Geographic distribution and composition of the parasite assemblage of the insectivorous bat, *Miniopterus natalensis* (Chiroptera: Miniopteridae), in South Africa

Dissertation for Master of Science Degree in Zoology

2012

Undertaken by: Simon Wood

Department of Zoology

The University of Cape Town

Private Bag X3, Rondebosch, 7701

Supervisor: Assoc. Prof. D.S. Jacobs

Department of Zoology

The University of Cape Town

Private Bag X3, Rondebosch, 7701

Co-Supervisor: Dr. K. Junker

The ARC-Onderstepoort Veterinary Institute

Private Bag X05, Onderstepoort, 0110

This dissertation was conducted in fulfilment of the requirements of a Masters of Science Degree in Zoology, MSc (Zoo), at the University of Cape Town.

TABLE OF CONTENTS

List of Figures

List of Tables

Declaration

I, Simon Wood, know the meaning of plagiarism and declare that all the work presented in this dissertation, save for that which is properly acknowledged, is my own.

Signed:_____ Date:

Acknowledgements

I would like to offer my heartfelt thanks and appreciation to my supervisors, Prof. David S. Jacobs and Dr. Kerstin Junker, for their incredible support and understanding during the course of this study. Furthermore, my thanks go to the identification experts Dr. Gert J. Venter, Ms Heloise I. Heyne (ARC-Onderstepoort Veterinary Institute), Dr. Eddie A. Ueckermann (ARC-Plant Protection Research Institute), Prof Ivan G. Horak (University of Pretoria) and Dr. Sonja Matthee (University of Stellenbosch), without whose invaluable expertise and assistance I would not have been able to complete this study. Thanks must also be given to my field assistants, Mr Jonathan Aronson, Mr Hassan Babiker, Ms Lizelle Odendaal and Ms Alicia Thomas, for their patience and good humour whilst processing all those bats in the wee hours of the morning despite being dead on their feet.

Thanks also to Cape Nature and the South African National Biodiversity Institute for allowing us access, accommodation and logistical support whilst in the field. Specific thanks go to the staff of the De Hoop Nature Reserve, Shongweni and Vanderkloof Dams, the owners/stewards of Koegelbeen Farm (Johan Cornelissen), Table Farm (Francie White), Steenkampskraal Mine (Sarel Mostert) and Sudwala Caves (Philip du Toit) for their help and guidance on site.

Funding, from the KW Johnstone Research Scholarship and the Postgraduate Entrance Level Scholarship, were provided by the National Research Foundation (NRF) via the UCT Postgraduate Funding Office as well as from a Grant to Prof. David S. Jacobs from the South African Research Chair Initiative (funded by the Department of Science and Technology). Opinions expressed and conclusions arrived at, are those of the author and are not necessarily to be attributed to the NRF.

Abstract

All free-living animal species have their own unique parasite assemblages. These parasites can have a significant impact on the fitness and ecology of their hosts, and through them the ecological systems in which they occur. Gaining knowledge about these parasites offers important information on the biology, systematics and phylogenies of their hosts. During this study the following were collected: flea, fly, mite, tick and helminth species from 96 Natal Long-Fingered bat (*Miniopterus natalensis* Smith, 1834) individuals sampled from seven localities across South Africa. This study aimed to both identify the species forming part of this parasite assemblage, and attempted to explain the distribution of the parasites and the factors influencing it. Each bat was euthanized and examined with the aid of a stereoscopic microscope for ectoparasites before having its gastro-intestinal tract removed for endoparasite recovery also using a stereo-microscope. Parasites were then identified and quantified. The parasite assemblage consisted of 610 ecto- and 2483 endoparasite individuals and included one flea, four fly, eight mite, one tick, and 11 helminth (one cestode, seven nematode and three trematode) species. Five undescribed mite species and two undescribed nematode species were recovered. Host sex was found to have no effect on infection intensity of ecto- or endoparasites. Host body mass had no effect on species number or infection intensity of either ecto- or endoparasites. However, there was a negative relationship between host body mass and endoparasite species diversity (r_5 = -0.84, $p<0.05$). Habitat heterogeneity displayed no significant relationship with ecto- or endoparasite species diversity or infection intensity. Finally, parasite species diversity was found to be unrelated to co-occurring bat species diversity.

CHAPTER 1

INTRODUCTION

1.1 Parasites, an Introduction

All free-living animal species have their own unique parasite assemblages. There are therefore many more parasites than free-living species in any given system. This means that they can have a significant impact on the fitness and ecology of their hosts and through them the ecological systems in which they occur (Hudson and Greenman 1998; Hudson *et al*. 1998; Torchin *et al*. 2001). Gaining knowledge about these parasites offers important information on the biology, systematics and the phylogenies of their hosts (Fritz 1983).

In fisheries biology, for example, parasite communities have been used to clarify the taxonomy of different host populations, such as in the work done by Oliva *et al.* (2008) on American chub mackerel, *Scomber japonicus* Houttuyn, 1782 (Scombridae). Furthermore, by understanding the various specialised traits and life-history strategies of parasites more can be learned about the parasite-avoidance strategies employed by their hosts. The indirect impacts on biodiversity and ecosystem processes of parasites through their hosts can be substantial. Parasitism and disease are significant causes of population regulation in many species [e.g. voles, Okulova and Aristova (1973); horses, Rubenstein and Hohmann (1989); bats, Lourenço and Palmeirim (2007); barn swallows, Møller and Rózsa (2005)], and by

regulating the populations of dominant or keystone species they can have far-reaching effects on ecosystem processes (Loreau *et al.* 2005).

Resistance to parasites is also energetically costly to hosts. It is necessary for the host to invest valuable resources in physiological and behavioural traits for the detection, prevention and response to parasite infection (Rigby *et al.* 2002). The immune system, in particular, requires large standing investments to remain effective and continually drains energy and resources in the repairing of damaged or parasite-consumed tissues (ter Hofstede and Fenton 2005). By studying the effects of parasites on their hosts more may be learned about the efficacy of their immune systems and its components such as the Major Histocompatibility Complex.

1.2 Host Dependency

Most ectoparasites and all endoparasites, by definition, are entirely dependent on their hosts for survival, inhabiting their exposed areas or internal organs, respectively (ter Hofstede *et al.* 2004). Hence, parasite distribution and ecology is largely determined by the distribution and habits of their hosts. It is common for these parasites to partition the available regions on their hosts, developing distinct morphologies which reflect their different host resource utilization (Dick 2007; Tello *et al.* 2008). Competition for host microhabitats is partly responsible for the evolution of these divergent morphologies resulting in greater species richness amongst parasites (Patterson *et al.* 2008). It has therefore been suggested that proximate factors like host attributes (as a parasite habitat), social groupings (which govern dispersion of host resources) and roost/den microhabitat, affect the degree

and diversity of parasitism in mammals (Patterson *et al.* 2008). Bat flies, for example, spend most of their life on their hosts and so follow their hosts' geographical distribution closely, only leaving their hosts as larvae (Marshall 1982; Dick and Gettinger 2005). Mites are similarly host-dependent sharing their hosts' geographic distribution. They are often host-limited, and are forced to complete their entire life-cycle on the body of their host (Christe *et al.* 2000).

Endoparasite life-cycles can be quite complex, involving a number of intermediate hosts. Trematodes, like *Paralecithodenrium* Travassos, 1921 from bats (Mc Allister & Bursey 2009), are heteroxenous, their indirect life-cycle often involving a first and second intermediate host as well as a final host. The first intermediate host often is a mollusc, such as a freshwater snail (Yamaguti 1971; Olson *et al.* 2003). Cestodes are also heteroxenous, but their life-cycle usually includes only a single intermediate host (Llewllyn 1987; Olson *et al.* 2001). Nematodes can either have indirect life-cycles, e.g. in *Litomosoides yutajensis* Guerrero, Martin & Bain, 2003, a vector-transmitted filarial worm from a mormoopid bat (Guerrero *et al*. 2006), or a direct (monoxenous) one, as seen in *Strongylacantha glycirrhiza* Beneden, 1873 from rhinolophoids (Anderson 2000) as well as other Trichostrongyloidea, such as Molineidae from bats. Their eggs are passed into the environment with the hosts' faeces and subsequent hosts are infected when third-stage larvae developing from these eggs either penetrate the skin or are ingested (Durette-Desset *et al.* 1994).

The ecological factors which determine the degree to which parasites are host specific are difficult to isolate (Krasnov *et al.* 2004a; Krasnov *et al.* 2005; Krasnov *et al.* 2006). As a general rule, where a parasite's mode of transmission is linked with host behaviour that exposes the parasite to a variety of hosts, selection tends to favour host switching, which leads to a decrease in host specificity (Poulin 2007). It is widely believed that ectoparasite host specificity is influenced by the behaviour and ecology of both the parasite and its host (Wenzel *et al.* 1966; Marshall 1981, 1982; Kunz 1982; Kunz and Lumsden 2003; Krasnov *et al.* 2004a; ter Hofstede and Fenton 2005; Poulin 2007).

Although several bat fly lineages have reduced or even lost their wings, the majority (79%) of New World species are volant (Dittmar *et al.* 2006) which influences host specificity. Volancy coupled with the tendency to leave the host when disturbed (Wenzel *et al.* 1966), should lead to frequent inter-host transfers and lower host specificity (Dick and Patterson 2007). This would in turn increase their potential distribution range by giving them access to a wider range of hosts. Recent studies on parasite host choice also support this 'flexible' host specificity with parasites being selective about host species and age (juveniles generally have higher infection rates) but making no distinction between male or female hosts within that species (Overal 1980; Bertola *et al.* 2005; Dick and Dick 2006).

Previously, the assumption that hosts and parasites share a specialized, exclusive evolutionary association made it seem unlikely that parasites would change host species (Brooks *et al.* 2006), especially in the case of endoparasites, given their

limited mobility when compared to the volant ectoparasites. However, this was based on the premise that it is the host species itself, rather than a certain biological characteristic or combination of characteristics of the host, that the parasite is tracking (Brooks and McLennan 1993; Brooks *et al*. 2006). When taking host traits into consideration, in place of a purely taxonomic approach, parasites may indeed be able to switch hosts if the trait they were tracking was shared among multiple hosts (Brooks *et al*. 2006). This process has become known as ecological fitting: where present day associations might be shaped in part by the distribution of phylogenetically conservative traits (Janzen 1985).

An example of this is the platyhelminth communities of a total of 75 anuran species from six localities in two distinctly different ecosystems; temperate forest and grassland in the United States, and tropical dry and wet forests in Mexico and Costa Rica (Brooks *et al.* 2006). Here all six communities investigated exhibited a similar structure in terms of genera and families parasitising the frogs. This suggests that endoparasite communities may also be subject to a degree of host switching and consequently display reduced host specificity similar to that found in ectoparasites (Olson *et al.* 2001).

There is much support for the effect of host age on parasite infection intensity and species abundance in ectoparasites of bats, but little to no data on endoparasites (Overal 1980; Komeno and Linhares 1999; Bertola *et al.* 2005; Dick and Dick 2006). The differences in ectoparasite infection intensity in juvenile bats when compared to adults can be attributed to poor grooming and reduced immune systems at this early

developmental stage resulting in an increase in parasite infection intensity until effective grooming behaviour is established (Marshall 1982; Komeno and Linhares 1999; Lučan 2006). However, it is likely that due to reduced foraging efficiency and body mass (Hamilton and Barclay 1998; Adams and Pedersen 2000) juvenile bats may harbour smaller burdens of endoparasites and, consequently, smaller species diversity.

1.3 Ectoparasites of Bats

The arthropod ectoparasites of bats belong to the Siphonaptera (fleas), Diptera (flies), Hemiptera (true bugs), Dermaptera (earwigs), and Acari (ticks and mites) and comprise more than 687 species (Whitaker 1988). Of the four orders Dermaptera, Hemiptera, Diptera and Siphonaptera, six families occur exclusively on bats (Marshall 1982). A recent survey of bat flies on Paraguayan bats by Dick and Gettinger (2005) determined that 87% of 31 streblid species were restricted to a single bat species and are thus highly host specific. With so many arthropod species intimately associated with bats, studies of these ectoparasites may offer valuable insight into biological, systematic and phylogenetic aspects of their hosts (Fritz 1983) as well as the biology of the parasites themselves.

The survival and reproductive costs exacted on the bats' fitness by these ectoparasites are currently not well understood (Bender 2000). However, parasites such as bat flies take blood meals from their host many times daily and will often die within hours of being removed from their host (Fritz 1983). Hosts also increase their

time spent grooming as the ectoparasite infection intensity increases, thereby reducing the time and energy available to the bat for feeding and other activities (ter Hofstede and Fenton 2005). To avoid costs incurred by these ectoparasites, some non-bat hosts may live in habitats unsuitable for the parasites (Hart 1992) or periodically change roosts from those with high ectoparasite abundance to those with lower abundance (e.g. caribou, Downes *et al.* 1986; cliff swallows, Brown and Brown 1992; great tits, Christe *et al.* 1994; badgers, Butler and Roper 1996).

A study on bats in Belize by ter Hofstede and Fenton (2005) compared the differences in grooming behaviour and roosting preference (cavity, foliage, or both) between bat species based on ectoparasite density (bat flies and mites). Cavity-roosting species generally had higher densities of bat flies and mites. It was also found that there were differences in grooming behaviour at the species level, where bat species with higher ectoparasite density (from cavity roosts) groomed more often than those species with lower densities (from the more ephemeral foliage roosts). This suggests that ectoparasite densities and grooming behaviour may be related to bat roosting preferences (ter Hofstede and Fenton 2005; Patterson *et al.* 2007). Thus, despite grooming having a direct effect on ectoparasite mortality (Marshall 1981, 1982), it is only an effective measure if other less energetically costly measures, e.g. roost switching, fail (Marshall 1981, 1982; ter Hofstede and Fenton 2005; Patterson *et al.* 2007).

The degree of ectoparasite infection may be related to a number of factors. Host roosting preference has been shown to have an effect on parasite densities. Cavity-

roosting bats having typically higher ectoparasite densities than foliage roosters (ter Hofstede and Fenton 2005). Host colony or group size also influences the density of infection, ectoparasites with limited mobility generally show increased abundance with increasing host group size (Kunz 1976; Lewis and Lewis 1994; Cote and Poulin 1995). For example, the distribution of bat wing mites is not related to environmental variables. Instead, group size may be the more important factor for mites (Sheeler-Gordon and Owen 1999).

Few studies have been done on African bat ectoparasites and these are mostly taxonomic (Streblidae and Streblinae Revision, Jobling 1936; African Ascodipterinae species descriptions, Maa 1965) with the occasional ecological report (diet and ectoparasites of Kenyan bats, Whitaker and Mumford 1978), showing that there is a great need for further research in this field in Africa.

1.4 Endoparasites of Bats

In addition to their ectoparasite assemblage, bats harbour a wide variety of endoparasites as well. These endoparasites include protozoans (not considered in this study) and helminths. As previously mentioned, the latter include trematodes, cestodes and nematodes (Agrawal 1967; Ubelaker 1970; Ubelaker *et al.* 1977; Cuartes-Calle and Muñoz-Arango 1999). The trematodes are the most diversified and prevalent of these groups (Nickel and Hansen 1967; Blankespoor and Ulmer 1970; Ubelaker 1970; Coggins 1988; Pistole 1988; Hilton and Best 2000), and are found principally in the digestive tracts of bats (Coggins 1988).

Thus far most work done on vertebrate helminth communities has focused mainly on the identification of factors contributing to the hierarchical organization of helminth communities with little insight into their ecology (Bush *et al.* 1990; Esch *et al.* 1990). Those few studies which have investigated the ecology of helminth communities of bats (Nickel and Hansen 1967; Coggins *et al.* 1982; Lotz and Font 1994) are specific to American bat populations while bats in general have been largely neglected (Esteban *et al.* 2001).

The handful of studies on African bat helminths are predominantly taxonomic, e.g. *Litomosa chiropterorum* Ortlepp, 1932 found in South African *Miniopterus natalensis* Smith, 1834 populations (Junker *et al.* 2008), a comparison of species of the cestode genus *Vampirolepis* Spasskii, 1954 with description of a new species from a hipposiderid bat in Tanzania (Jenzen and Howell 1983) or works on trematode parasites of bats (Dubois 1956; Saoud and Ramadan 1977a,b); in addition, many of these are focused on bats in Egypt (Baruš 1973; Saoud and Ramadan 1976; 1977a,b). Those few that have investigated African bat parasite ecology showed great variation in general community structure and ecology depending on the hosts involved. For example, a study on eight different bat species across Egypt found intensity of helminth infection between host sexes was either equal or varied depending on host species. Certain trematode genera showed noticeable preference to particular host species, and infections with trematodes, cestodes or nematodes were found in some cases to be antagonistic to each other (Saoud and Ramadan 1976).

As in the case of ectoparasites, gaining further insight into the ecology of bat helminth communities is essential to improving our understanding of the biological, systematic and phylogenetic aspects of their bat hosts.

1.5 Bats as Parasite Hosts

The widespread success of bats is due to their ability to exploit diverse trophic niches, roosting sites, habitats, and to employ varied movement patterns and sensory modalities (Kalko 1997; Patterson *et al.* 2003). This is made possible by their key innovations of flight and echolocation (Thewissen and Babcock 1992; Teeling *et al.* 2000; Simmons *et al.* 2008). Bats are especially valuable to local environments as pollinators, seed dispersers and insectivores, which in turn generate numerous indirect effects on the health and vitality of their immediate environment (Wilson 1989; Rainey *et al.* 1995). This ecological variation coupled with their diverse social systems, ranging from small family groups to colonies of millions, means that bat species should differ considerably in their susceptibility to different pathogens and pests (Hill and Smith 1984; Patterson *et al.* 2008).

Being wide-ranging, volant animals, bats often move rapidly and frequently between perch and roost sites, interacting with many other bat species during their foraging, roosting and reproductive activities (Dick and Patterson 2007). They roost in a wide variety of structures from foliage and leaf tents to mines and caves (Patterson *et al.* 2007), with the larger long-lived roosts often housing several bat species at once (Goodwin and Greenhall 1961). This offers parasites (ectoparasites in particular) a

great many opportunities to find new hosts and disperse to new locations, which should lead to non-specific host-parasite associations over evolutionary time (Dick and Patterson 2007).

However, there are benefits to parasites being host specific. Some parasites have limited dispersal capabilities (e.g. mites, Christe *et al.* 2000), while others have become so morphologically, behaviourally or physiologically adapted to their host that they cannot survive on a new host (Tompkins and Clayton 1999). For example, fleas can often be adapted to the specific blood composition of their particular host and so be incompatible with another (Krasnov *et al.* 2002). The reason such parasites become so specifically adapted to their host is in an attempt to bypass their hosts defences. Defences such as roost site selection, grooming and specific immunological defences are countered by the ectoparasites through quiescent developmental stages, evasive movements, difficult-to-dislodge body shapes and attachment organs, and the development of immunocompatibility with their hosts (Marshall 1981; Salzet *et al.* 2000; Khokhlova *et al.* 2004; Dick and Patterson 2007).

Endoparasitic helminths, especially heteroxenous ones, are picked up by bats from what they eat (Holmes 1964; Phillips 1966) and so the greater a bat's specialization on a particular prey item the more likely they are to become parasitized by the specific helminth using that prey item as an intermediate host (Hilton and Best 2000). Conversely, the more diverse a bat's diet the more diverse will be its endoparasite assemblage. The feeding habits and foraging strategies of bats, thus,

appear to have a strong influence on, e.g., trematode prevalence and type (Marshall and Miller 1979; Coggins 1988; Esteban *et al.* 2001). Trematodes are predominantly found in those insectivorous bats that are prone to ingest infected aquatic insects (Ubelaker 1970; Coggins 1988; García-Vargas *et al.* 1996; Pérez-Ponce de León 2001). However, there is some evidence suggesting that lepidopterans may serve as an additional, less common, intermediate host (Ubelaker 1970). Nematodes and cestodes of bats on the other hand employ mainly beetles as their primary intermediate hosts (Morgan and Hawkins 1951; Skrjabin *et al.* 1952, 1954; Yamaguti 1961; Ubelaker 1970; Kinsella 1991).

In Texas, the Big Brown bat [*Eptesicus fuscus* Beauvois, 1796 (Vespertilionidae)], e.g., had a higher intensity of trematodes than did the co-occurring Brazilian Free-Tailed bat [*Tadarida brasiliensis* Geoffroy, 1824 (Molossidae)] which instead had higher infection intensities of nematodes (Holmes 1964). This was attributed to the fact that *T. brasiliensis* feeds mostly on moths with only a small percentage (<1%) of its diet being made up of insects with aquatic larvae, while *E. fuscus*' diet consisted primarily of beetles but with >15% being composed of insects with aquatic larvae (Holmes 1964).

1.6 *Miniopterus natalensis*

This study focused on the Natal long-fingered bat, *M. natalensis* (Figure 1), because it has a wide geographic distribution across several biomes in South Africa, occurs in large colonies numbering thousands of individuals (Mills and Hess 1997) and has a

diverse diet including dipterans, hemipterans, isopterans and, to a lesser extent, lepidopterans and coleopterans (Jacobs 2000; Schoeman and Jacobs 2003).

Figure 1: *Miniopterus natalensis* in profile

They are gregarious cave dwellers (Skinner and Smithers 1990) which migrate seasonally between wintering roosts occupied by both sexes, and female-only summer maternity roosts where the young are born and raised (Mills and Hess 1997). Despite these migrations, ringing studies indicate a high degree of fidelity to both roost types (van der Merwe 1973). Its migratory nature has resulted in *M. natalensis* being capable of occupying a wide range of vegetation types between seasons. These range from moist mist-belt forests to dry savanna bushveld (Taylor 2000), only being restricted to regions that offer suitable caves or cave-like structures (e.g. mines and tunnels) as roosting sites (Mills and Hess 1997).

