	0.06		
Sex code	1	0.81	0.37		
Total length	1	2.83	0.09		
Parameter estimate					
Effect	**Level of effect**	**Estimate**	**Standard error**	**Wald statistic**	**p-value**
Intercept		-0.78	1.78	0.19	0.66
Habitat type	natural	-0.46	0.17	7.01	0.01*
Pair	Somerset West	0.62	0.25	6.01	0.01*
Pair	Stellenbosch 1	0.01	0.28	0.00	0.97
Pair	Porterville	0.28	0.27	1.06	0.30
Sex code	0	0.15	0.17	0.81	0.37
Total length		0.14	0.08	2.83	0.09
Scale		7.19	0		

*indicates significant differences (p < 0.05)

Table 4: Breakdown of GLZ model and analysis for mean *Androlaelaps fahrenholzi* abundance on *Rhabdomys pumilio* in fragment and natural localities of the Cape Floristic Region, South Africa, 2009.

Model	Model p-value	% Deviance explained	Dispersion corrected		
Model(poisson, log link): y = habitat type + pair + sex code + total length	0*	89.44	yes		
All effects					
Effect	Degrees of freedom	Wald statistic	p-value		
Intercept	1	0.05	0.82		
Habitat type	1	12.39	0*		
Pair	3	4.32	0.23		
Sex code	1	1.99	0.16		
Total length	1	0.05	0.82		
Parameter estimate					
Effect	Level of effect	Estimate	Standard error	Wald statistic	p-value
Intercept		0.26	1.12	0.05	0.82
Habitat type	natural	-0.38	0.11	12.39	0*
Pair	Somerset West	0.17	0.17	1.02	0.31
Pair	Stellenbosch 1	-0.17	0.18	0.88	0.35
Pair	Porterville	0.25	0.16	2.41	0.12
Sex code	0	0.15	0.11	1.99	0.16
Total length		0.01	0.05	0.05	0.82
Scale		1.90	0		

*indicates significant differences (p < 0.05)