Distinct morphological variation between *M. natalensis* colonies, but not between sexes, has been reported by Miller-Butterworth *et al.* (2003), particularly with regards to wing morphology and aspect ratio (AR). These changes in AR between colonies relate to the close association between *M. natalensis* subpopulation locations and the major biomes they inhabit, where intraspecific variation in wingspan and echolocation flexibility has enabled them to utilize both open and cluttered habitats (Jacobs 1999). This indicates that different populations of this bat species may be adapted to local environmental conditions; such as vegetation type, climatic conditions or regional prey differences.

1.7 Aims and Hypotheses

The aims of this study were to describe the geographic range and composition of parasite assemblages of the common and wide-spread bat, *M. natalensis*, in South Africa to alleviate the current lack of data. Species composition, species richness, prevalence and intensity were used as the main parasitological descriptors (Bush *et al.* 1997) to determine the influence of host sex and size as well as habitat heterogeneity on parasite assemblages as outlined in the hypotheses below.

1.7.1 Host Sex Hypothesis

There are no distinct behavioural or physiological differences between male and non-reproductive female bats, so exposure to both ecto- and endoparasites would be similar in both sexes. Hence, it was predicted that there should be no difference

in the prevalence and infection intensities of either ecto- or endoparasites between males and non-reproductive females.

1.7.2 Host Body Size Hypothesis

Larger bats, i.e. bats with greater body mass, would have a higher food intake and thus a higher chance of exposure to parasite infection through their diet. Larger hosts also provide more opportunities, e.g. increased surface area, for colonisation by parasites. If so, there should be (1) a positive correlation between host body mass and ecto- and endoparasite species diversity, and (2) a positive correlation between host body mass and endoparasite infection intensity.

1.7.3 Habitat Heterogeneity Hypothesis

Habitats with high plant diversity are associated with high insect diversity. Insectivorous bats foraging in these habitats should be exposed to higher diversities of possible intermediate hosts and therefore also to the infective stages of parasites. Thus both ecto- and endoparasite species diversity, as well as their infection intensities, should vary between colonies across biomes according to the varying levels of plant diversity. Bats occurring in regions with more heterogeneous, or variable, flora (i.e. Grassland, Albany Thicket and Fynbos) should harbour (1) more ecto- and endoparasite species, (2) should have higher intensities of infection by those parasites, and (3) colonies of bats in roosts shared by more bat species should have more ectoparasite species than those colonies in roosts with fewer host species due to the increased host and associated parasite diversity.

CHAPTER 2

MATERIALS AND METHODS

2.1 Study Sites

This study was done at seven sites across South Africa (Figure 2) during a single summer season from mid-September 2009 to early January 2010. Potentially confounding factors such as seasonal migration and hibernation could thus be minimized or eliminated altogether. The seven sites served as representatives of six of the eight major South African biomes namely Albany Thicket, Fynbos, Grassland, Nama Karoo, Savanna and Succulent Karoo respectively (Mucina and Rutherford 2006). Sampling was done at the Sudwala Caves in Mpumulanga (Grassland biome), Koegelbeen Sinkhole (Savanna) and Vanderkloof Dam (Nama Karoo) in the Northern Cape, Steenkampskraal mine (Succulent Karoo) and De Hoop Nature Reserve (Fynbos) in the Western Cape, Table Farm (Albany Thicket) in the Eastern Cape, and Shongweni Dam (Savanna) in KwaZulu-Natal. These biomes are characterised below.

Albany Thicket

There is no formal "Thicket Biome" in the scientific literature. However, it is recognised that the vegetation which replaces forest (where a degree of fire protection is still evident, but rainfall is too low), does not fit within the "Forest" type, since it has neither the required height nor the many strata below the canopy. A conspicuous grassy ground layer is also absent. Subtropical thicket is closed

shrubland to low forest dominated by evergreen and succulent trees, shrubs and vines, many of which have stem spines. Albany thicket is found in semi-arid areas of the Eastern and Western Cape, with annual rainfalls of 200 to 950 mm. Altitude varies from sea level to 1600 m, and the region's geology is dominated by the sandstone and quartzite of the Cape Supergroup. (Low and Rebelo 1996; Mucina and Rutherford 2006)

Fynbos

The Fynbos Biome is considered by many to be synonymous with the Cape Floristic Region or Cape Floral Kingdom, which is the smallest of the six Floral Kingdoms in the world. This is due to the overwhelming contribution to the region's species richness and specificity made by the Fynbos Biome's two key vegetation groups, Fynbos and Renosterveld. The Region is characterized by its richness in plant species (8 700 species) and its high endemicity (68% of plant species are confined to the Cape Floral Kingdom), even though it makes up less that 6% of the area of the country. This region is dominated by the quartzitic Cape Fold Belt with altitude ranging from near sea level to 1500 m above sea level, and extremely nutrient deficient soils, experiencing predominantly winter rainfall ranging from 250 to 800 mm per year. (Rutherford and Westfall 1986, 1994)

Grassland

The Grassland Biome is found chiefly on the high central plateau of South Africa, and the inland areas of KwaZulu-Natal and the Eastern Cape. The topography is mainly flat and rolling, but includes the escarpment itself, altitude varies from near sea level

to 2850 m. Grasslands are dominated by a single layer of grasses. The amount of cover depends on rainfall and the degree of grazing; and trees are absent, except in a few localized habitats. Geophytes (bulbs) are often abundant. Frosts, fire and grazing maintain the grass dominance and prevent the establishment of trees. Rainfall ranges from 280 to 1820 mm per year, and most major geological and soil types occur within the biome. (Rutherford and Westfall 1986, 1994; Mucina and Rutherford 2006)

Nama Karoo

The Nama Karoo Biome occurs on the central plateau of the western half of South Africa, at altitudes between 500 and 2000 m, with most of the biome falling between 1000 and 1400 m. It is the second-largest biome in the region. The geology underlying the biome is varied, as the distribution of this biome is determined primarily by rainfall. The rain falls in summer, and varies between 100 and 520 mm per year. This also determines the predominant soil type of lime-rich, weakly developed soil over rock. Although less than 5% of rain reaches the rivers, the high erodibility of soils poses a major problem where overgrazing occurs. The dominant vegetation is a grassy, dwarf shrubland. Grasses tend to be more common in depressions and on sandy soils, and less abundant on clayey soils. Grazing rapidly increases the relative abundance of shrubs. (Rutherford and Westfall 1986, 1994)

Savanna

The Savanna Biome is well developed over the lowveld and Kalahari region, covering over one-third of South Africa. It is characterized by a grassy ground layer and a

distinct upper layer of woody plants. Where this upper layer is nearer the ground the vegetation may be referred to as Shrubveld, where it is dense it is known as Woodland, and the intermediate stages are locally known as Bushveld. The environmental factors delimiting this biome are complex: altitude ranges from sea level to 2000 m; rainfall varies from 235 to 1000 mm per year; frost may occur from 0 to 120 days per year; and almost every major geological and soil type occurs within the biome. (Rutherford and Westfall 1986, 1994)

Succulent Karoo

The Succulent Karoo Biome covers a flat to gently undulating plain, with some hilly and "broken" veld, mostly situated to the west and south of the Great Escarpment (the semicircle of mountain ranges roughly paralleling South Africa's coastline), and north of the Cape Fold Belt (the folded sedimentary sequence of rocks in the south-western corner of South Africa). The altitude is mostly below 800 m, but in the east it may reach 1500 m. A variety of geological units occur in the region. There is little difference between the soils of the Succulent Karoo and Nama Karoo Biomes, both are lime-rich, weakly developed soils on rock. This biome is primarily determined by the low winter rainfall and extreme summer aridity, with rainfall varying between 20 and 290 mm per year. The vegetation is dominated by dwarf, succulent shrubs. Mass flowering displays of annuals, mainly Daisies (Asteraceae), occur in spring, often on degraded or fallow lands. Grasses are rare, except in some sandy areas. The number of plant species, mostly succulents, is very high and unparalleled elsewhere in the world for an arid area of this size. (Rutherford and Westfall 1986, 1994)

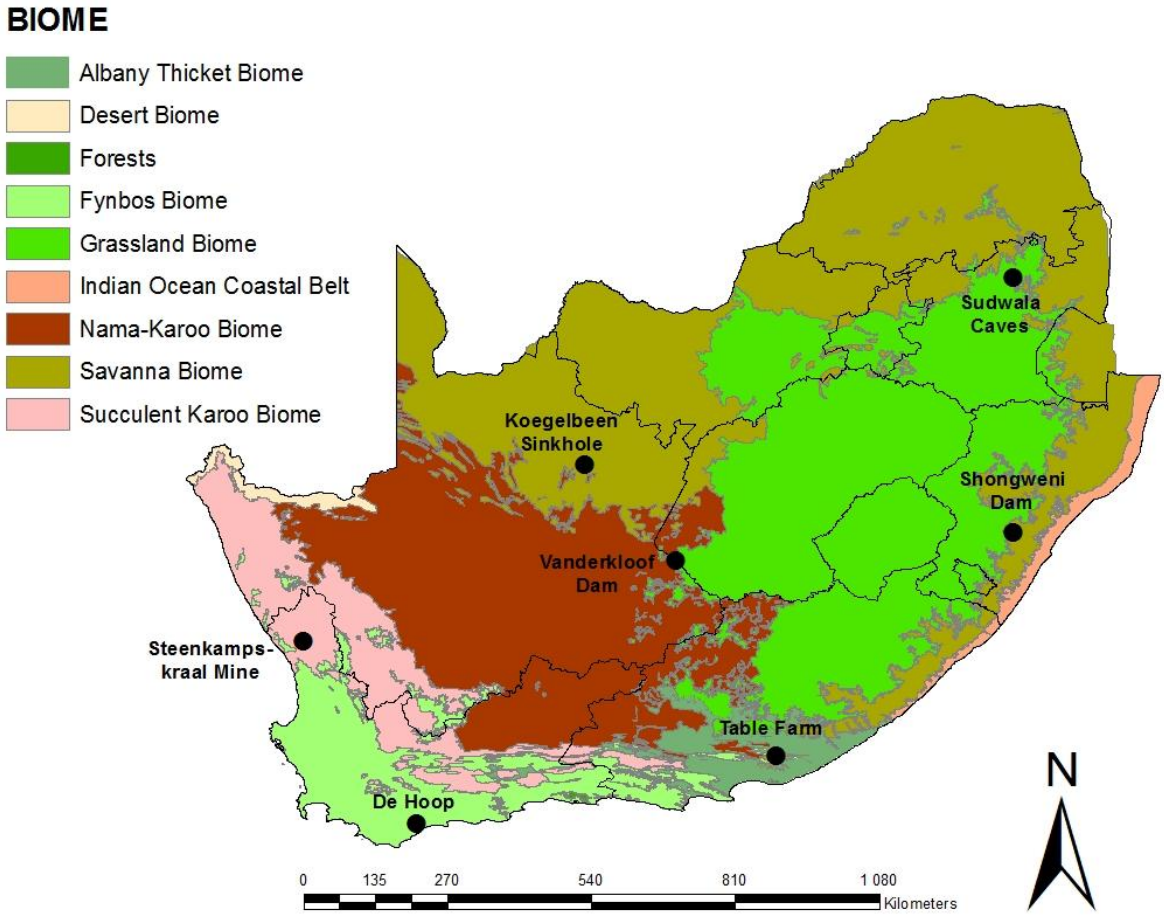

Figure 2: Location of study sites within South African biomes

**map produced using ArcGIS v9.2 (ESRI, 1999-2006)*

Table 1: Collection data for *Miniopterus natalensis* in South Africa

Sample Sites	Biome	Bats Captured			GPS Co-ordinates	
		Male (62)	Female (34)	Total (96)	Latitude	Longitude
De Hoop Guano Cave*	Fynbos	10	3	13	34° 25' 26" S	20° 21' 34" E
Koegelbeen Sinkhole	Savanna	10	9	19	28° 23' 24" S	23° 11' 60" E
Shongweni Dam	Savanna	10	1	11	29° 51' 42" S	30° 43' 08" E
Steenkampskraal Mine	Succulent Karoo	2	0	2	31° 21' 37" S	18° 26' 57" E
Sudwala Caves*	Grassland	10	10	20	25° 20' 15" S	30° 37' 57" E
Table Farm*	Albany Thicket	10	10	20	33° 17' S	26° 25' E
Vanderkloof Dam*	Nama Karoo	10	1	11	29° 59' 50" S	24° 43' 30" E

** = heterogeneous habitat, unmarked = homogeneous habitat*

2.2 Bat Capture

Adult male bats and adult non-reproductive females were sampled at each of the sites to eliminate potential confounding factors caused by age or reproductive status. Table 1 lists the number of males and females recovered from each locality. Bats were captured as they emerged at dusk using mist nets placed about 3 m from the entrance to their cave roosts. Where sufficient bats could not be captured using this method, a harp-trap placed close to the entrance to the cave was used. Immediately upon capture and successful identification, bats were placed temporarily in individual cloth bags to separate them and their parasites from other bats during capture. Bats were identified using callipers and a discriminant function derived from total body length and hind foot length (Stoffberg *et al.* 2004), to distinguish *Miniopterus natalensis* from the morphologically similar and co-occurring *Miniopterus fraterculus* Thomas & Schwann, 1906 (Miniopteridae). After bats were collected and identified, they and the contents of their holding bags were placed into glass jars with sealable lids where they and their ectoparasites were euthanized using Halothane (Close *et al.* 1997; Leach *et al.* 2004).

Following euthanasia, the bats' gastro-intestinal tracts (GITs) were removed and placed in plastic screw top jars to which boiling water was added. This rapidly killed any helminths without damaging or shrinking them, thus making later identification easier. Following this, the dissected bats, their GITs and their ectoparasites were all placed in individual, clearly labelled plastic screw top jars filled with 70% ethanol for transportation to the University of Cape Town and preservation until dissection.

Gloves, holding bags, callipers and euthanasia jars were thoroughly cleansed between use on different host individuals and stringent measures were in place at all times to prevent ectoparasite cross-contamination. These included bats being removed from nets immediately after capture to prevent ectoparasites from moving between captured bats. Each bat was handled separately and their individual containers clearly labelled and kept apart. Finally, the nets were constantly monitored and cleared of ectoparasites that may have escaped their hosts upon capture. These escapees were not used in analyses since they could not be assigned to individual bats.

Other bat species found at each sample site were identified and recorded from their echolocation calls. This was done using the Avisoft Ultra-SoundGate 416 System to record the calls and BatSound Pro software (Version 3.20, Pettersson Elektronik AB, Upsala, Sweden) to identify species from them. This information was used to determine if differences in potential bat host species diversity influenced parasite species diversity (Prediction 3, Habitat Heterogeneity Hypothesis).

2.3 Host Preservation and Parasite Processing

At the University of Cape Town the preserved hosts, including the contents of their transport jars, were examined under a stereoscopic microscope and all ectoparasites removed by hand, after which the ectoparasites where preserved according to the procedures described by Whitaker (1988). Ectoparasites were counted and their location on the host (i.e. fur, flight membranes, ears and nose) recorded before

being stored by host and taxonomic group in individual plastic eppendorf tubes, filled with 70% ethanol, for later clearing and mounting.

The GITs that had been preserved in 70% ethanol were transferred to the ARC-Onderstepoort Veterinary Institute (ARC-OVI), where identification of both helminths and ectoparasites was done; mites were identified at the ARC-Plant Protection Research Institute (ARC-PPRI). Each GIT was separated into stomach, small intestine and large intestine (caecum and colon). Helminths were removed from each part of the GIT with the aid of a stereo-microscope, using a combination of fine forceps and soft-tipped paint brushes depending on the fragility of the parasites. All helminths were stored by host in individual eppendorf's containing 70% ethanol. For identification purposes, nematodes were cleared in lactophenol, while cestodes and trematodes were mounted in Hoyer's medium. Measurements were taken, for identification, under a compound microscope (Olympus BX 50) equipped with differential interference contrast and a digital imaging system, including digital image analysis software (AnalySIS™). The number of each parasite taxon (endo- and ecto-) was then determined for each bat at each site and for both host sexes.

2.4 Final Specimen Storage

On completion of the project, bat specimens were sent to the collections of those museums closest to where they were originally sampled. These were the Iziko South African Museum in Cape Town (accession numbers: SAM ZM 41832-41844), the McGregor Museum in Kimberly (accn no.'s: MMK/M/7314-7345), the Ditsong

Museum of Natural History (formerly the Transvaal Museum) in Pretoria (accn no's: TM 48463-48482) and the Durban Natural History Museum (accn no.'s: DM13283-DM13313). Parasite voucher specimens were stored in the National Collection of Animal Helminths housed at the ARC-OVI in Pretoria.

2.5 Parasite Assemblages

Ectoparasites were identified by the following experienced parasitologists: Bat flies (Diptera): Dr. Gert J. Venter and Ms Chantel de Beer, ARC-OVI, Gauteng, South Africa; ticks (Acari): Ms. Heloise I. Heyne, ARC-OVI in collaboration with Prof. Ivan G. Horak, University of Pretoria, Gauteng, South Africa; mites (Acari): Dr. Eddie A. Ueckermann, ARC-PPRI, Gauteng, South Africa; fleas (Siphonaptera): Dr. Sonja Matthee, University of Stellenbosch, Western Cape, South Africa. Helminth identification was done under the guidance of Dr. Kerstin Junker, ARC-OVI.

Each endo- and ectoparasite was identified to order, and where possible genus and species. Prevalence and intensity of infection were used as quantitative descriptors of parasite assemblages and employed in accordance with Bush *et al.* (1997). Prevalence was defined as the proportion of sampled bats infected by a parasite. Infection intensity was defined as the number of individual ecto- or endoparasites per infected host, these values were then used to test the host body size hypothesis. When used to test the host sex and habitat heterogeneity hypotheses infection intensities were calculated by the number of ecto- and endoparasites collected from

each host divided by the host's forearm length (mm) to standardise for variation in body sizes.

2.6 Parasite Diversity

In this study parasite diversity was taken as species richness, i.e. the maximum number of ecto- or endoparasite species identified per sample site. This was done instead of using a diversity index to allow for comparisons with previous studies. However, for possible future comparisons Shannon's diversity indices (Shannon and Weaver 1949) were also calculated, since this is the most commonly used measure of general ecological diversity [e.g. bats, Magurran (1988), Medellín *et al* (2000) and Seneviratne *et al* (2009); bird parasites, Cattadori *et al* (2005); eel parasites, Sures and Streit (2001); goat parasites, Silvestre *et al* (2000)].

Shannon's diversity index, also known as the Shannon index or Shannon-Weaver index, is popular because it accounts for both abundance and evenness of the species present (Magurran 1988). The indexes 'H' value represents not only the number of species present but how the abundance of the species is distributed (Magurran 1988). For example, high values of 'H' would be representative of more diverse communities with more evenly distributed species (Magurran 1988).

This index was calculated for each parasite species at each site using the following formula:

$$H = -\sum_{i=1}^{S} p_i \ln p_i$$

where p_i is the relative abundance of each species *i*, calculated as the proportion of individuals of a given species to the total number of individuals in the community: $\frac{n_i}{N}$, and *S* is the number of species (i.e. the species richness) at a site.

2.7 Testing Hypotheses

2.7.1 Host Sex Hypothesis

Factorial MANOVA analyses (with log-transformed data if normality was not found), grouping by sample site, were used to test whether ecto- and endoparasite infection intensity differed between host sexes by using the pooled intensity values of male and female bats, respectively, from all sample sites. Sites were excluded where host collection or parasite recovery from both bat sexes was unsuccessful (Steenkampskraal Mine and Vanderkloof Dam – Table 1). Note that ecto- and endoparasite data were analysed separately. Since no significant differences were found between the sexes, the data for both sexes were subsequently pooled to make analyses in the following hypotheses more robust.

2.7.2 Host Body Size Hypothesis

Linear regressions were used to test whether host body size was related to parasite species diversity and infection intensity, using the following variables: host body mass (g), host body condition index (BCI), ecto- and endoparasite species diversity, and ecto- and endoparasite infection intensity. Ecto- and endoparasite data were analysed separately, and log transformed when not normally distributed.

For each bat host the BCI was calculated by dividing host body mass by forearm length (Speakman and Racey 1986). Using linear regressions the relationship between host body condition and parasite species diversity and parasite infection intensity was determined.

2.7.3 Habitat Heterogeneity Hypothesis

To evaluate whether or not bats found in the habitats from heterogeneous biomes (Grassland, Albany Thicket and Fynbos) have higher parasite species diversity and infection intensities than those in the homogenous biomes (Nama Karoo, Succulent Karoo and Savanna), Kruskal-Wallis ANOVA was used when data were not normally distributed. When testing the first prediction, comparing parasite species across the biomes sampled, a random subset of the data was taken (using a random number generator) to account for unequal sampling across the sites, and data from Steenkampskraal Mine were excluded since only two bats were sampled there (Table 1). In testing the second prediction, comparing infection intensities across biomes, neither of these steps were necessary since the data were found to be sufficient and normally distributed to allow the use of parametric ANOVA to compare parasite infection intensities from hosts across biomes. Finally, to test the third prediction, a random subset of the parasite species diversity data was taken, log-transformed and a general linear regression performed to determine whether a correlation existed between bat host diversity within colonies and ectoparasite species number.

2.8 Data Analysis

All statistical tests were done using Statistica version 9.0 (Statsoft Inc., 2009).

Data were tested for normality using the Lilliefors test, and stepwise multiple regression was used to assess covariation among dependent and independent variables in all tests.

CHAPTER 3

RESULTS: PARASITE ASSEMBLAGES

3.1 Parasite Assemblages

In this study 96 adult bats, 62 males and 34 females, were collected from seven sample sites across South Africa (Table 2). Of those bats, 93 (97%) were host to ectoparasites and 91 (95%) to endoparasites (Tables 3 & 4). Table 2 details the hosts average measurements across sample sites used in analyses testing the affects of host mass and infection intensity on parasite distribution and diversity.

Table 2: *Miniopterus natalensis* sampled at the seven sites

Sample Sites	**Host Sex**	**Avg. Mass (g) ± SD**	**Avg. FA (mm) ± SD**	**Avg. BCI ± SD**
DE HOOP GUANO CAVE	Female (3)	9.27 ± 0.78	46.60 ± 0.50	0.20 ± 0.02
	Male (10)	10.62 ± 0.63	45.83 ± 0.77	0.23 ± 0.01
De Hoop Guano Cave Total	13	10.31 ± 0.86	46.01 ± 0.78	0.22 ± 0.02
KOEGELBEEN SINKHOLE	Female (9)	12.06 ± 0.53	46.67 ± 1.32	0.26 ± 0.01
	Male (10)	11.21 ± 0.58	46.05 ± 0.81	0.24 ± 0.01
Koegelbeen Sinkhole Total	19	11.61 ± 0.69	46.34 ± 1.10	0.25 ± 0.01
SHONGWENI DAM	Female (1)	10.60 ± 0	43.46 ± 0	0.24 ± 0
	Male (10)	12.71 ± 0.77	45.66 ± 0.91	0.28 ± 0.02
Shongweni Dam Total	11	12.52 ± 0.97	45.46 ± 1.09	0.28 ± 0.02
STEENKAMPSKRAAL MINE	Male (2)	12.81 ± 0.26	46.65 ± 0.67	0.27 ± 0.01
Steenkampskraal Mine Total	2	12.81 ± 0.26	46.65 ± 0.67	0.27 ± 0.01
SUDWALA CAVES	Female (10)	11.02 ± 0.67	46.25 ± 0.76	0.24 ± 0.01
	Male (10)	10.92 ± 0.59	45.10 ± 0.81	0.24 ± 0.01
Sudwala Caves Total	20	10.97 ± 0.62	45.68 ± 0.97	0.24 ± 0.01
TABLE FARM CAVE	Female (10)	11.00 ± 0.52	45.06 ± 1.28	0.24 ± 0.01
	Male (10)	11.84 ± 0.72	45.83 ± 1.31	0.26 ± 0.02
Table Farm Cave Total	20	11.42 ± 0.75	45.44 ± 1.32	0.25 ± 0.02
VANDERKLOOF DAM	Female (1)	12.06 ± 0	46.30 ± 0	0.26 ± 0
	Male (10)	12.88 ± 0.72	45.80 ± 0.52	0.28 ± 0.02
Vanderkloof Dam Total	11	12.80 ± 0.72	45.85 ± 0.52	0.28 ± 0.02
GRAND TOTAL	96	11.53 ± 1.07	45.82 ± 1.06	0.25 ± 0.02

Avg. = average, g = grams, SD = standard deviation, FA = forearm length, BCI = body condition index

Ectoparasite species collected belonged to the Acari, including the tick *Ixodes simplex* Neumann, 1906 (Ixodidae) and the mites *Calcarmyobia rhinolophia* Radford, 1940) (Myobiidae), *Ichoronyssus miniopteri* Zumpt & Patterson, 1952 (Laelapidae), five potentially new species of *Macronyssus* Kolenati, 1858 (Macronyssidae) and *Spinturnix semilunaris* De Meillon & Lavoipierre, 1944 (Spinturnicidae). Dipteran parasites were represented by *Nycteribia schmidlii* Schiner, 1853 and *Penicillidia fulvida* Bigot, 1885 (both Nycteribiidae), as well as the streblid genera *Ascodipteron* Adensamer, 1896 and *Brachytarsina* Macquart, 1851. A single flea (Siphonaptera), *Oxyparius isomalus* Waterston, 1915 (Ischnopsyllidae) was present. Table 7 (Appendices) lists each study site and the species found there.

Endoparasite species collected were the trematodes *Anchitrema sanguineum* Sonsino, 1894 (Anchitrematidae) as well as *Paralecithodendrium khalili* Saoud & Ramadan, 1977 and *Paralecithodendrium parvouterus* Bhalerao, 1926 (both Lecithodendriidae). Cestodes were represented by Hymenolepididae. Nematodes included the order Enoplida, represented by *Aonchotheca* Lopez-Neyra, 1947 and specimens assigned to Capillariinae (both Trichuridae). Spirurida included, the filaria *Litomosa chiropterorum* Ortlepp, 1932 (Onchocercidae) and specimens belonging to *Physaloptera* Rudolphi, 1819 (Physalopteridae). The Strongylida were represented by *Molinostrongylus ornatus* Mönnig, 1927 and two potentially new species of *Molinostrongylus* Skarbilovitch, 1934 (Molineidae). Table 8 (Appendices) lists each study site and the species found there.

Ectoparasites showing noticeably restricted distributions included: *C. rhinolophia* (Sudwala Caves, Shongweni Dam and Vanderkloof Dam)*, Brachytarsina* sp. (Koegelbeen Sinkhole), *Macronyssus* sp. (Sudwala Caves), *Macronyssus* sp. D (Sudwala Caves) and *Macronyssus* sp. E (Shongweni Dam) (Table 3). Endoparasites with a limited geographic range included: *A. sanguineum* (Sudwala Caves), *P. khalili* (Sudwala Caves, Shongweni Dam), *P. parvouterus* (Koegelbeen Sinkhole, Sudwala Caves), Hymenolepididae (Sudwala Caves, Shongweni Dam, Table Farm Cave), Capillariinae (Shongweni Dam), *M. ornatus* (De Hoop Guano Cave, Sudwala Caves, Table Farm Cave), *Molinostrongylus* sp. B (Table Farm Cave) and *Physaloptera* sp. (De Hoop Guano Cave, Table Farm Cave) (Table 4).

Figure 3 summarizes the diversity of parasite species found across the seven sample sites: Total (ecto-/endo-) parasite species found at De Hoop Guano Cave (6/3), Koegelbeen Sinkhole (4/3), Sudwala Caves (5/4), Shongweni Dam (6/3), Steenkampskraal Mine (3/2), Table Farm Cave (6/3) and Vanderkloof Dam (5/2).

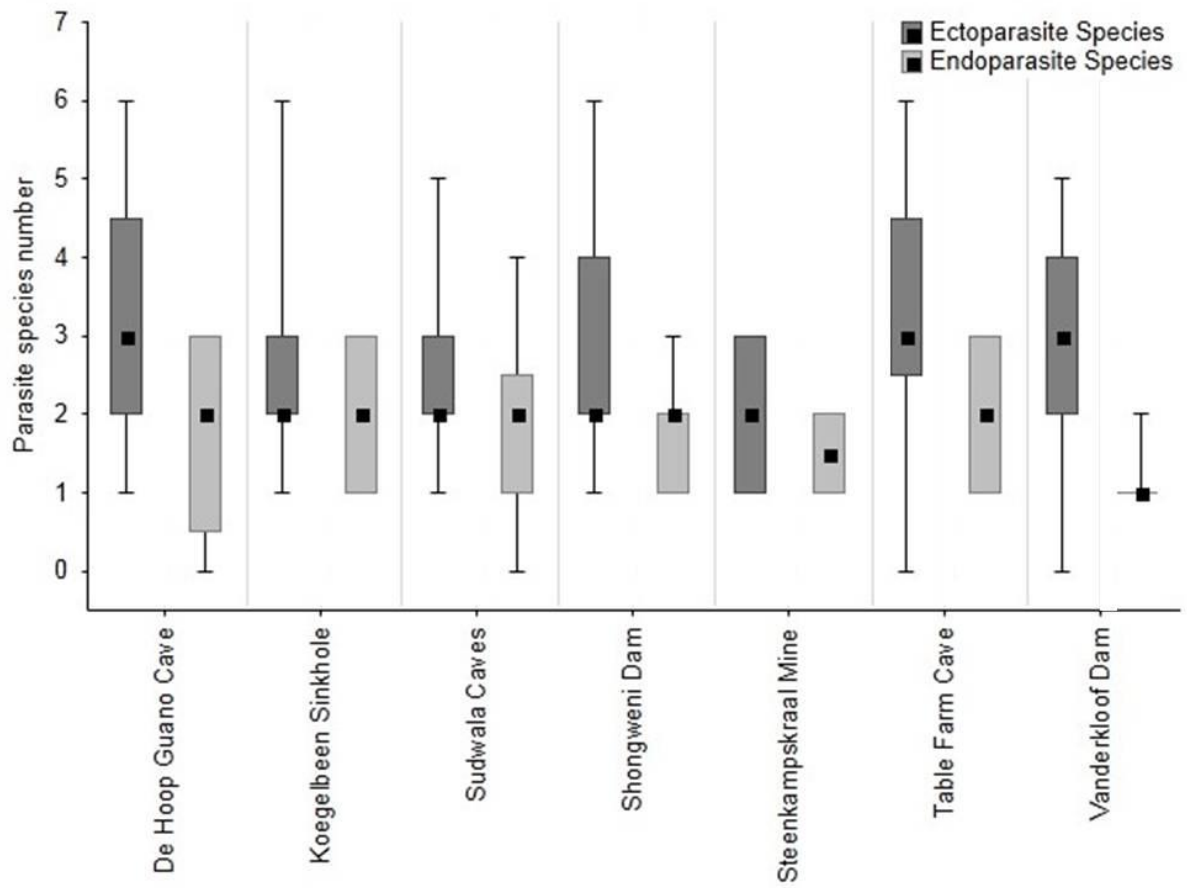

Figure 3: Box & Whisker plot of the number of parasite species infecting *Miniopterus natalensis* across sample sites in South Africa

Boxes represent the inter-quartile ranges of the number of parasite species per site, with the central dots being the median of each range. The bars indicate the maximum and minimum number of species obtained at each site. Due to low sample sizes at some sites (e.g. Steenkampskraal Mine) their boxes' inter-quartile range and max/min bars are the same.

There were approximately 1.3 times more species of ectoparasites (Figure 4) across all sample sites than endoparasites (Figure 5). Ectoparasites comprised 610 individuals from 14 species (Table 3). Endoparasites comprised only 11 species, but were four times more numerous with 2483 individuals (Tables 3 & 4). Five of the ectoparasite species and two of the endoparasites species collected are considered new to science (Tables 3 & 4).

The parasites with the highest overall prevalences, but varying abundance (the total number of individuals recovered is indicated following prevalence), were the ectoparasitic bat fly *N. schmidlii* (76%; n = 202) and the endoparasitic nematode *L. chiropterorum* (68%; n = 703). This was followed by the ectoparasitic mite *S. semilunaris* (41%; n = 66) and the endoparasitic nematode *Aonchotheca* sp. (27%; n = 42). The least prevalent parasites were the ectoparasitic *Brachytarsina* sp., *Macronyssus* sp. and *Macronyssus* sp. D and E, as well as the endoparasites *A. sanguineum*, Capillariinae and *Molinostrongylus* sp. B, all of which had a prevalence of 1% and were represented by a single specimen (Figures 4 & 5, Tables 3 & 4).

The parasites with the highest intensity of infection were the ectoparasitic mite *I. miniopteri*, with a total of 78 specimens collected from all infected hosts and a mean intensity (MI) of 2.9 ± 3.1 and a range of 1-13, and the endoparasitic trematode *P. khalili* [n = 1435, MI = 102.5 ± 191.0 (1-738)]. These were followed by *N. schmidlii* [n = 202, MI = 2.8 ± 2.2 (1-14)] and the trematode *P. parvouterus* [n = 102, MI = 14.6 ± 11.2 (1-33)]. (Figures 4 & 5, Tables 3 & 4). The least abundant parasites were the ectoparasitic *Ascodipteron* sp., *C. rhinolophia*, *Macronyssus* sp. E and *P. fulvida*, and the endoparasitic *A. sanguineum* and *Molinostrongylus* sp. B., all of which were represented by a single specimen in a single host only (Figures 4 & 5, Tables 3 & 4).

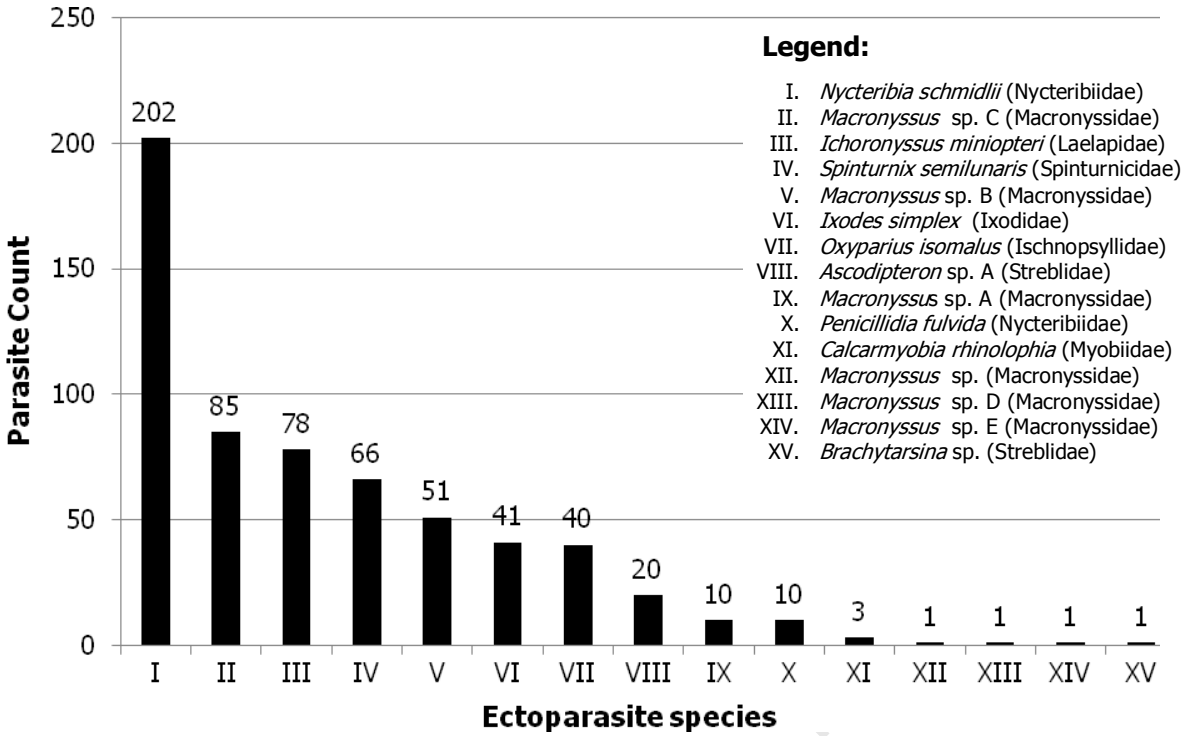

Figure 4: Total number of ectoparasites per species recovered from *Miniopterus natalensis* across all sample sites in South Africa

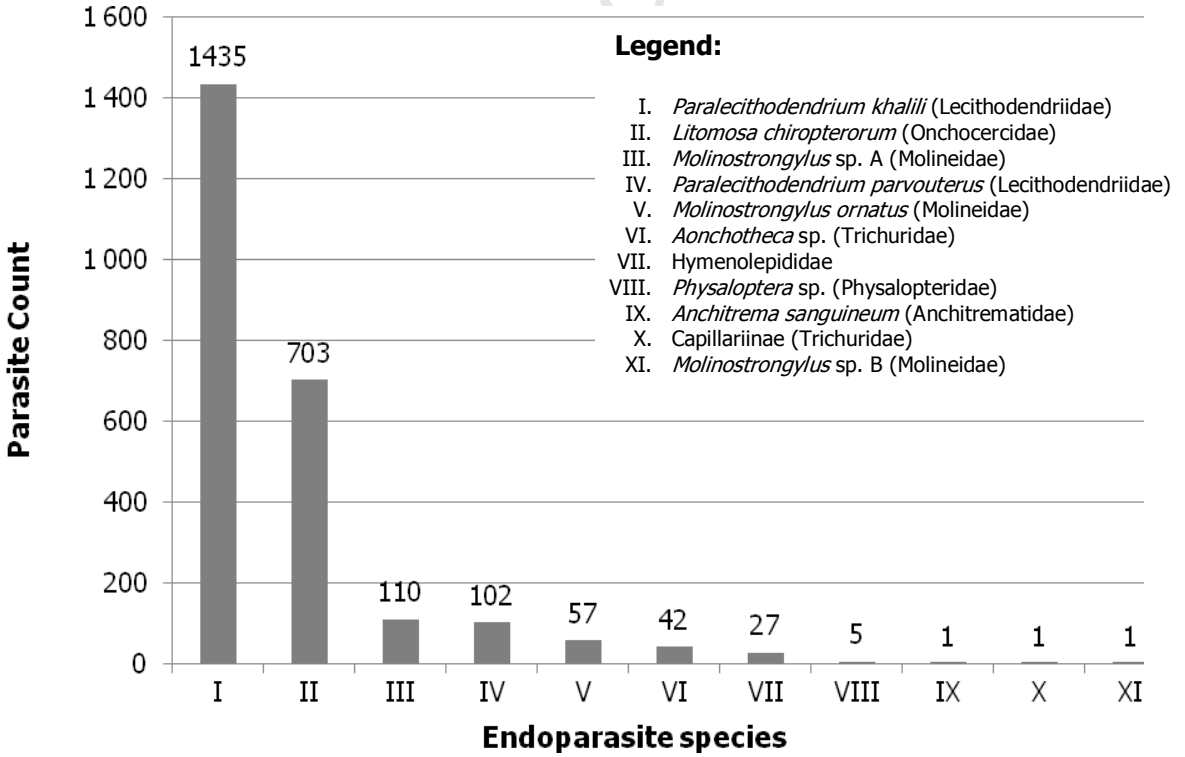

Figure 5: Total number of endoparasites per species recovered from *Miniopterus natalensis* across all sample sites in South Africa

Table 3: Ectoparasites found on *Miniopterus natalensis* in South Africa

Ectoparasite species	DHC (n=13)				KGB (n=19)				SDC (n=20)				SHD (n=11)			
	No. H	**No. Ecp**	**P%**	**MI ± SD (r)**	**No. H**	**No. Ecp**	**P%**	**MI ± SD (r)**	**No. H**	**No. Ecp**	**P%**	**MI ± SD (r)**	**No. H**	**No. Ecp**	**P%**	**MI ± SD (r)**
ACARI	12	91	92	3.6 ± 3.1 (1-13)	13	52	68	2.6 ± 3.4 (1-15)	17	53	85	1.7 ± 1.9 (1-11)	9	25	82	1.6 ± 0.8 (1-3)
Ixodes simplex	2	5	15	2.5 ± 2.1 (1-4)	2	2	11	1 ± 0 (1)	8	12	40	1.5 ± 0.8 (1-3)	-	-	-	-
Calcarmyobia rhinolophia	-	-	-	-	-	-	-	-	1	1	5	1.0 ± 0 (1)	1	1	9	1.0 ± 0 (1)
Ichoronyssus miniopteri	8	42	62	5.3 ± 4.2 (1-13)	3	5	16	1.7 ± 0.6 (1-2)	2	2	10	1.0 ± 0 (1)	3	5	27	1.7 ± 1.2 (1-3)
Macronyssus sp.	-	-	-	-	-	-	-	-	1	1	5	1.0 ± 0 (1)	-	-	-	-
Macronyssus sp. A	-	-	-	-	1	2	5	2.0 ± 0 (2)	4	4	20	1 ± 0 (1)	-	-	-	-
Macronyssus sp. B	6	24	46	4.0 ± 3.3 (1-10)	4	13	21	3.3 ± 3.3 (1-8)	3	4	15	1.3 ± 0.6 (1-2)	3	4	27	1.3 ± 0.6 (1-2)
Macronyssus sp. C	-	-	-	-	3	19	16	6.3 ± 7.6 (1-15)	9	25	45	2.8 ± 3.4 (1-11)	2	4	18	2.0 ± 1.4 (1-3)
Macronyssus sp. D	-	-	-	-	-	-	-	-	1	1	5	1.0 ± 0 (1)	-	-	-	-
Macronyssus sp. E	-	-	-	-	-	-	-	-	-	-	-	-	1	1	9	1.0 ± 0 (1)
Spinturnix semilunaris	9	20	69	2.2 ± 1.1 (1-4)	7	11	37	1.6 ± 1.0 (1-3)	2	3	10	1.5 ± 0.7 (1-2)	6	10	55	1.7 ± 0.8 (1-3)
DIPTERA	8	22	62	1.8 ± 0.7	17	44	39	2.2 ± 1.4	18	46	90	2.0 ± 1.1 (1-4)	9	63	82	4.5 ± 3.8 (1-14)
Ascodipteron sp.	3	3	23	1.0 ± 0 (1)	2	2	11	1.0 ± 0 (1)	6	11	30	1.8 ± 1.7 (1-4)	4	4	36	1.0 ± 0 (1)
Brachytarsina sp.	-	-	-	-	1	1	5	1.0 ± 0 (1)	-	-	-	-	-	-	-	-
Nycteribia schmidlii	8	16	62	2.0 ± 0.5 (1-3)	16	39	84	2.4 ± 1.5 (1-5)	17	35	85	2.1 ± 1.1 (1-4)	9	58	82	6.4 ± 3.4 (2-14)
Penicillidia fulvida	1	3	8	3.0 ± 0 (3)	1	2	5	2.0 ± 0 (2)	-	-	-	-	1	1	9	1.0 ± 0 (1)
SIPHONAPTERA	-	-	-	-	11	21	58	1.9 ± 0.9 (1-4)	-	-	-	-	-	-	-	-
Oxyparius isomalus	-	-	-	-	11	21	58	1.9 ± 0.9 (1-4)	-	-	-	-	-	-	-	-
TOTAL	12	113	92	3.1 ± 2.7 (1-13)	19	117	100	2.3 ± 2.3 (1-15)	20	99	100	1.8 ± 1.6 (1-11)	11	88	100	2.9 ± 3.0 (1-14)

No. H = no. of infected hosts, No. Ecp. = no. of ectoparasites, n = sample size, P% = parasite prevalence, MI = mean infection intensity, r = range. DHC = De Hoop Guano Cave, KGB = Koegelbeen Sinkhole, SDC = Sudwala Caves, SHD = Shongweni Dam

Table 3 (cont.): Ectoparasites found on *Miniopterus natalensis* in South Africa

Ectoparasite species	SKK (n=2)				TF (n=20)				VKD (n=33)				TOTAL (96)			
	No. H	No. Ecp	P%	MI ± SD (r)	No. H	No. Ecp	P%	MI ± SD (r)	No. H	No. Ecp	P%	MI ± SD (r)	No. H	No. Ecp	P%	MI ± SD (r)
ACARI	2	2	50	1.0 ± 0 (1)	17	79	85	1.8 ± 1.4 (1-8)	8	35	52	2.1 ± 1.5 (1-6)	78	337	81	2.2 ± 2.2 (1-15)
Ixodes simplex	-	-	-	-	11	22	55	2.0 ± 1.3 (1-5)	-	-	-	-	23	41	24	1.8 ± 1.2 (1-5)
Calcarmyobia rhinolophia	-	-	-	-	-	-	-	-	1	1	3	1.0 ± 0 (1)	3	3	3	1.0 ± 0 (1)
Ichoronyssus miniopteri	-	-	-	-	5	12	25	2.4 ± 3.1 (1-8)	6	12	18	2.0 ± 1.6 (1-5)	27	78	28	2.9 ± 3.1 (1-13)
Macronyssus sp.	-	-	-	-					-	-	-	-	1	1	1	1.0 ± 0 (1)
Macronyssus sp. A	-	-	-	-	2	2	10	1.0 ± 0 (1)	1	2	3	2.0 ± 0 (2)	8	10	8	1.3 ± 0.5 (1-2)
Macronyssus sp. B	-	-	-	-	3	5	15	1.7 ± 1.2 (1-3)	1	1	3	1.0 ± 0 (1)	20	51	21	2.6 ± 2.5 (1-10)
Macronyssus sp. C	1	1	25	1.0 ± 0 (1)	12	20	60	1.7 ± 0.9 (1-4)	6	16	18	2.7 ± 2.0 (1-6)	33	85	34	2.6 ± 3.0 (1-15)
Macronyssus sp. D	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1.0 ± 0 (1)
Macronyssus sp. E	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1.0 ± 0 (1)
Spinturnix semilunaris	1	1	25	1.0 ± 0 (1)	12	18	60	1.5 ± 1 (1-4)	2	3	6	1.5 ± 0.7 (1-2)	39	66	41	1.7 ± 1.0 (1-4)
DIPTERA	1	4	25	4.0 ± 0 (4)	17	39	85	2.2 ± 1.5 (1-6)	7	15	24	1.9 ± 1.5 (1-5)	77	233	80	2.4 ± 2.0 (1-14)
Ascodipteron sp.	-	-	-	-	-	-	-	-	-	-	-	-	15	20	16	1.3 ± 0.8 (1-4)
Brachytarsina sp.	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1.0 ± 0 (1)
Nycteribia schmidlii	1	4	25	4.0 ± 0 (4)	15	36	75	2.4 ± 1.6 (1-6)	7	14	21	2.0 ± 1.5 (1-5)	73	202	76	2.8 ± 2.2 (1-14)
Penicillidia fulvida	-	-	-	-	3	3	15	1.0 ± 0 (1)	1	1	3	1.0 ± 0 (1)	7	10	7	1.4 ± 0.8 (1-3)
SIPHONAPTERA	1	3	25	3.0 ± 0 (3)	4	4	20	1.0 ± 0 (1)	8	12	24	1.5 ± 0.8 (1-3)	24	40	25	1.7 ± 0.9 (1-4)
Oxyparius isomalus	1	3	25	3.0 ± 0 (3)	4	4	20	1.0 ± 0 (1)	8	12	24	1.5 ± 0.8 (1-3)	24	40	25	1.7 ± 0.9 (1-4)
TOTAL	2	9	100	2.3 ± 1.5 (1-4)	19	122	95	1.8 ± 1.4 (1-8)	10	62	30	1.9 ± 1.3 (1-6)	93	610	97	2.2 ± 2.1 (1-15)

No. H = no. of infected hosts, No. Ecp. = no. of ectoparasites, n = sample size, P% = parasite prevalence, MI = mean infection intensity, r = range. SKK = Steenkampskraal Mine, TF = Table Farm Cave, VKD = Vanderkloof Dam

Table 4: Endoparasites found in *Miniopterus natalensis* in South Africa

Endoparasite species	DHC (n=13)				KGB (n=19)				SDC (n=20)				SHD (n=11)			
	No. H	**No. Enp.**	**P%**	**MI ± SD (r)**	**No. H**	**No. Enp.**	**P%**	**MI ± SD (r)**	**No. H**	**No. Enp.**	**P%**	**MI ± SD (r)**	**No. H**	**No. Enp.**	**P%**	**MI ± SD (r)**
TREMATODA	-	-	-	-	1	33	5	33 ± 0 (33)	12	1499	60	78.9 ± 167.4 (1-738)	2	6	18	3.0 ± 2.8 (1-5)
Anchitrema sanguineum	-	-	-	-	-	-	-	-	1	1	5	1.0 ± 0 (1)	-	-	-	-
Paralecithodendrium khalili	-	-	-	-	-	-	-	-	1	1429	5	119.1 ± 202.5 (2-738)	2	6	18	2.0 ± 2.8 (1-5)
Paralecithodendrium parvouterus	-	-	-	-	-	33	-	33 ± 0 (33)	1	69	5	11.5 ± 8.5 (1-20)	-	-	-	-
CESTODA	-	-	-	-	-	-	-	-	4	8	20	2.0 ± 2.0 (1-5)	4	5	36	1.3 ± 0.5 (1-2)
Hymenolepididae	-	-	-	-	-	-	-	-	4	8	20	2.0 ± 2.0 (1-5)	4	5	36	1.3 ± 0.5 (1-2)
NEMATODA	9	52	43	2.5 ± 1.8 (1-6)	19	188	46	4.7 ± 3.8 (1-13)	11	25	29	1.7 ± 1.0 (1-4)	11	177	61	14.8 ± 11.5 (2-41)
Strongylida	6	22	46	2.8 ± 1.8 (1-6)	14	96	74	6.9 ± 3.8 (2-13)	5	10	25	2.0 ± 1.4 (1-4)	-	-	-	-
Molinostrongylus ornatus	6	19	46	3.2 ± 2.4 (1-6)	-	-	-	-	3	6	15	2.0 ± 1.7 (1-4)	-	-	-	-
Molinostrongylus sp. A	6	3	46	1.5 ± 0.7 (1-2)	14	96	74	6.9 ± 3.8 (2-13)	3	4	15	2.0 ± 1.4 (1-3)	-	-	-	-
Molinostrongylus sp. B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Spirurida	9	29	69	2.4 ± 1.6 (1-5)	14	71	74	5.0 ± 3.9 (1-12)	1	2	5	2.0 ± 0 (2)	11	175	100	15.9 ± 11.2 (4-41)
Litomosa chiropterorum	9	25	69	2.8 ± 1.6 (1-5)	14	71	74	5.0 ± 3.9 (1-12)	1	2	5	2.0 ± 0 (2)	11	175	100	15.9 ± 11.2 (4-41)
Physaloptera sp.	3	4	23	1.3 ± 0.6 (1-2)	-	-	-	-	-	-	-	-	-	-	-	-
Enoplida	1	1	8	1.0 ± 0 (1)	12	21	63	1.8 ± 0.9 (1-3)	9	13	45	1.4 ± 0.7 (1-3	1	2	9	2.0 ± 0 (2)
Aonchotheca sp.	1	1	8	1.0 ± 0 (1)	12	21	63	1.8 ± 0.9 (1-3)	9	13	45	1.4 ± 0.7 (1-3)	-	-	-	-
Capillariinae	-	-	-	-	-	-	-	-	-	-	-	-	1	2	9	2.0 ± 0 (2)
TOTAL	9	52	100	2.5 ± 1.8 (1-6)	19	221	100	5.4 ± 5.8 (1-33)	18	1532	90	40.3 ± 123.1 (1-738)	11	188	100	10.4 ± 11.2 (1-41)

No. H = no. of infected hosts, No. Enp. = no. of endoparasites, n = sample size, P% = parasite prevalence, MI = mean infection intensity, r = range. DHC = De Hoop Guano Cave, KGB = Koegelbeen Sinkhole, SDC = Sudwala Caves, SHD = Shongweni Dam

Table 4 (cont.): Endoparasites found in *Miniopterus natalensis* in South Africa

Endoparasite species	SKK (n=2)				TF (n=20)				VKD (n=11)				TOTAL (n=96)			
	No. H	**No. Enp.**	**P %**	**MI ± SD (r)**	**No. H**	**No. Enp.**	**P%**	**MI ± SD (r)**	**No. H**	**No. Enp.**	**P%**	**MI ± SD (r)**	**No. H**	**No. Enp.**	**P%**	**MI ± SD (r)**
TREMATODA	-	-	-	-	-	-	-	-	-	-	-	-	22	1538	23	69.9 ± 156.8 (1-738)
Anchitrema sanguineum	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1.0 ± 0 (1)
Paralecithodendrium khalili	-	-	-	-	-	-	-	-	-	-	-	-	14	1435	15	102.5 ± 191.0 (1-738)
Paralecithodendrium parvouterus	-	-	-	-	-	-	-	-	-	-	-	-	7	102	7	14.6 ± 11.2 (1-33)
CESTODA	-	-	-	-	7	14	35	2.0 ± 1.5 (1-5)	-	-	-	-	15	27	16	1.8 ± 1.4 (1-5)
Hymenolepididae	-	-	-	-	7	14	35	2.0 ± 1.5 (1-5)	-	-	-	-	15	27	16	1.8 ± 1.4 (1-5)
NEMATODA	2	16	67	5.3 ±4.5 (1-10)	20	252	49	7.4 ± 12.8 (1-64)	11	208	85	16 ± 13.5 (1-39)	83	918	86	6.7 ±9.6 (1-64)
Strongylida	1	1	50	1.0 ± 0 (1)	10	35	50	3.2 ± 3.1 (1-11)	3	4	27	1.3 ± 0.6 (1-2)	42	168	44	4.0 ± 3.5 (1-13)
Molinostrongylus ornatus	-	-	-	-	9	32	45	3.6 ± 3.4 (1-11)	-	-	-	-	18	57	19	3.2 ± 2.8 (1-11)
Molinostrongylus sp. A	1	1	50	1.0 ± 0 (1)	1	2	5	2.0 ± 0 (2)	3	4	27	1.3 ± 0.6 (1-2)	23	110	24	4.8 ± 3.9 (1-13)
Molinostrongylus sp. B	-	-	-	-	1	1	5	1.0 ± 0 (1)	-	-	-	-	1	1	1	1.0 ± 0 (1)
Spirurida	2	15	100	7.5 ± 3.5 (5-10)	19	214	95	10.7 ± 15.9 (1-64)	9	202	82	22.4 ± 10.9 (5-39)	69	708	72	10.3 ± 12.2 (1-64)
Litomosa chiropterorum	2	15	100	7.5 ± 3.5 (5-10)	19	213	95	11.2 ± 16.1 (1)	9	202	82	22.4 ± 10.9 (5-39)	65	703	68	10.8 ± 12.4 (1-64)
Physaloptera sp.	-	-	-	-	1	1	5		-	-	-	-	4	5	4	1.3 ± 0.5 (1-2)
Enoplida	-	-	-	-	3	3	15	1.0 ± 0 (1)	1	2	9	2.0 ± 0 (2)	27	42	28	1.6 ± 0.8 (1-3)
Aonchotheca sp.	-	-	-	-	3	3	15	1.0 ± 0 (1)	1	2	9	2.0 ± 0 (2)	26	42	27	1.5 ± 0.8 (1-3)
Capillariinae	-	-	-	-	-	-	-	-	-	-	-	-	1	2	1	2.0 ± 0 (2)
TOTAL	2	16	100	5.3 ± 4.5 (1-10)	20	266	100	6.5 ± 11.8 (1-64)	11	208	100	16.0 ± 13.5 (1-39)	90	2483	94	14.2 ± 59.1 (1-738)

No. H = no. of infected hosts, No. Enp. = no. of endoparasites, n = sample size, P% = parasite prevalence, MI = mean infection intensity, r = range. SKK = Steenkampskraal Mine, TF = Table Farm Cave, VKD = Vanderkloof Dam

3.2 Shannon's Diversity Index

Excepting Shongweni Dam (1.26) and Steenkampskraal Mine (1.21), the ectoparasite Shannon's Diversity Index (SDI) was relatively uniform (1.79 ± 0.11) (Table 5). In contrast, endoparasite SDI's showed more variation and were much lower, being below one at five of the seven sites sampled, excepting De Hoop Guano Cave (1.16) and Koegelbeen Sinkhole (1.23) which were approximately 3.5 times higher than the average endoparasite SDI's (Table 5).

Vanderkloof Dam had an especially low endoparasite SDI (0.15) with only three species present, two of which (*Aonchotheca* sp. and *Molinostrongylus* sp. A) were represented by only two and four individuals, respectively, as opposed to the 202 specimens representing the dominant helminth species (*L. chiropterorum*) there (Table 4).

Table 5: Shannon's Diversity Indices of parasite communities of *Miniopterus natalensis* across sample sites in South Africa

Sample Sites	**Biome**	**Shannon's Diversity Index (H)***	
		Ectoparasites	**Endoparasites**
Sudwala Caves	Grassland	1.80	0.32
Koegelbeen Sinkhole	Savanna	1.89	1.23
Table Farm	Albany Thicket	1.88	0.72
Vanderkloof Dam	Nama Karoo	1.78	0.15
Shongweni Dam	Savanna	1.26	0.32
Steenkampskraal Mine	Succulent Karoo	1.21	0.23
De Hoop Guano Cave	Fynbos	1.61	1.16

**Using the formula* $\mathrm{H} = -\sum_{i=1}^{S} p_i \ln p_i$*, where* p_i *is the relative abundance of each species i, calculated as the proportion of individuals of a given species to the total number of individuals in the community:* $\frac{n_i}{N}$*, and S is the number of species (i.e. the species richness) at a site.*

CHAPTER 4

RESULTS: TESTING HYPOTHESES

4.1 Host Sex Hypothesis

There was no difference in infection intensity (Tables 6 & 7) between host sexes for either ectoparasites (MANOVA: $F_{(9,21)} = 1.22$, $p>0.05$; Figure 6) or endoparasites (MANOVA: $F_{(5,51)} = 1.78$, $p>0.05$; Figure 7).

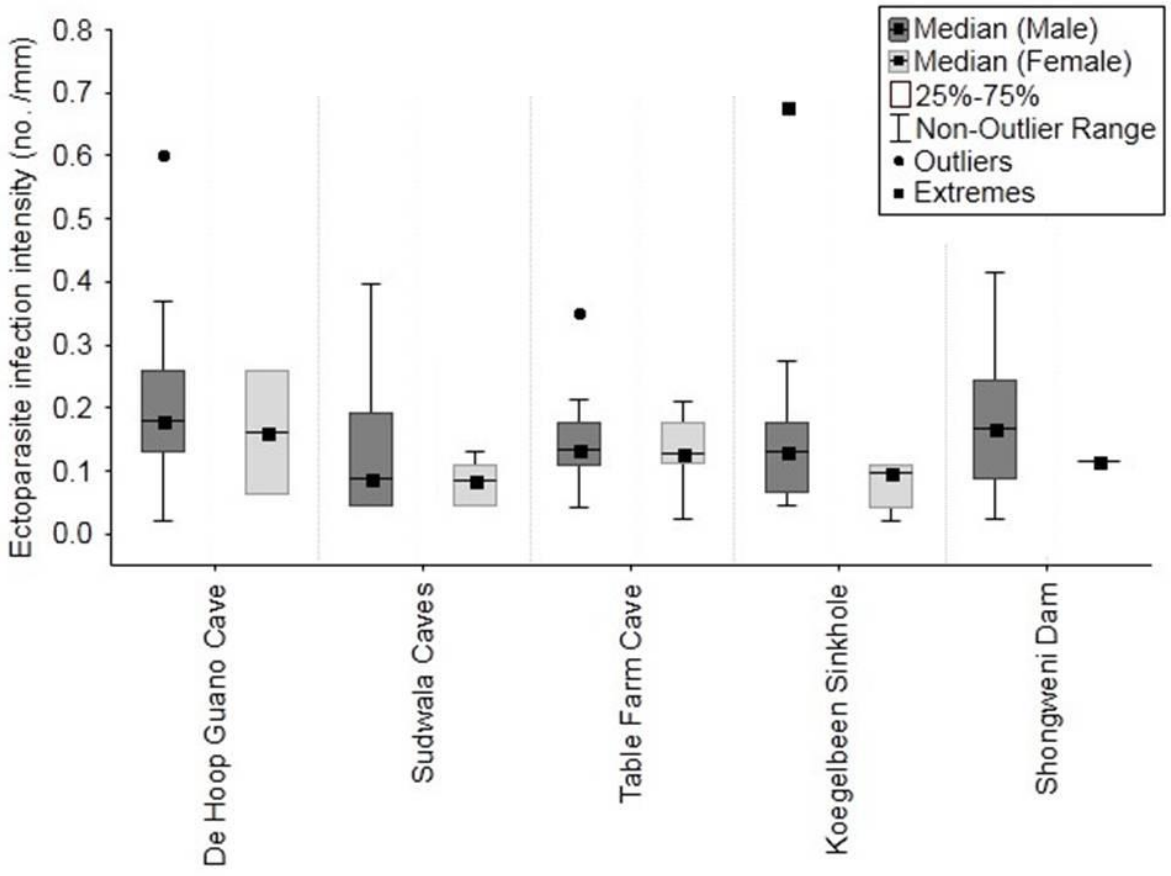

Figure 6: Box-and-Whisker plot of ectoparasite infection intensity in male and female *Miniopterus natalensis* across sample sites in South Africa. $F_{(9,21)} = 1.22$, $p>0.05$.

Note: no./mm represents no. of endoparasites divided by host forearm length (mm)

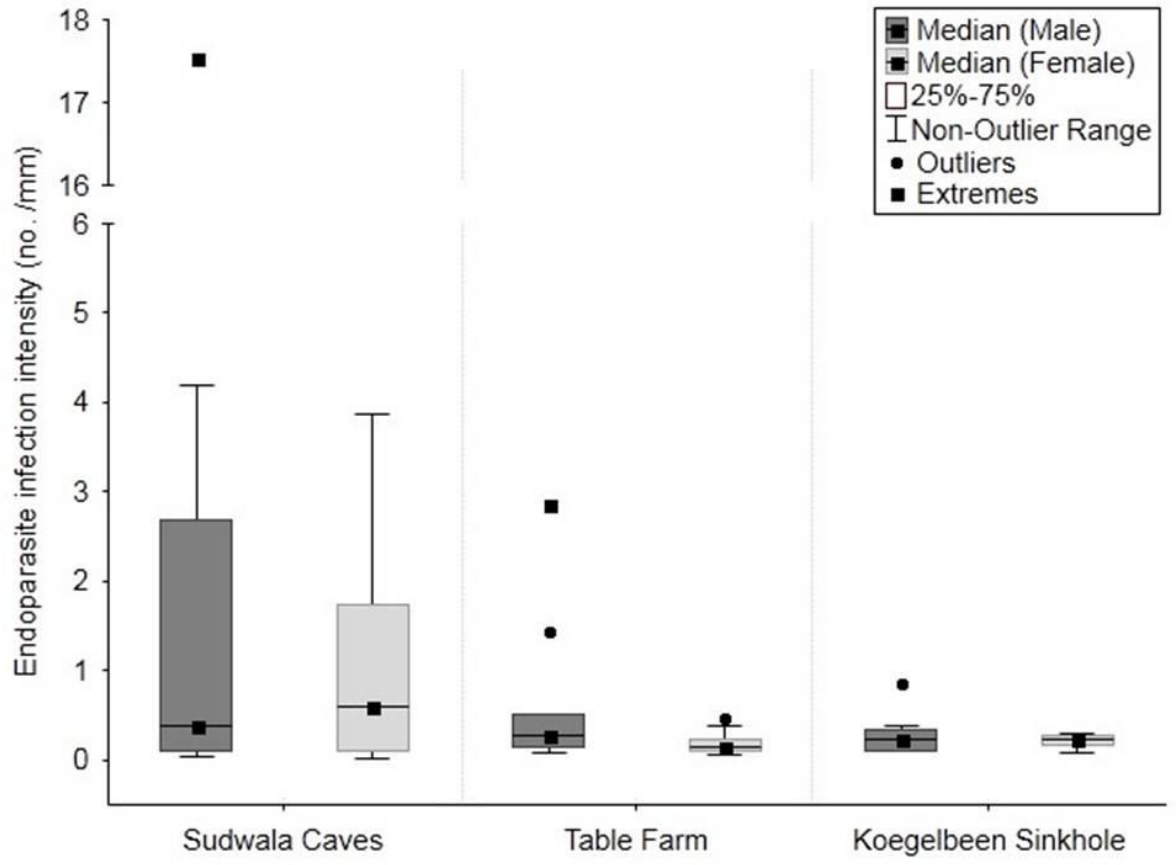

Figure 7: Box-and-Whisker plot of endoparasite infection intensity in male and female *Miniopterus natalensis* across sample sites in South Africa. $F_{(5,51)} = 1.78$, $p>0.05$.

Note: no./mm represents no. of endoparasites divided by host forearm length (mm)

However, Figure 7 shows two extremes which may have distorted the results in the endoparasites. These extremes were excluded and the data retested, but this still resulted in no significant differences in endoparasite infection intensity between the biomes. This allowed for the data from males and females to be pooled in subsequent analyses, thereby making the results of those analyses more robust.

Table 6: Ectoparasite and Endoparasite Infection Intensities, corrected for size, in *Miniopterus natalensis*, South Africa

Host Code	Host Sex	Sample Site	Biome	Biome Group	Host F.L. (mm)	No. of Ecp.	Ecp. Inf. Int.	No. of Enp.	Enp. Inf. Int.
011009Mn01SDC	Male	Sudwala Caves	Grass-land	Hetero-geneous	45.5	18	0.40	798	17.54
011009Mn02SDC	Male				44.7	10	0.22	187	4.18
011009Mn03SDC	Male				44.02	3	0.07	28	0.64
011009Mn04SDC	Male				44.5	2	0.04	52	1.17
011009Mn05SDC	Male				46.3	5	0.11	2	0.04
011009Mn06SDC	Male				46.6	9	0.19	4	0.09
011009Mn07SDC	Male				45.1	7	0.16	5	0.11
011009Mn08SDC	Male				45.02	3	0.07	6	0.13
011009Mn09SDC	Male				44.7	2	0.04	-	-
011009Mn10SDC	Male				44.6	2	0.04	-	-
031009Mn11SDC	Female				45.29	2	0.04	1	0.02
031009Mn12SDC	Female				46.93	3	0.06	100	2.13
031009Mn13SDC	Female				46.83	5	0.11	5	0.11
031009Mn14SDC	Female				45.78	5	0.11	2	0.04
031009Mn15SDC	Female				46.12	6	0.13	28	0.61
031009Mn16SDC	Female				45.5	2	0.04	26	0.57
031009Mn17SDC	Female				46	5	0.11	80	1.74
031009Mn18SDC	Female				46.06	2	0.04	5	0.11
031009Mn19SDC	Female				47.85	4	0.08	61	1.27
031009Mn20SDC	Female				46.17	4	0.09	179	3.88
Average					**45.68 ± 0.97**	**4.95 ± 3.86**	**0.11 ± 0.08**	**87.17 ± 186.65**	**1.91 ± 4.10**
101009Mn01KGB	Male	Koegelbeen Sinkhole	Savanna	Homo-geneous	45.12	3	0.07	5	0.11
101009Mn02KGB	Male				45.72	31	0.68	14	0.31
101009Mn03KGB	Female				45.34	5	0.11	10	0.22
131009Mn04KGB	Female				47.69	8	0.17	18	0.38
131009Mn05KGB	Male				45.46	8	0.18	5	0.11
131009Mn06KGB	Female				47	5	0.11	4	0.09
131009Mn07KGB	Male				45.67	3	0.07	7	0.15
131009Mn08KGB	Male				46.17	6	0.13	16	0.35
131009Mn09KGB	Male				46.65	7	0.15	5	0.11
131009Mn10KGB	Male				46.92	4	0.09	7	0.15
131009Mn11KGB	Male				45.28	2	0.04	39	0.86
131009Mn12KGB	Male				47.53	13	0.27	11	0.23
131009Mn13KGB	Male				46.93	3	0.06	12	0.26
141009Mn14KGB	Female				46.36	4	0.09	6	0.13
161009Mn15KGB	Female				45.81	5	0.11	13	0.28
161009Mn16KGB	Female				45.81	2	0.04	10	0.22
161009Mn17KGB	Female				45.73	5	0.11	14	0.31

No. of Ecp.= number of ectoparasites, No. of Enp.= number of endoparasites, F.L. = forearm length, mm = millimetres, Inf. Int. = infection intensity, corrected for size

Host Code	Host Sex	Sample Site	Biome	Biome Group	Host F.L. (mm)	No. of Ecp.	Ecp. Inf. Int.	No. of Enp.	Enp. Inf. Int.
161009Mn18KGB	Female	Koegelbeen Sinkhole	Savanna	Homo-geneous	47.03	1	0.02	12	0.26
161009Mn19KGB	Female				47.29	2	0.04	13	0.27
Average					**46.29 ± 0.82**	**6.16 ± 6.64**	**0.13 ± 0.14**	**11.63 ± 7.80**	**0.25 ± 0.17**
071209Mn01TF	Male				45.1	8	0.18	11	0.24
071209Mn02TF	Male				44.44	3	0.07	4	0.09
071209Mn03TF	Male				45.1	-	-	11	0.24
071209Mn04TF	Male				45.18	6	0.13	7	0.15
071209Mn05TF	Male				46.6	2	0.04	15	0.32
071209Mn06TF	Male				45.8	16	0.35	23	0.50
071209Mn07TF	Male				45.54	8	0.18	4	0.09
071209Mn08TF	Male				45.5	5	0.11	130	2.86
071209Mn09TF	Male				47.22	10	0.21	19	0.40
071209Mn10TF	Male				44.32	5	0.11	64	1.44
071209Mn11TF	Female				42.64	9	0.21	3	0.07
071209Mn12TF	Female				44.14	1	0.02	9	0.20
071209Mn13TF	Female				45.02	5	0.11	10	0.22
071209Mn14TF	Female				46.72	6	0.13	6	0.13
071209Mn15TF	Female				45.32	8	0.18	6	0.13
071209Mn16TF	Female				46.68	6	0.13	22	0.47
071209Mn17TF	Female				45.3	9	0.20	4	0.09
071209Mn18TF	Female				44.29	5	0.11	17	0.38
071209Mn19TF	Female				46.2	6	0.13	8	0.17
071209Mn20TF	Female				44.3	4	0.09	5	0.11
Average					**45.28 ± 1.12**	**6.42 ± 3.34**	**0.14 ± 0.07**	**18.90 ± 29.41**	**0.42 ± 0.65**
101209Mn01VKD	Male	Vanderkloof Dam	Nama Karoo	Homo-geneous	46.22	2	0.04	16	0.35
101209Mn02VKD	Male				45.4	4	0.09	39	0.86
101209Mn03VKD	Male				45.12	12	0.27	22	0.49
101209Mn04VKD	Male				46.14	13	0.28	35	0.76
101209Mn05VKD	Male				45.22	11	0.24	14	0.31
101209Mn06VKD	Male				46.72	3	0.06	3	0.06
101209Mn07VKD	Male				45.9	3	0.07	5	0.11
101209Mn08VKD	Male				46.19	5	0.11	15	0.32
101209Mn09VKD	Male				45.42	4	0.09	27	0.59
101209Mn10VKD	Male				45.68	5	0.11	30	0.66
101209Mn11VKD	Female				46.3	-	-	2	0.04
Average					**45.80 ± 0.52**	**6.20 ± 4.13**	**0.14 ± 0.09**	**18.91 ± 12.81**	**0.41 ± 0.28**
181209Mn01SHD	Male	Shongweni Dam	Savanna	Homo-geneous	45.88	4	0.09	26	0.57
181209Mn02SHD	Male				44.27	9	0.20	9	0.20

No. of Ecp.= number of ectoparasites, No. of Enp.= number of endoparasites, F.L. = forearm length, mm = millimetres, Inf. Int. = infection intensity, corrected for size

Host Code	Host Sex	Sample Site	Biome	Biome Group	Host F.L. (mm)	No. of Ecp.	Ecp. Inf. Int.	No. of Enp.	Enp. Inf. Int.
181209Mn03SHD	Male	Shongweni Dam	Savanna	Homo-geneous	46.89	15	0.32	41	0.87
181209Mn04SHD	Male				46.53	5	0.11	13	0.28
181209Mn05SHD	Male				46.94	10	0.21	19	0.40
181209Mn06SHD	Male				45.2	3	0.07	11	0.24
181209Mn07SHD	Male	Shongweni Dam	Savanna	Homo-geneous	45.3	6	0.13	26	0.57
181209Mn08SHD	Male				45.68	19	0.42	4	0.09
181209Mn09SHD	Male				45.28	11	0.24	19	0.42
181209Mn10SHD	Male				44.62	1	0.02	13	0.29
181209Mn11SHD	Female				43.46	5	0.12	8	0.18
Average					**45.46 ± 1.09**	**8.00 ± 5.44**	**0.18 ± 0.12**	**17.18 ± 10.62**	**0.38 ± 0.23**
040110Mn01SKK	Male	Steenkamps-kraal Mine	Succulent Karoo	Homo-geneous	46.17	8	0.17	5	0.11
040110Mn02SKK	Male				47.12	1	0.02	11	0.23
Average					**46.65 ±0.67**	**4.50 ± 4.95**	**0.10 ± 0.11**	**8.00 ± 4.24**	**0.17 ± 0.08**
010310Mn01DHC	Male	De Hoop Guano Cave	Fynbos	Hetero-geneous	46.6	11	0.24	1	0.10
010310Mn02DHC	Male				44.9	27	0.60	6	0.13
010310Mn03DHC	Male				45.3	6	0.13	13	0.29
010310Mn04DHC	Male				45.34	6	0.13	-	-
010310Mn05DHC	Male				46.34	12	0.26	3	0.06
010310Mn06DHC	Male				44.42	10	0.23	4	0.09
010310Mn07DHC	Male				46.28	2	0.04	3	0.06
010310Mn08DHC	Male				46.48	6	0.13	8	0.17
010310Mn09DHC	Male				46.14	17	0.37	10	0.22
010310Mn10DHC	Male				46.5	1	0.02	4	0.09
010310Mn11DHC	Female				46.6	3	0.06	-	-
010310Mn12DHC	Female				47.1	-	-	1	0.02
010310Mn13DHC	Female				46.1	12	0.26	-	-
Average					**45.92 ± 0.74**	**9.42 ± 7.29**	**0.21 ± 0.16**	**5.30 ± 3.95**	**0.12 ± 0.08**

No. of Ecp.= number of ectoparasites, No. of Enp.= number of endoparasites, F.L. = forearm length, mm = millimetres, Inf. Int. = infection intensity, corrected for size

4.2 Host Body Size Hypothesis

All data were pooled across sites and sex, and log transformed to conform with assumptions. No relationship was found between the number of ectoparasite species (r_5 = -0.39, p>0.05) and average host body mass using linear regressions. However, the number of endoparasite species was negatively correlated with average host body mass (r_5 = -0.84, p<0.05; Figure 8), contrary to predictions (Figure 8).

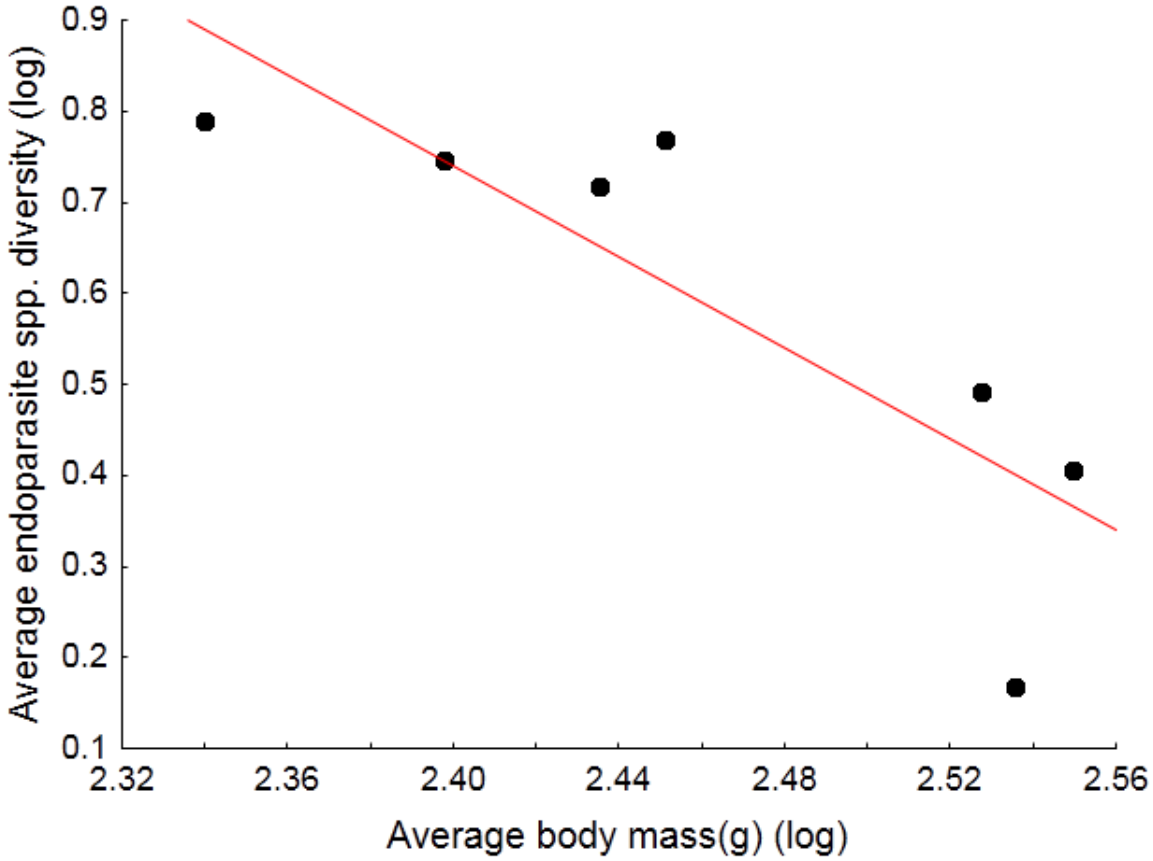

Figure 8: Plot of average endoparasites species diversity (log), collected from *Miniopterus natalensis*, against average host body mass (g) (log) across sample sites in South Africa. r_5 = -0.84, p<0.05.

Similarly, general linear regressions were performed to determine the relationship between average host body mass and average parasite infection intensity. Both average host body mass and average parasite infection intensity were log transformed. However, the infection intensities of neither ecto- nor endoparasites

showed a significant relationship with average host body mass (r_5 = -0.39, p>0.05 and r_5 = -0.05, p>0.05 respectively).

There was also no relationship between average body condition index (BCI) and the average infection intensities of either ecto- (r_5 = -0.34, p>0.05) or endoparasite (r_5 = 0.26, p>0.05). Similarly there was also no relationship between average BCI and average number of ectoparasite species (r_5 = 0.01, p>0.05). However, the number of endoparasite species was negatively correlated with average BCI (r_5 = -0.83, p<0.05) (Figure 9).

Within site analyses of each of these predictions found no significant correlations for the ecto- or endoparasites at any site (average host body mass - ecto's: r's < 0.34; p's > 0.28 and endo's: r's < 0.44; p's > 0.05) (BCI - ecto's: r's < 0.37; p's > 0.25 and endo's: r's < 0.36; p's > 0.11), except at Shongweni Dam where a significant positive relationship was found between average endoparasite infection intensity and average host body mass (r = 0.615, p<0.05).

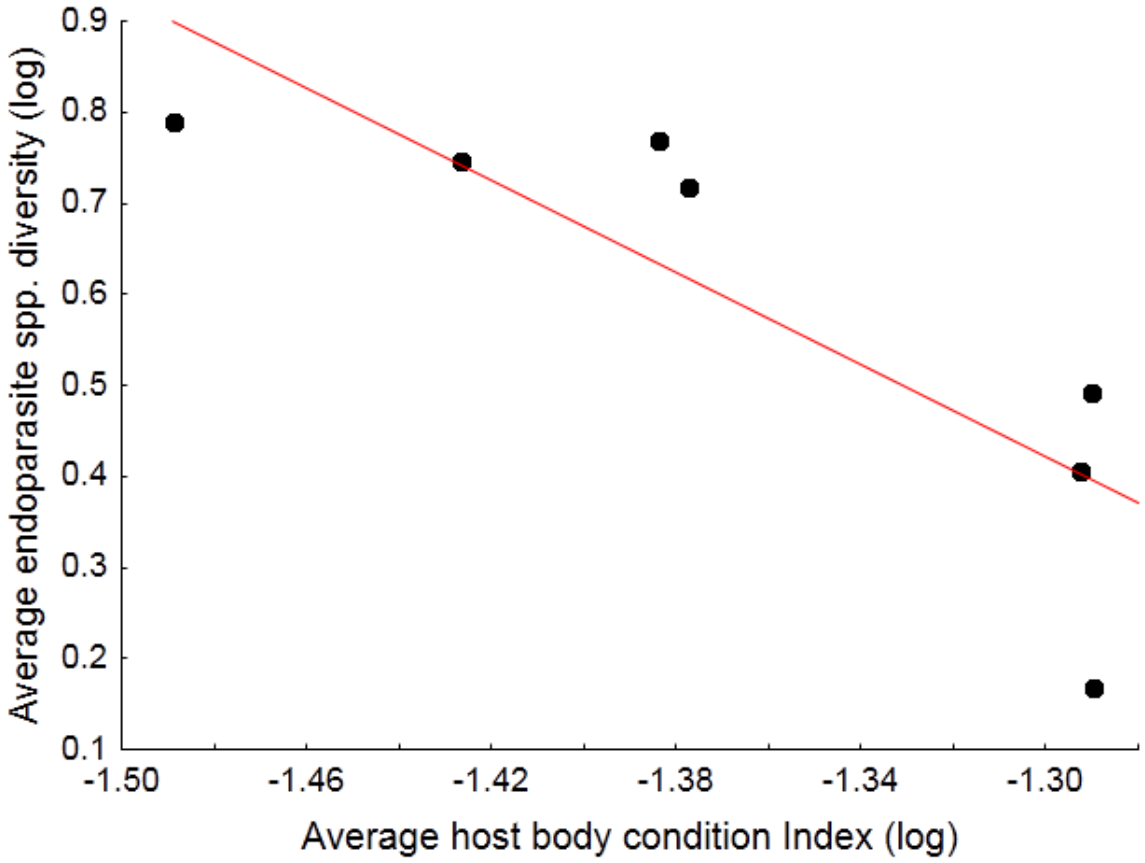

Figure 9: Plot of average host body condition (log) and average endoparasite species diversity (log), collected from *Miniopterus natalensis*, across sites in South Africa. r_5 = -0.83, $p<0.05$.

Note: Body Condition (Index) increases from left to right

4.3 Habitat Heterogeneity Hypothesis

Prediction 1

Kruskal-Wallis ANOVA's performed on the total number of parasite species at each sample site (excluding Steenkampskraal Mine) showed little variation between the heterogeneous and homogeneous habitats into which the sample sites were grouped for these analyses. Neither ecto- nor endoparasite species numbers were

significantly affected by habitat heterogeneity ($H_{(4,60)}$ = 3.67, p>0.05 and $H_{(5,56)}$ = 14.64, p=0.05 respectively; Figures 10 & 11).

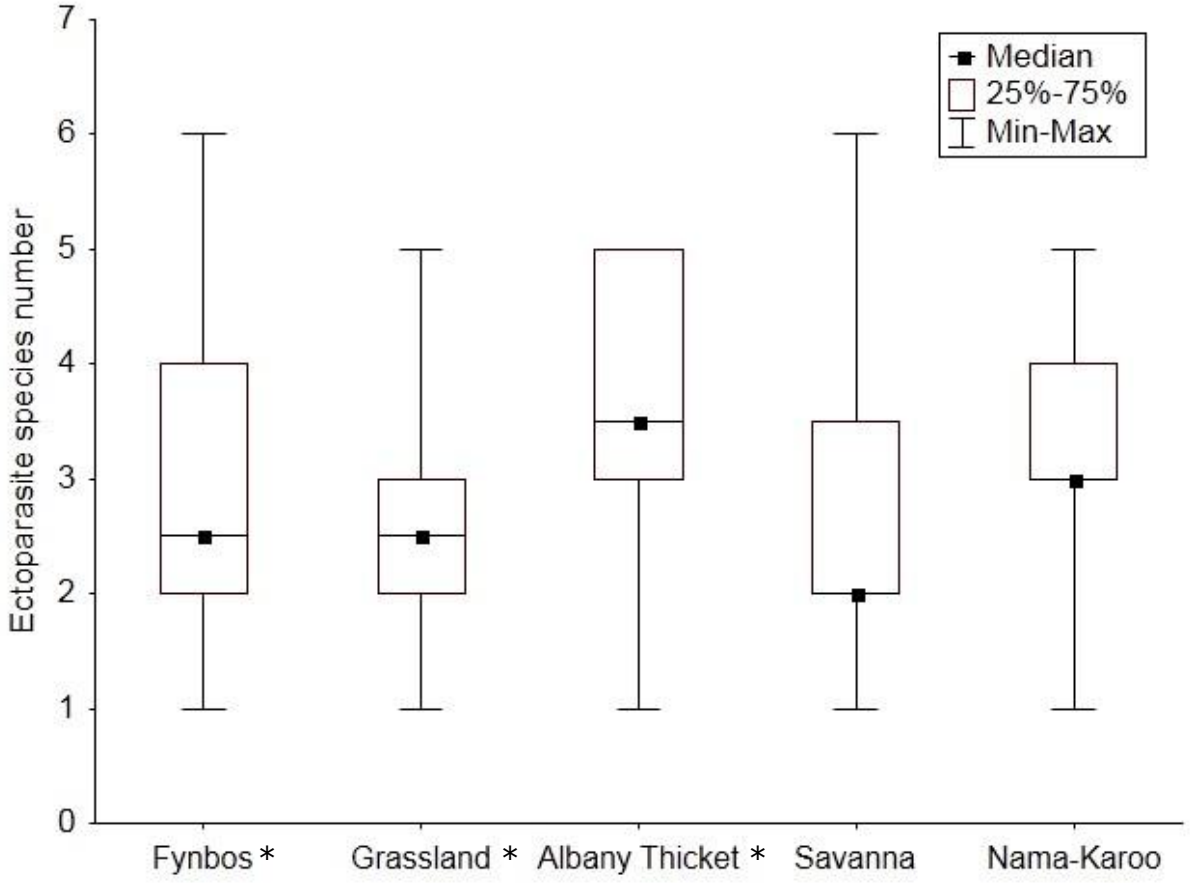

Figure 10: Box-and-Whisker plot of ectoparasite species counts from *Miniopterus natalensis* across sample sites in South Africa. $H_{(4,60)}$ = 3.67, p>0.05.

** = heterogeneous habitat, unmarked = homogeneous habitat*

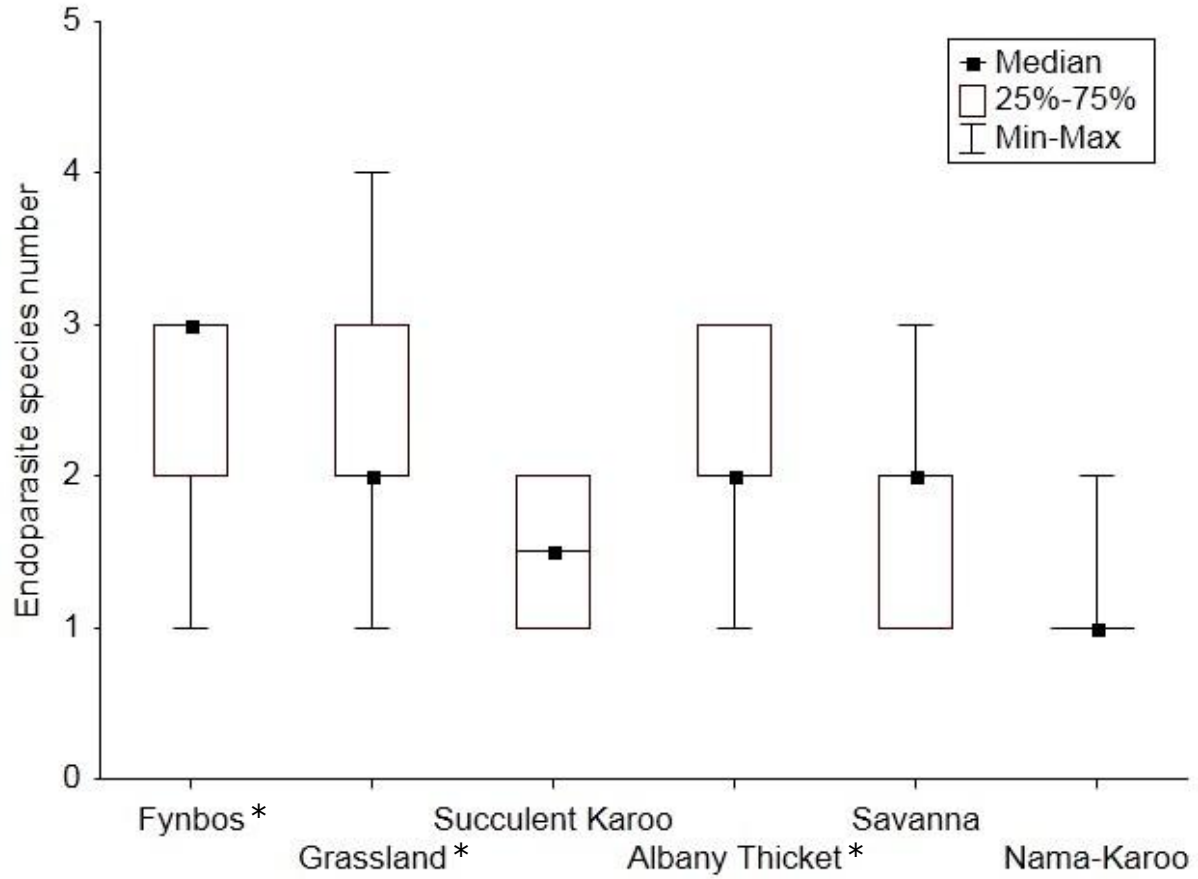

Figure 11: Box-and-Whisker plot of endoparasite species counts from *Miniopterus natalensis* across sample sites in South Africa. $H_{(5,56)}$ = 14.64, p=0.05.

** = heterogeneous habitat, unmarked = homogeneous habitat*

Prediction 2

Using Kruskal-Wallis ANOVA's, no significant difference was found between habitat heterogeneity and parasite infection intensity between the sites for either ecto- ($H_{(5,93)}$ = 6.73, p>0.05; Figure 12) or endoparasites ($H_{(5,91)}$ = 10.83, p>0.05; Figure 13) in these parasite assemblages.

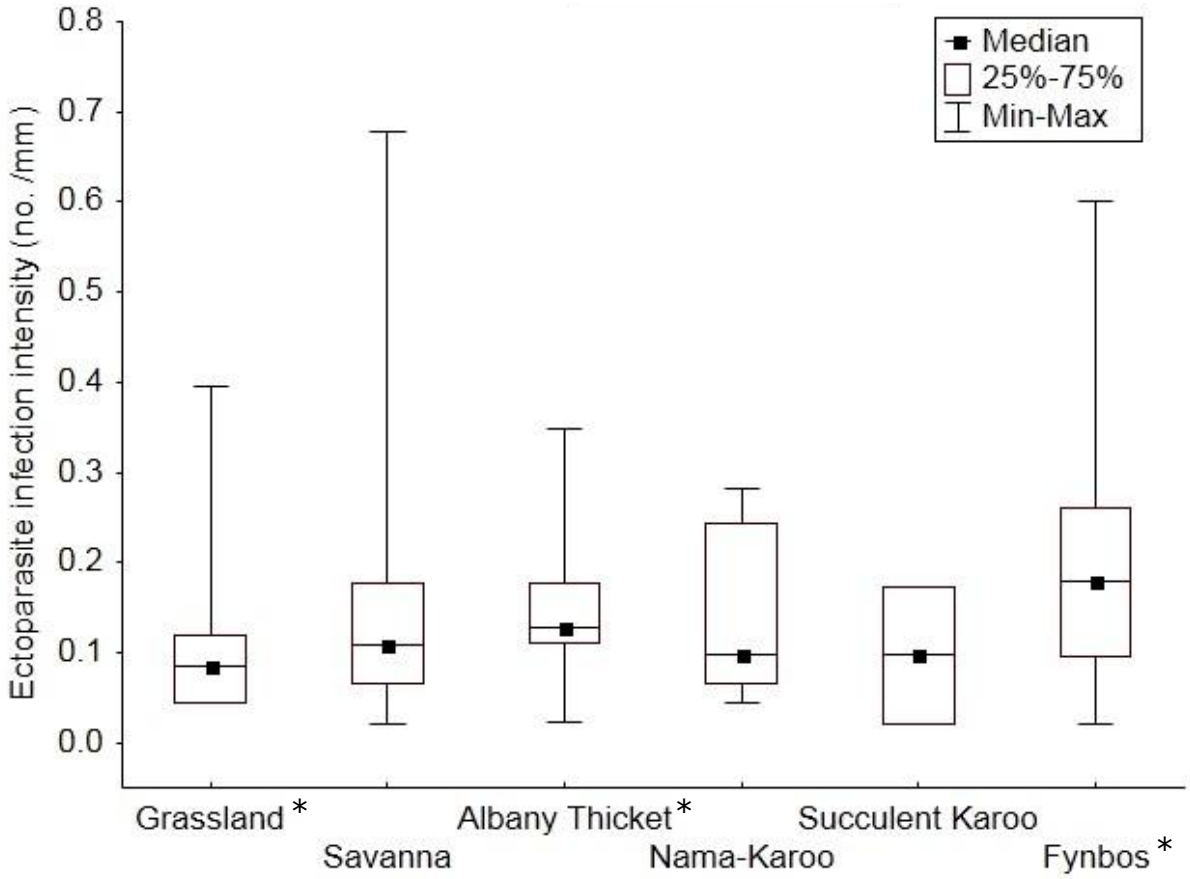

Figure 12: Box-&-Whisker plot of ectoparasite infection intensities on *Miniopterus natalensis* across sample sites in South Africa. $H_{(5,93)} = 6.73$, $p>0.05$.

no./mm represents no. of endoparasites divided by host forearm length (mm)
** = heterogeneous habitat, unmarked = homogeneous habitat*

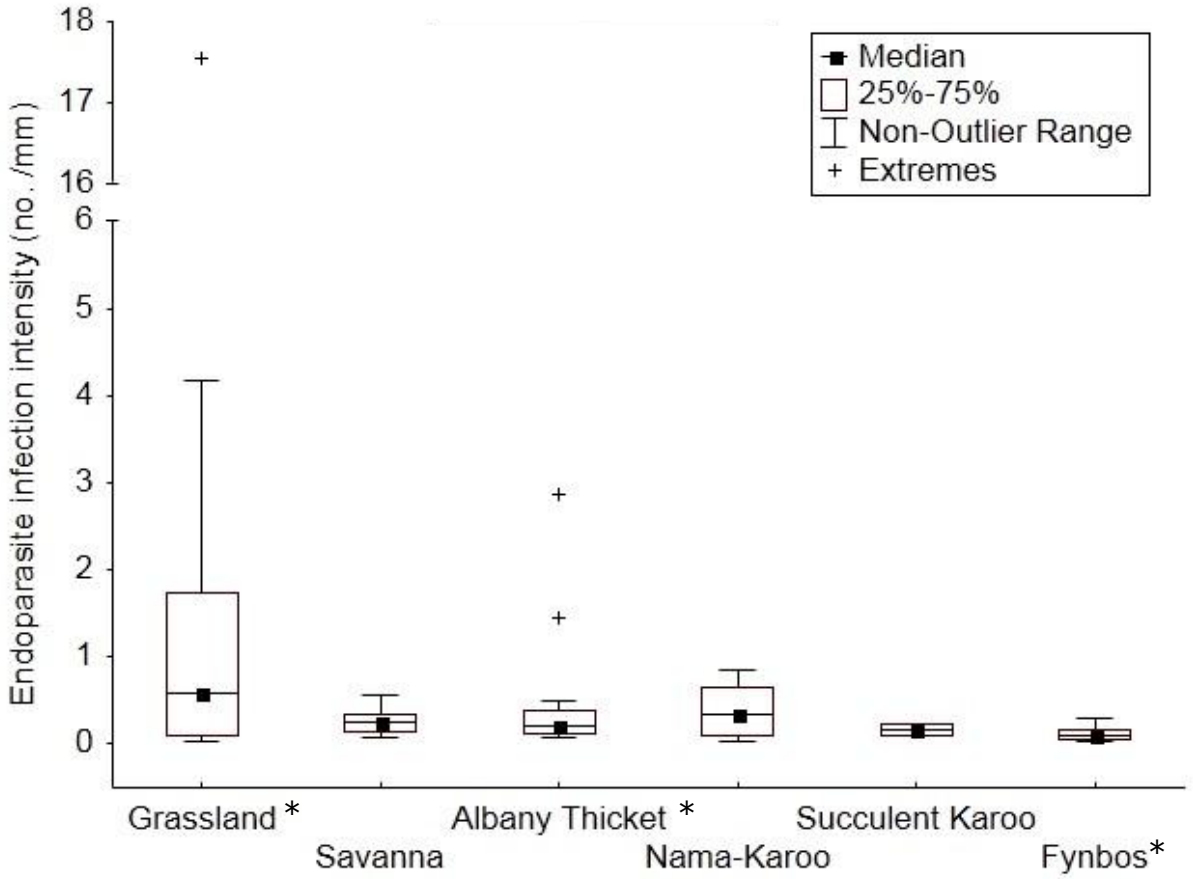

Figure 13: Box-&-Whisker plot of endoparasite infection intensities in *Miniopterus natalensis* across sample sites in South Africa. $H_{(5,91)} = 10.83$, $p>0.05$.

no./mm represents no. of endoparasites divided by host forearm length (mm)
** = heterogeneous habitat, unmarked = homogeneous habitat*

However, Figure 13 shows three extreme data points that may have affected the significance of the results. After removing these extremes and retesting the data there were still no significant differences found in endoparasite infection intensity between biomes.

Prediction 3

Bat species that co-occurred with *Miniopterus natalensis* at each sample site were as follows. De Hoop Guano Cave: *Myotis tricolor* Temminck, 1832 (Vespertilionidae), *Nycteris thebaica* Geoffroy Saint-Hilaire, 1818 (Nycteridae), *Rhinolophus capensis* Lichtenstein, 1823 and *Rhinolophus clivosus* Cretzschmar, 1828 (both Rhinolophidae); Koegelbeen Sinkhole: *R. clivosus*, *Rhinolophus darlingi* Andersen, 1905 and *Rhinolophus denti* Thomas, 1904 (Rhinolophidae); Shongweni Dam: *M. fraterculus* and *M. tricolor;* (Steenkampskraal Mine) *R. capensis*; Sudwala Caves: *M. fraterculus*, *Rhinolophus blasii* Peters, 1866, *R. clivosus* and *R. darling* (Rhinolophidae); Table Farm: *R. capensis*; Vanderkloof Dam: *Neoromicia capensis* Smith, 1829 (Vespertilionidae).

There was no relationship ($r_{(4)}$ = -0.04, p>0.05) between bat species diversity and co-occurring ectoparasite species diversity (Figure 14).

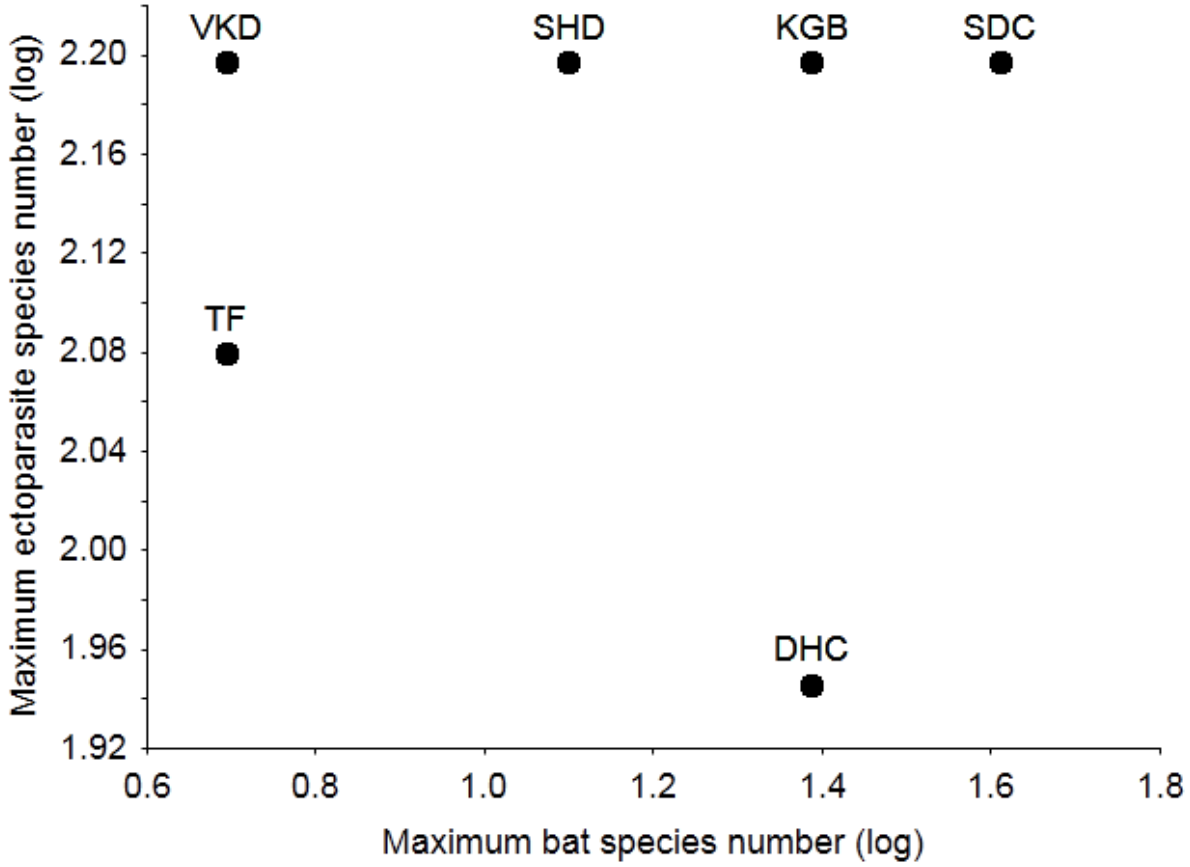

Figure 14: General Linear Model of total number of ectoparasite species (log) versus total number of bat species (log) across sample sites. $r_{(4)} = -0.04$, $p>0.05$.

DHC = De Hoop Guano Cave, KGB = Koegelbeen Sinkhole, SHD = Shongweni Dam, SDC = Sudwala Caves, TF = Table Farm, VKD = Vanderkloof Dam

CHAPTER 5

DISCUSSION

The present study has yielded an extensive list of both external and internal parasites infecting *Miniopterus natalensis* in South Africa. The parasite assemblage of *M. natalensis* comprises 14 species of ectoparasites, five of which are as yet undescribed (*Macronyssus* sp. A-E), and 11 species of endoparasites, two of which are considered new species (*Molinostrongylus* sp. A & B). The presence of the three trematodes, *Anchitrema sanguineum, Paralecithodendrium khalili* and *Paralecithodendrium parvouterus* in *M. natalensis* in South Africa represents new geographic as well as new host-parasite records, while one new host-parasite record, *Ichoronyssus miniopteri*, was found for ectoparasites. Five ectoparasites and eight endoparasites displayed noticeably restricted distributions relative to the other species in the assemblage, which suggests that within site factors may be affecting their distribution. However, these within site affects will need to be investigated more closely in future studies, as sample sizes at each site in this study were too small and inconsistent for reliable within site analyses beyond those already performed.

M. natalensis was found to share most of its parasites with the closely related *Miniopterus schreibersii* Kuhl, 1817 (Miniopteridae; Miller-Butterworth *et al.* 2005). These parasites were: The mites *Calcarmyobia rhinolophia* (Uchikawa 1985), *I. miniopteri* (Domrow 1959) and *Spinturnix semilunaris* (Uchikawa *et al.* 1994), the tick *Ixodes simplex* (Kolonin 2007), the dipterans *Nycteribia schmidlii* and *Penicillidia*

fulvida (Blackwell 1980), as well as the flea *Oxyparius isomalus* (Gibson *et al.* 2005); both hosts also share the trematodes *A. sanguineum* and *P. parvouterus* as well as the nematodes *Litomosa chiropterorum* and *Molinostrongylus ornatus* (Gibson *et al.* 2005).

5.1 Host Sex Hypothesis

A number of studies pertaining to both ecto-and endoparasites of bats, have reported that there is little variation in infection intensity between host sexes (Overal 1980; Hilton and Best 2000; Bertola *et al.* 2005; Dick and Dick 2006). This was borne out by the results of the present study where no significant relationship was found between host sex and infection intensity (ectoparasites: $F_{(9,21)} = 1.22$, $p>0.05$, and endoparasites: $F_{(5,51)} = 1.78$, $p>0.05$; Figures 6 & 7). On the other hand, Saoud and Ramadan (1976), while finding no sex-related differences in the prevalence of helminths in *Rhinopoma hardwickii cystops* Thomas, 1903 (Rhinopomatidae) and *Taphozous* (*Liponycteris*) *nudiventris nudiventris* Cretzschmar, 1830 (Emballonuridae) in Egypt, reported the prevalence of helminths in female *Asellia tridens tridens* Geoffroy, 1813 (Hipposideridae) to be almost twice that found in males, 42.4% versus 21.7% respectively. The authors speculated that this might have been the result of differences in the habits and ecology of the two sexes. In avian hosts, e.g. Helmeted guineafowl, *Numida meleagris* Linnaeus, 1758 (Numididae), pre-breeding differences in the foraging behaviour of males and females, with females increasing their protein- , i.e. arthropod-, intake and males often passing their catch to the female during courtship, have been suggested to be the reason for higher intensities of infections seen in females (Davies *et al.* 2008).

Given that sampling in the present study included only non-breeding adults, there was little difference in general biology, behaviour & body chemistry between the sexes, which would not have been the case if pregnant females were also used. It is perhaps therefore not surprising that no differences in parasite abundance were found between host sexes. Inclusion of breeding females would have resulted in factors such as fluctuating hormone levels, differences in foraging behaviour, as well seasonal social clustering may have resulted in differences between sexes (Fenton 1969; Krasnov *et al.* 2002; Lučan 2006; Seneviratne *et al.* 2009). In *Myotis daubentonii* Kuhl, 1817 (Vespertilionidae), for example, the aggregation of females in large colonies during the breeding period leads to increased transmission rates of the mite *Spinturnix andegavinus* Kolenati, 1857 (Spinturnicidae) (Lučan 2006). Furthermore, pregnant females foraged for prolonged periods to meet the energy demands of developing embryos (Lučan 2010), thus increasing the possibility of exposure to infected intermediate hosts.

5.2 Host Body Size Hypothesis

Based on work done by Miller-Butterworth *et al*. (2003) it is known that *M. natalensis* exhibit significant morphological variation between colonies and so may show noticeable differences in their parasite species diversities and infection intensities. Similar differences in body size were found in the current data, where the largest bat weighed over 14 g and the smallest less than 9 g, despite all specimens being fully mature bats. There was a small but noticeable difference in average body

mass between sites, ranging from just over 10 g in bats at the De Hoop Guano Cave to more than 12 g at Vanderkloof Dam and Steenkampskraal Mine.

It is worth noting that these are a naturally small bat species, so relatively small changes in mass such as reported here have much greater impact on them than for larger species averaging 30 g or more, such as those used in other studies (Poulin 1997; Arneberg 2002; George-Nascimento *et al.* 2004).

Body mass is an excellent proxy for host body size and can serve as a more reliable measurement than the subjective measurements of body length, width or depth (Patterson *et al.* 2008). It has been suggested that a positive relationship exists between host body mass and parasite infection intensity and species richness (Arneberg 2002; George-Nascimento *et al.* 2004) where host body mass may be an important factor in cases where greater food intake results in greater parasite intake, or where available energy and space on/within the host limits parasite population density (Arneberg *et al.* 1998).

However, in the current study the relationship between host body size and parasite species diversity was reversed, bats that weighed less harboured more endoparasite species (Figure 8). This is contrary to what Guégan and Hugueny (1994) and Patterson *et al.* (2008) found. At first this would seem to be counter-intuitive due to reduced volume in smaller bats logically restricting available space for habitation, which would increase interspecies competition in the endoparasites (Poulin and George-Nascimento 2007). However, it should be borne in mind that such effects would be most noticeable once a host nears carrying capacity for the maximum

biomass of parasites it can harbour (Poulin and George-Nascimento 2007). Moreover, when considered from the perspective of the bat's health, BCI's showed that smaller bats had lower BCI's and that the lower BCI's correlated significantly with increased endoparasite species (Figure 9) just as body size had. A possible explanation might be that the smaller bats were smaller because they were less healthy for a number of reasons, such as an innate weaker immune system and prior parasitic infection. This in turn might have compromised their ability to fight off infection, making them more susceptible to colonisation by a variety of endoparasites when compared to bigger bats.

Within site analyses found no significant correlation between ecto- or endoparasite species diversity and host body mass or BCI. Admittedly, BCI is a fairly crude measure of body health on which to base realistic predictions. However, future work looking into the immune system genetics of these bats in relation to their parasite species diversity and infection intensities would provide a much better measure of the overall health of the bats relative to their parasite burdens. Unfortunately, this was beyond the scope of this study.

The second prediction within the Host Body-size Hypothesis was that there was a positive correlation between host body mass and parasite infection intensities. Larger hosts have been shown, across species, to accumulate more parasites by offering them more infection opportunities by eating more, ranging wider and living longer (Marshall 1981; Poulin 1997). They also provide more microhabitats in which more parasites may live (Poulin and George-Nascimento 2007). However, in *M.*

natalensis there were no significant relationships for either parasite group when compared across sites (ectoparasites: r_5 = -0.39, p>0.05, and endoparasites: r_5 = -0.05, p>0.05). It must be noted that the majority of previous studies focused on average body size between different host species rather than body size within host species, and that when this is controlled for the significance of body size as an influencing factor is reduced. However, even in studies which focused on a single host species (Moura *et al.* 2003), where a statistically significant relationship between host body size and parasite abundance was not found, it was noted that a trend still existed favouring larger host body size. The absence of a correlation between body mass and intensity of infection in the present study might be explained by the fact that ectoparasites are more mobile on the hosts and so small within species increases in host body mass has only a minor affect on the space available. Furthermore, competition amongst parasites and bat grooming limits intensity of infection (Saoud and Ramadan 1976; Komeno and Linhares 1999; ter Hofstede and Fenton 2005; Patterson *et al.* 2008; Tello *et al.* 2008). However, recent work done by Dick (2005) found that in co-occurring bat fly species high abundance of one species was significantly correlated with high abundance of another. He suggested that this might be evidence for a mutualistic relationship amongst co-occurring bat flies, in contrast with other studies prioritising density compensation instead (Gotelli and McCabe 2002; Gotelli and Rhode 2002).

In the case of endoparasites, the present results mirror those of Botella and Esteban (1995) in their study on the vespertilionid bats *Myotis myotis* Borkhausen, 1797, and *Myotis blythii*, Tomes 1857, in Spain, where no significant relationship was found

between physalopteran helminth infection intensities and host body weight. Work done on bat endoparasites in Egypt (Saoud and Ramadan 1976) indicated that intestinal infection with one group of helminths may be antagonistic to other groups. It was found that where there were abundant trematodes or nematodes in a host there would be a scarcity of cestodes, and antagonistic interaction was even observed between different trematode species. This suggests that the effects of host body size on infection intensities may be mitigated by increased competition, with a suitable equilibrium being established. However, knowledge on this subject, particularly with regards to endoparasites, is still scant and therefore this, presently, remains speculation.

Within site analyses also found no significant correlation between ecto- or endoparasite infection intensities and host body mass or BCI, except at Shongweni Dam where a positive correlation was found between host body mass and endoparasite infection intensity. This may have been due to the foraging and roosting conditions at Shongweni Dam: Wet, humid, lush vegetation and the roost was close to large bodies of standing water. The roost itself was a short abandoned tunnel in the side of the dam wall, relatively exposed, with water streaming down the walls and sludgy pools of mud and waste along the length of the floor, possibly reducing the health of the bats roosting there. However, since BCI was not significantly correlated with infection intensity here and since there were no significant correlations at Vanderkloof Dam, which had a very similar roosting environment; it seems more likely that the foraging environment was responsible for this significant relationship. The habitat at Shongweni Dam was mesic and highly

vegetated, but arid and sparsely vegetated at Vanderkloof Dam. Furthermore, the endoparasite community at Shongweni Dam was predominantly composed of *L. chiropterorum* from the body cavity and a hymenolepidid cestode from the intestine. Both these helminths are comparatively large and would likely have more impact on their host than the smaller trematodes or smaller nematodes. It is therefore possible that due to the composition of the helminth assemblage at Shongweni Dam, larger hosts would have been able to support higher infection intensities. While *L. chiropterorum* was present at Vanderkloof Dam as well, it was slightly less prevalent and cestodes were absent (Table 4).

5.3 Habitat Heterogeneity Hypothesis

Miniopterus natalensis is known to be both physiologically and behaviourally adapted to a wide array of local environmental conditions (Miller-Butterworth *et al.* 2003), which combined with varying prey availability suggested that parasite infection intensity and species diversity would vary across biomes.

Several studies have shown endoparasite species diversity and infection intensity in bats to be strongly correlated with both geographical and seasonal variation (Marshall and Miller 1979; Coggins 1988; Esteban *et al.* 2001), and it is commonly held that large-scale relationships, spanning great distances and multiple habitats, exist between plant and insect diversity (Hawkins and Porter 2003). This means that insectivorous bats foraging in habitats with higher plant diversity should in turn be exposed to higher diversities of insect prey which act as intermediate hosts to the parasites infecting these bats. While this assumption was borne out by work done by

Esteban *et al.* (2001) on *Pipistrellus* (*Pipistrellus*) *pipistrellus* Schreiber, 1774 (Vespertilionidae) populations in Spain where mean number of helminth species per infected bat, mean infracommunity abundance and mean infracommunity diversity all showed significant differences between localities, this was not the case in the present study. The results presented herein did not support the argument that bats from more variable habitats would have more varied ecto- and endoparasite species. Instead, habitat heterogeneity did not in fact have a significant effect on the species diversity of either ecto- (Figure 10) or endoparasites (Figure 11) when compared to homogenous habitats.

Previous authors had attributed differences between sites to different environmental conditions and subsequent variation in foraging habitats and their plant/insect diversity at each location (Marshall and Miller 1979; Coggins 1988; Esteban *et al.* 2001), generally expecting those regions with higher rainfall and moderate climates to be the area's most likely to have high plant diversity and correspondingly high insect diversity. Yet, despite great geographical, and hence habitat, differences in the current study, the Shannon's Diversity Indices (Table 5), showed more or less consistent ectoparasite species diversity across sample sites (excepting a few outliers, De Hoop Guano Cave & Koegelbeen Cave). In the case of the outliers, the increase in the SDI at these sites seems to be due to a higher evenness of the distribution of the parasite species that are present, rather than a higher number of species at these sites. This evenness may be due to site specific conditions. For example, De Hoop Guano Cave is located on the edge of the large De Hoop Vlei, which would have allowed the bats greater access to a wider range of insect prey.

These intermediate insect hosts may in turn have possessed more diverse parasites available for infection of the bats when they consumed the insects. However, in direct contrast to this, Koegelbeen Sinkhole was located in the middle of arid Karoo scrub with only a few small local farm dams available as open water sources. One possible explanation might be that factors contributing to plant/insect diversity are diverse and highly specific to the regions and flora involved, and difficult to predict. For example, the floristically rich South African Grassland biome was found to be as equally rich in insect diversity as the Fynbos biome despite being subject to droughts and highly fluctuating temperatures (Procheş and Cowling 2006, 2007; Procheş *et al.* 2009). Alternatively, perhaps the increased endoparasite diversities at these sites were due to them being large, relatively well established maternity colonies. This means many bats from smaller surrounding colonies would congregate at these colonies for breeding and the rearing of offspring (Fenton 1969). A direct result of such aggregation would be the general parasite assemblages at these sites becoming much more heterogeneous than usual, not to mention the effects of increased genetic mixing of the hosts as suggested by the findings of Miller-Butterworth *et al.* (2003). The lack of data and comparative literature make it impossible to determine the exact cause at present.

It is likely that the consistent parasite species diversity was due to *M. natalensis* undertaking short distance migration between biomes. It is known to be able to disperse over great distances across different biomes (Miller-Butterworth *et al.* 2003). *Miniopterus natalensis* is present throughout South Africa, Mozambique, Zimbabwe, Botswana, Namibia, Angola, Zambia, Malawi and the southern regions of

the Democratic Republic of Congo (Hayman and Hill 1971). In South Africa *M. natalensis* has been found to disperse from Koegelbeen in the centre of the country all the way to Steenkampskraal on the coast (a distance of over 500 kms), and that genetic differences between populations across the country are not very pronounced (Miller-Butterworth *et al.* 2003). Alternatively, or in conjunction, it is possible that the parasites are not particularly host specific at the intermediate and primary host level, tracking host traits instead of species (Janzen 1985).

Environmental factors might not only influence parasite communities indirectly by being associated with higher insect diversity, but through rainfall/humidity and temperature they have a direct influence on the survival of the free-living stages of parasitic helminths (Mas-Coma *et al.* 2008, 2009). In this context vegetation cover can also play an important role (Brouat *et al.* 2007). Helminth eggs can survive in the environment for extended periods but are very susceptible to desiccation (Anderson 2000). Therefore, soil moisture conditions must be sufficiently high and temperatures not too extreme to prevent the eggs drying out (Anderson 2000). Seen in this light, differences across biomes may also have less of an impact on *M. natalensis* since they only roost in caves, which act as a stable, buffered home environment (Barr 1967; Howarth 1980). These in turn shelter them, and their parasites, from many of the fluctuations of the surrounding environment. It is suggested that this wide dispersal, limited genetic diversity, ecological fitting and buffered roosting environment may all help to mitigate the effects of habitat heterogeneity on parasite assemblage diversity in these bats.

Based on previous studies that suggested that differences in local environmental conditions, and consequently available prey would not only cause bat populations to vary in parasite species diversity but in intensity of infection as well (Hilton and Best 2000; Esteban *et al.* 2001; Dick and Gettinger 2005; Junker *et al.* 2008), it was expected that *M. natalensis* from more variable habitats would have higher intensities of ecto- and endoparasites. However, parasite infection intensity was not significantly different between heterogeneous and homogeneous habitats in either ecto- (Figure 12) or endoparasites (Figure 13).

When taken with the results from the second hypothesis, this suggests that infection intensity in *M. natalensis* parasite assemblages is primarily governed by availability of food to the host and its ability to fend off parasites either through grooming, roost switching, immune responses or parasite competition rather than through external environmental factors and (intermediate-host) insect diversity. Although site specific environmental and insect diversity variation must not be discounted, as shown by the second hypothesis results for Shongweni Dam.

It must also be noted that currently little is known about the identity of the intermediate hosts of the heteroxenous helminths of bats, making further conjecture unreliable without this vital information.

Behavioural patterns of the bats themselves and co-occurrence of different species at a given roosting site might also contribute to habitat heterogeneity. A number of studies (Nickel and Hansen 1967; Blankespoor and Ulmer 1970; Coggins *et al.* 1982)

have identified a general trend of increasing endoparasite infection following winter hibernation and peaking in autumn. They suggest that this trend is caused by the loss of most of the hosts' parasites during hibernation followed by reinvasion in spring. The reinvasion is then facilitated by the swarming and varied emergence patterns of the hosts bringing a greater variety of individuals into closer proximity with one another than is normally the case in the roost. This produces a much more heterogeneous assemblage of parasites available for reinfection (Coggins *et al.* 1982).

From this one would expect colonial bats (particularly cave roosters) roosting together with other bat species to be more likely to have a high diversity of parasite species, due to the increased number of parasite species available for cross-infection. When this is coupled with ecological fitting potentially increasing the likelihood of host-switching, it seems logical that the greater the species diversity in such colonies the greater the chance for cross-species infection (Janzen 1985; Keesing *et al.* 2006).

In the current study, however, no significant correlations between co-occurring bat species diversity and ectoparasite species diversity was found (Figure 14). While it would stand to reason that the greater the number of bat species sharing a particular roost the more diverse the available parasite assemblage from which the bats can be infected, this result is not in fact surprising since similar bat species were found across all these roosting caves. Marked segregation between most bat

species within each cave has also been observed, as well as their having different emergence times (Thomas 2011). These factors would limit interspecies interaction and so reduce the potential for cross-infection by ectoparasites.

CHAPTER 6

CONCLUSIONS

In conclusion, *Miniopterus natalensis* is a bat species found over a huge area (approx. 1.2 million km^2), its geographic range spanning marked differences in both climate and habitat. These range from desert in the West to temperate in the East, with Savannas in the central region, and include two globally recognised biodiversity hotspots (the Cape Floristic Region and the Maputoland-Pondoland-Albany Region, Mittermeier *et al.* 2004). Yet there is little genetic difference between *M. natalensis* populations (Miller-Butterworth *et al.* 2003), which seems to have resulted in a fairly homogeneous parasite species assemblage across the country. It is suggested that in addition to the host's wide dispersal and limited genetic diversity the effects of ecological fitting and a buffered roosting environment might have contributed to this stable parasite assemblage.

This study has provided valuable data on not only the ectoparasite communities of *M. natalensis* but on its endoparasite communities as well; data which have been scarce to non-existent until now. This includes the recovery of five new ectoparasite and two new endoparasite species, which are currently awaiting classification. Furthermore, this study has undertaken a far more comprehensive review of South African bat parasites than any other study to date by sampling from seven sites across six biomes across the country, instead of being limited to just one or two sites as has unfortunately been the case until now.

There is still, however, much uncertainty in the present results and the interpretations thereof. Key among the reasons for this uncertainty was the inability to achieve a suitable sample size for a project of this scale in the fieldwork period available, making this something that must be improved upon in future studies before more reliable predictions and interpretations can be made. Another concern was that many of the sample sites were not located in the centre of biomes and often incorporated a number of different habitats which made teasing apart individual habitat effects on the data very difficult and unreliable. This bias can also be remedied with more extensive sampling in the future. Finally, more studies are required in which parasite assemblages are compared across South African bat species to provide a greater insight into the potential mechanisms governing parasite species diversity and levels of infection.

Bordes *et al.* (2010) point out how the study of parasite species diversity is of great significance since it functions as an important means for estimating parasite pressure, and is an important selective force in the evolution of hosts and their habitat (Bordes and Morand 2009), despite the substantial variation in the relationship between parasite species diversity and host traits. The impact of parasite species diversity on host energetic demand, body condition, life history traits and behaviour are all of vital importance in understanding the nature of the parasite host relationship; nevertheless, the lack of clear general patterns in the studies done to date can be discouraging. However, Bordes *et al.* (2010) suggest that this is because most studies to date have focused only on factors governing host availability to parasites, which is only half of the equation. They suggest that

much more focus must be placed on parasites' compatibility with their hosts, on their ability to overcome host defences and the nature and evolution of those defences in the hosts. Some research has already been done on these factors including studies on basal metabolic rate (Morand and Harvey 2000; Krasnov *et al.* 2004b; Korallo *et al.* 2007), T-cell mediated immune response (Møller and Rózsa 2005) and Histocompatibility complex diversity (Hedrick 1994; Wegner *et al.* 2003; Harf and Sommer 2005; Sĭmková *et al.* 2006; Goüy de Bellocq *et al.* 2008). However, essentially no work has been done in this field on bats and their parasites and so there is still much work to be done to improve our understanding of bat parasite ecology.

BIBLIOGRAPHY

ADAMS, R. A. & PEDERSEN, S. C. 2000. *Ontogeny, functional ecology, and evolution of bats*. Cambridge University Press, Cambridge.

AGRAWAL, V. 1967. Two new trematodes from the intestine of a yellow bat, *Nycticeius kuhlii* from Lucknow, India. *Revista de Biologia Tropical,* 15**,** 207–214.

ANDERSON, R. C. 2000. *Nematode parasites of vertebrates: Their development and transmission*. 2nd edition. CAB International, Oxfordshire.

ARNEBERG, P. 2002. Host population density and body mass as determinants of species richness in parasite communities: comparative analyses of directly transmitted nematodes of mammals. *Ecography,* 25**,** 88–94.

ARNEBERG, P., SKORPING, A. & READ, A. F. 1998. Parasite abundance, body size, life histories, and the energetic equivalence rule. *The American Naturalist,* 151**,** 497–513.

BARR, T. C. 1967. Observations on the ecology of caves. *The American Naturalist,* 101**,** 475–491.

BARUŠ, V. 1973. The finding of nematodes and acanthocephalans in Egyptian bats. *Folia Parasitologica (Praha),* 20**,** 213–222.

BENDER, J. D. 2000. *Metabolic response of the greater spear-nosed bat, Phyllostomus hastatus, to ectoparasitic batflies (Diptera: Streblidae).* Unpublished Master's thesis, Boston University, Boston.

BERTOLA, P. B., AIRES, C. C., FAVORITO, S. E., GRACIOLLI, G., AMAKU, M. & PINTO-DA-ROCHA, R. 2005. Bat flies (Diptera: Streblidae, Nycteribiidae) parasitic on bats (Mammalia: Chiroptera) at Parque Estadual da Cantareira, São Paulo, Brazil: parasitism rates and host-parasite associations. *Memórias do Instituto Oswaldo Cruz,* 100**,** 25–32.

BLACKWELL, M. 1980. Incidence, host specificity, distribution, and morphological variation in *Arthrorhynchus nycteribiae* and *A. eucampsipodae* (Laboulbeniomycetes). *Mycologia,* 72**,** 143–158.

BLANKESPOOR, H. D. & ULMER, M. J. 1970. Helminths from six species of Iowa bats. *Proceedings of the Iowa Academy of Science,* 77**,** 200–206.

BORDES, F. & MORAND, S. 2009. Parasite diversity: an overlooked metric of parasitic pressures. *Oikos,* 118**,** 801–806.

BORDES, F., MORAND, S. & KRASNOV, B. R. 2010. Does investment into "expensive" tissue compromise anti-parasitic defence? Testes size, brain size and parasite diversity in rodent hosts. *Oecologia,* [ePub ahead of print]**,** 1–10.

BOTELLA, P. & ESTEBAN, J. G. 1995. Histopathology of the stomach lesion caused by *Physaloptera brevivaginata* (Nematoda: Physalopteridae) in bats in Spain. *Folia Parasitologica,* 42**,** 143–148.

BROOKS, D. R., LEÓN-RÈGAGNON, V., MCLENNAN, D. A. & ZELMER, D. 2006. Ecological fitting as a determinant of the community structure of platyhelminth parasites of anurans. *Ecology,* 87**,** S76–S85.

BROOKS, D. R. & MCLENNAN, D. A. 1993. *Parascript: parasites and the language of evolution.* Smithsonian Institution Press, Washington D.C.

BROUAT, C., KANE, M., DIOUF, M., BÂ, K., SALL-DRAMÉ, R. & DUPLANTIER, J. M. 2007. Host ecology and variation in helminth community structure in *Mastomys* rodents from Senegal. *Parasitology,* 134**,** 437–450.

BROWN, C. R. & BROWN, M. B. 1992. Ectoparasitism as a cause of natal dispersal in cliff swallows. *Ecology,* 73**,** 1718–1723.

BUSH, A. O., AHO, J. M. & KENNEDY, C. R. 1990. Ecological versus phylogenetic determinants of helminth parasite community richness. *Evolutionary Ecology,* 4**,** 1–20.

BUSH, A. O., LAFFERTY, K. D., LOTZ, J. M. & SHOSTAK, A. W. 1997. Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *The Journal of Parasitology,* 83**,** 575–583.

BUTLER, J. M. & ROPER, T. J. 1996. Ectoparasites and sett use in European badgers. *Animal Behaviour,* 52**,** 621–629.

CATTADORI, I.M., HAYDON, D.T. & HUDSON, P.J. 2005. Parasites and climate synchronize red grouse populations. *Nature*, 433, 737-741.

CHRISTE, P., ARLETTAZ, R. & VOGEL, P. 2000. Variation in intensity of a parasitic mite (*Spinturnix myoti*) in relation to the reproductive cycle and immunocompetence of its bat host (*Myotis myotis*). *Ecology Letters,* 3**,** 207–212.

CHRISTE, P., OPPLIGER, A. & RICHNER, H. 1994. Ectoparasite affects choice and use of roost sites in the great tit, *Parus major*. *Animal Behaviour,* 47**,** 895–898.

CLOSE, B., BANISTER, K., BAUMANS, V., BERNOTH, E. M., BROMAGE, N., BUNYAN, J., ERHARDT, W., FLECKNELL, P., GREGORY, N. & HACKBARTH, H. 1997. Recommendations for euthanasia of experimental animals: Part 2. *Laboratory animals,* 31**,** 1.

COGGINS, J. R. 1988. Methods for the ecological study of bat endoparasites. *In:* KUNZ, T. H. (ed.) *Ecological and behavioral methods for the study of bats.* Smithsonian, Washington D.C.

COGGINS, J. R., TEDESCO, J. L. & RUPPRECHT, C. E. 1982. Seasonal changes and overwintering of parasites in the bat, *Myotis lucifugus* (Le Conte), in a Wisconsin hibernaculum. *The American Midland Naturalist,* 107**,** 305–315.

COTE, I. M. & POULIN, R. 1995. Parasitism and group size in social animals: a meta-analysis. *Behavioural Ecology,* 6**,** 159–165.

CUARTES-CALLE, C. & MUÑOZ-ARANGO, J. 1999. Nemátodos en la cavidad abdominal y el tracto digestivo de algunos murciélagos Colombianos. *Caldasia,* 21**,** 10–25.

DAVIES, O. R., JUNKER, K., JANSEN, R., CROWE, T. M. & BOOMKER, J. 2008. Age- and sex-based variation in helminth infection of helmeted guineafowl (*Numida meleagris*) with comments on Swainson's spurfowl (*Pternistis swainsonii*) and Orange River francolin (*Scleroptila levaillantoides*). *South African Journal of Wildlife Research,* 38**,** 163–170.

DICK, C. W. 2005. *Ecology and host specificity of bat flies (Diptera: Streblidae) and their chiropteran hosts.* PhD, Texas Tech University, Lubbock.

DICK, C. W. 2007. High host specificity of obligate ectoparasites. *Ecological Entomology,* 32**,** 446–450.

DICK, C. W. & DICK, S. C. 2006. Effects of prior infestation on host choice of bat flies (Diptera: Streblidae). *Journal of Medical Entomology,* 43**,** 433–436.

DICK, C. W. & GETTINGER, D. 2005. A faunal survey of streblid flies (Diptera: Streblidae) associated with bats in Paraguay. *The Journal of Parasitology,* 91**,** 1015–1024.

DICK, C. W. & PATTERSON, B. D. 2007. Against all odds: Explaining high host specificity in dispersal-prone parasites. *International Journal for Parasitology,* 37**,** 871–876.

DITTMAR, K., PORTER, M. L., MURRAY, S. & WHITING, M. F. 2006. Molecular phylogenetic analysis of nycteribiid and streblid bat flies (Diptera: Brachycera, Calyptratae): implications for host associations and phylogeographic origins. *Molecular Phylogenetics and Evolution,* 38**,** 155–170.

DOMROW, R. 1959. Acarina from Australian Bats. *Proceedings of the Linnean Society of New South Wales,* 83, 227-240.

DOWNES, C. M., THEBERGE, J. B. & SMITH, S. M. 1986. The influence of insects on the distribution, microhabitat choice, and behaviour of the Burwash caribou herd. *Canadian Journal of Zoology,* 64**,** 622–629.

DUBOIS, G. 1956. Contribution à l'étude des trématodes de chiroptères. *Revue Suisse de Zoology*, 63, 683–695.

DURETTE-DESSET, M.-C., BEVERIDGE, I. & SPRATT, D.M. 1994. The origins and evolutionary expansion of the Strongylida (Nematoda). *International Journal for Parasitology,* 24**,** 1139–1165.

ESCH, G. W., SHOSTAK, A. K., MARCOGLIESE, D. J. & GOATER, T. M. 1990. Patterns and process in helminth communities: an overview. *In:* ESCH, G. W., BUSH, A. O. & AHO, J. M. (eds.) *Parasite communities: Patterns and processes.* Chapman and Hall, London.

ESTEBAN, J. G., AMENGUAL, B. & COBO, J. S. 2001. Composition and structure of helminth communities in two populations of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) from Spain. *Folia Parasitologica,* 48**,** 143–148.

FENTON, M. B. 1969. Summer activity of *Myotis lucifugus* (Chiroptera: Vespertilionidae) at hibernacula in Ontario and Quebec. *Canadian Journal of Zoology,* 47**,** 597–602.

FRITZ, G. N. 1983. Biology and ecology of bat flies (Diptera: Streblidae) on bats in the genus *Carollia*. *Journal of Medical Entomology,* 20**,** 1–10.

GARCÍA-VARGAS, F. D., OSÓRIO, S. & DE LEÓN, G. P.-P. 1996. Helminth parasites of bats (Mormoopidae and Phyllostomidae) from the Estación de Biología Chamela, Jalisco State, México. *Bat Research News,* 37**,** 7–8.

GEORGE-NASCIMENTO, M., MUÑOZ, G., MARQUET, P. A. & POULIN, R. 2004. Testing the energetic equivalence rule with helminth endoparasites of vertebrates. *Ecology Letters,* 7**,** 527–531.

GIBSON, D. I., BRAY, R. A. & HARRIS, E. A. 2005. *Host-Parasite Database of the Natural History Museum, London* [Online]. London. Available: http://www.nhm.ac.uk/research-curation/research/projects/host-parasites/index.html [Accessed March 2012].

GOODWIN, G. G. & GREENHALL, A. M. 1961. A review of the bats of Trinidad and Tobago: descriptions, rabies infection, and ecology. *Bulletin of the American Museum of Natural History,* 122**,** 187–302.

GOTELLI, N. J. & MCCABE, D. J. 2002. Species co-occurrence: A meta-analysis of J.M. Diamond's assembly rules model. *Ecology,* 83**,** 2091–2096.

GOTELLI, N. J. & RHODE, K. 2002. Co-occurrence of ectoparasites of marine fishes: A null model analysis. *Ecology Letters,* 5**,** 86–94.

GOÜY DE BELLOCQ, J., CHARBONNEL, N. & MORAND, S. 2008. Coevolutionary relationship between helminth diversity and MHC class II polymorphism in rodents. *Journal of Evolutionary Biology,* 21**,** 1144–1150.

GUÉGAN, J. F. & HUGUENY, B. 1994. A nested parasite species subset pattern in tropical fish: Host as major determinant of parasite infracommunity structure. *Oecologia,* 100**,** 184–189.

GUERRERO, R., BAIN, O., ATTOUT, T. & MARTIN, C. 2006. The infective larva of *Litomosoides yutajensis* Guerrero *et al*., 2003 (Nematoda: Onchocercidae), a *Wolbachia*-free filaria from bat. *Parasite*, 13, 127–130.

HAMILTON, I. M. & BARCLAY, R. M. R. 1998. Ontogenetic influences on foraging and mass accumulation by big brown bats (*Eptesicus fuscus*). *Journal of Animal Ecology,* 67**,** 930–940.

HARF, R. & SOMMER, S. 2005. Association between major histocompatibility complex class II DRB alleles and parasite load in the hairy-footed gerbil, *Gerbillurus paeba*, in the southern Kalahari. *Molecular Ecology,* 14**,** 85–91.

HART, B. L. 1992. Behavioral adaptations to parasites: an ethological approach. *Journal of Parasitology,* 78**,** 256–265.

HAWKINS, B. A. & PORTER, E. E. 2003. Does herbivore diversity depend on plant diversity? The case of California butterflies. *The American Naturalist,* 161**,** 40–49.

HAYMAN, R. W. & HILL, J. E. 1971. Part 2: Order Chiroptera. *In:* MEESTER, J. & SETZER, H. W. (eds.) *The mammals of Africa. An identification manual.* Smithsonian Institution Press, Washington D.C.

HEDRICK, P. W. 1994. Evolutionary genetics of the major histocompatibility complex. *The American Naturalist,* 143**,** 945–964.

HILL, J. E. & SMITH, J. D. 1984. *Bats, a natural history.* British Museum (Natural History), London.

HILTON, C. D. & BEST, T. L. 2000. Gastrointestinal helminth parasites of bats in Alabama. *Occasional Papers of the North Carolina Museum of Natural Sciences and the North Carolina Biological Survey,* 12**,** 57–66.

HOLMES, J. C. 1964. Factors influencing the trematodes fauna of bats. *Proceedings of the First International Congress on Parasitology,* 1**,** 490–492.

HOWARTH, F. G. 1980. The zoogeography of specialized cave animals: A bioclimatic model. *Evolution,* 34**,** 394–406.

HUDSON, P. & GREENMAN, J. 1998. Competition mediated by parasites: biological and theoretical progress. *Trends in Ecology and Evolution,* 13**,** 387–390.

HUDSON, P. J., DOBSON, A. P. & NEWBORN, D. 1998. Prevention of population cycles by parasite removal. *Science,* 282**,** 2256–2258.

JACOBS, D. S. 1999. Intraspecific variation in wingspan and echolocation call flexibility might explain the use of different habitats by the insectivorous bat, *Miniopterus schreibersii* (Vespertilionidae: Miniopterinae). *Acta Chiropterologica,* 1**,** 93–103.

JACOBS, D. S. 2000. Community level support for the allotonic frequency hypothesis. *Acta Chiropterologica,* 2**,** 197–207.

JANZEN, D. H. 1985. On ecological fitting. *Oikos,* 45**,** 308–310.

JENZEN, L. A. & HOWELL, K. M. 1983. *Vampirolepis schmidti* sp. n. (Cestoidea: Hymenolepididae) from *Triaenopis persicus* (Hipposideridae) of Tanzania. *Proceedings of the Helminthological Society of Washington,* 50**,** 135–137.

JOBLING, B. 1936. A revision of the subfamilies of the Streblidae and the genera of the subfamily Streblinae (Diptera Acalypterae) including a redescription of *Metelasmus pseudopterus* Coquillett and a description of two new species from Africa. *Parasitology,* 28**,** 355–380.

JUNKER, K., BAIN, O. & BOOMKER, J. 2008. Helminth parasites of Natal long-fingered bats, *Miniopterus natalensis* (Chiroptera: Miniopteridae), South Africa. *The Onderstepoort Journal of Veterinary Research,* 75**,** 261–265.

KALKO, E. K. V. 1997. Diversity in tropical bats. *In:* ULRICH, H. (ed.) *Tropical biodiversity and systematics. Proceedings of the International Symposium on Biodiversity and Systematics in Tropical Ecosystems.* Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.

KEESING, F., HOLT, R. D. & OSTFELD, R. S. 2006. Effects of species diversity on disease risk. *Ecology Letters,* 9**,** 485–498.

KHOKHLOVA, I. S., SPINU, M., KRASNOV, B. R. & DEGEN, A. A. 2004. Immune response to fleas in a wild desert rodent: effect of parasite species, parasite burden, sex of host and host parasitological experience. *Journal of Experimental Biology,* 207**,** 2725–2733.

KINSELLA, J. M. 1991. Comparison of helminths of three species of mice, *Podomys floridanus*, *Peromyscus gossypinus*, and *Peromyscus polionotus*, from southern Florida. *Canadian Journal of Zoology,* 69**,** 3078–3083.

KOLONIN, G. V. 2007. Mammals as hosts of Ixodid ticks (Acarina, Ixodidae). *Entomological Review,* 87**,** 401–412.

KOMENO, C. A. & LINHARES, A. X. 1999. Bat flies parasitic on some phyllostomid bats in Southeastern Brazil: parasitism. Rates and host-parasite relantionships. *Memórias do Instituto Oswaldo Cruz,* 94**,** 151–156.

KORALLO, N. P., VINARSKI, M. V., KRASNOV, B. R., SHENBROT, G. I., MOUILLOT, D. & POULIN, R. 2007. Are there general rules governing parasite diversity? Small mammalian hosts and gamasid mite assemblages. *Diversity and Distributions,* 13**,** 353–360.

KRASNOV, B. R., KHOKHLOVA, I. S., OGUZOGLU, I. & BURDELOVA, N. V. 2002. Host discrimination by two desert fleas using an odour cue. *Animal Behaviour,* 64**,** 33–40.

KRASNOV, B. R., MORAND, S., MOUILLOT, D., SHENBROT, G. I., KHOKHLOVA, I. S. & POULIN, R. 2006. Resource predictability and host specificity in fleas: the effect of host body mass. *Parasitology,* 133**,** 81–88.

KRASNOV, B. R., MOUILLOT, D., SHENBROT, G. I., KHOKHLOVA, I. S. & POULIN, R. 2004a. Geographical variation in host specificity of fleas (Siphonaptera) parasitic on small mammals: the influence of phylogeny and local environmental conditions. *Ecography,* 27**,** 787–797.

KRASNOV, B. R., POULIN, R., SHENBROT, G. I., MOUILLOT, D. & KHOKHLOVA, I. S. 2005. Host specificity and geographic range in haematophagous ectoparasites. *Oikos,* 108**,** 449–456.

KRASNOV, B. R., SHENBROT, G. I., KHOKHLOVA, I. S. & DEGEN, A. A. 2004b. Flea species richness and parameters of host body, host geography and host "milieu". *Journal of Animal Ecology,* 73**,** 1121–1128.

KUNZ, T. H. 1976. Observations on the winter ecology of the bat fly *Trichobius corynorhini* Cockerell (Diptera: Streblidae). *Journal of Medical Entomology,* 12**,** 631–636.

KUNZ, T. H. 1982. Roosting ecology of bats. *In:* KUNZ, T. H. (ed.) *Ecology of bats.* Plenum Press, New York.

KUNZ, T. H. & LUMSDEN, L. F. 2003. Ecology of cavity and foliage roosting bats. *In:* KUNZ, T. H. & FENTON, M. B. (eds.) *Bat ecology.* University of Chicago Press, Chicago.

LEACH, M. C., BOWELL, V. A., ALLAN, T. F. & MORTON, D. B. 2004. Measurement of aversion to determine humane methods of anaesthesia and euthanasia. *Animal Welfare,* 13**,** 77–86.

LEWIS, R. E. & LEWIS, J. H. 1994. Siphonaptera of North America north of Mexico: Ischnopsyllidae. *Journal of Medical Entomology,* 31**,** 348–368.

LLEWLLYN, J. 1987. Phylogenetic inference from platyhelminth life-cycle stages. *International Journal for Parasitology,* 17, 281–289.

LOREAU, M., ROY, J. & TILMAN, D. 2005. Linking ecosystem and parasite ecology. *In:* THOMAS, F., GUÉGAN, J. F. & RENAUD, F. (eds.) *Parasitism and Ecosystems.* Oxford University Press, Oxford.

LOURENÇO, S. I. & PALMEIRIM, J. M. 2007. Can mite parasitism affect the condition of bat hosts? Implications for the social structure of colonial bats. *Journal of Zoology*, 273, 181–188.

LOTZ, J. M. & FONT, W. F. 1994. Excess positive associations in communities of helminths of bats: a refined null hypothesis and a test of the facilitation hypothesis. *Journal of Parasitology,* 80**,** 398–413.

LOW, A. B. & REBELO, A. G. (eds.) 1996. *Vegetation of South Africa, Lesotho and Swaziland.* DEAT, Pretoria.

LUČAN, R. K. 2006. Relationships between the parasitic mite *Spinturnix andegavinus* (Acari: Spinturnicidae) and its bat host, *Myotis daubentonii* (Chiroptera: Vespertilionidae): seasonal, sex- and age-related variation in infestation and

possible impact of the parasite on the host condition and roosting behaviour. *Folia Parasitologica,* 53**,** 147–152.

LUČAN, R. K. 2010. Population ecology of Daubenton's bat. PhD Thesis, University of South Bohemia, Czech Republic, 126 pp; http://theses.cz/id/fm1k1k/Luan_PhD_Th4.pdf

MAA, T. C. 1965. Ascodipterinae of Africa. *Journal of Medical Entomology,* 1**,** 311–326.

MAGURRAN, A. E. 1988. *Ecological Diversity and its Measurement*. Princeton University Press, Princeton.

MARSHALL, A. G. 1981. *The ecology of ectoparasitic insects.* Academic, London.

MARSHALL, A. G. 1982. Ecology of insects ectoparasitic on bats. *In:* KUNZ, J. H. (ed.) *Ecology of Bats.* Plenum Publishing, London.

MARSHALL, M. E. & MILLER, G. C. 1979. Some digenetic trematodes from Ecuadorian bats including five new species and one new genus. *Journal of Parasitology,* 65**,** 909–917.

MAS-COMA, S., VALERO, M. A. & BARGUES, M. D. 2008. Effects of climate change on animal and zoonotic helminthiases. *In:* DE LA ROCQUE, S., HENDRICKX, G. & MORAND, S. (eds.) *Climate Change: Impact on the Epidemiology and Control of Animal Diseases.* World Organization for Animal Health (OIE), Science & Technology Review, Paris.

MAS-COMA, S., VALERO, M. A. & BARGUES, M. D. 2009. Climate change effects on trematodiases, with emphasis on zoonotic fascioliasis and schistosomiasis. *Veterinary Parasitology,* 163**,** 264–280.

Mc ALLISTER, C. T. & BURSEY, C. R. 2009. New host and geographic distribution records for helminths (Trematoda, Nematoda) in three species of Vespertilionid bats (Chiroptera) from the pine ridge of Dawes County, Nebraska, U.S.A. *Comparative Parasitology,* 76**,** 117–121.

MEDELLÍN, R.A., EQUIHUA, M. & AMIN, M.A. 2000. Bat diversity and abundance as indicators of disturbance in neotropical rainforests. *Conservation Biology*, 14, 1666-1675.

MILLER-BUTTERWORTH, C. M., JACOBS, D. S. & HARLEY, E. H. 2003. Strong population substructure is correlated with morphology and ecology in a migratory bat. *Nature,* 424**,** 187–191.

MILLER-BUTTERWORTH, C. M., EICK, G., JACOBS, D. S., SCHOEMAN, M. C. & HARLEY, E. H. 2005. Genetic and phenotypic differences between South african long-fingered bats, with a Global miniopterine phylogeny. *Journal of Mammalogy*, 86(6),1121–1135.

MILLS, G. & HESS, L. 1997. *The complete book of southern African mammals.* Struik Publishers, Cape Town.

MITTERMEIER, R. A., ROBLES-GIL, P., HOFFMAN, M., PILGRIM, J. D., BROOKS, T. M., MITTERMEIER, C. G., LAMOREUX, J. L. & FONSECA, G. 2004. *Hotspots revisited: Earth's biologically richest and most threatened terrestrial ecoregions.* Cemex & Conservation International, Mexico City.

MØLLER, A. P. & RÓZSA, L. 2005. Parasite biodiversity and host defences: chewing lice and immune response of their avian hosts. *Oecologia,* 142**,** 169–176.

MORAND, S. & HARVEY, P. H. 2000. Mammalian metabolism, longevity and parasite species richness. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* 267**,** 1999–2003.

MORGAN, B. B. & HAWKINS, P. A. 1951. *Veterinary helmintholog.* Burgess Publishing Company, Minneapolis.

MOURA, M. O., BORDIGNON, M. O. & GRACIOLLI, G. 2003. Host characteristics do not affect community structure of ectoparasites on the fishing bat *Noctilio leporinus* (L., 1758) (Mammalia: Chiroptera). *Memórias do Instituto Oswaldo Cruz,* 98**,** 811–815.

MUCINA, L. & RUTHERFORD, M. C. 2006. *The vegetation of South Africa, Lesotho and Swaziland.* South African National Biodiversity Institute, Pretoria.

NICKEL, P. A. & HANSEN, M. F. 1967. Helminths of bats collected in Kansas, Nebraska, and Oklahoma. *The American Midland Naturalist,* 78**,** 481–486.

OKULOVA, N. M. & ARISTOVA, V. A. 1973. Influence of ectoparasites on a population of the northern red-backed vole in southwestern Siberia. *Soviet Journal of Ecology,* 4**,** 522–527.

OLIVA, M. E., VALDIVIA, I. M., COSTA, G., FREITAS, N., PINHEIRO DE CARVALHO, M. A., SÁNCHEZ, L. & LUQUE, J. L. 2008. What can metazoan parasites reveal about the taxonomy of *Scomber japonicus* Houttuyn in the coast of South America and Madeira Islands? *Journal of Fish Biology,* 72**,** 545–554.

OLSON, P. D., CRIBBB, T. H., TKACHD, V. V., BRAYA, R. A. & LITTLEWOOD, D. T. J. 2003. Phylogeny and classification of the Digenea (Platyhelminthes: Trematoda). *International Journal for Parasitology,* 33**,** 733-755.

OLSON, P. D., LITTLEWOOD, D. T. J., BRAY, R. A. & MARIAUX, J. 2001. Interrelationships and evolution of the tapeworms (Platyhelminthes: Cestoda). *Molecular Phylogenetics and Evolution,* 19**,** 443–467.

OVERAL, W. L. 1980. Host-relations of the bat fly *Megistopoda aranea* (Diptera: Streblidae) in Panama. *The University of Kansas Science Bulletin,* 52**,** 1–20.

PATTERSON, B. D., DICK, C. W. & DITTMAR, K. 2007. Roosting habits of bats affect their parasitism by bat flies (Diptera: Streblidae). *Journal of Tropical Ecology,* 23**,** 177–189.

PATTERSON, B. D., DICK, C. W. & DITTMAR, K. 2008. Parasitism by bat flies (Diptera: Streblidae) on neotropical bats: effects of host body size, distribution, and abundance. *Parasitology Research,* 103**,** 1091–1100.

PATTERSON, B. D., WILLIG, M. R. & STEVENS, R. D. 2003. Trophic strategies, niche partitioning, and patterns of ecological organization. *In:* KUNZ, T. H. & FENTON, M. B. (eds.) *Bat Ecology.* University of Chicago Press, Chicago.

PÉREZ-PONCE DE LEÓN, G. 2001. The diversity of digeneans (Platyhelminthes: Cercomeria: Trematoda) in vertebrates in Mexico. *Comparative Parasitology,* 68**,** 1–8.

PHILLIPS, G. L. 1966. Ecology of the big brown bat (Chiroptera: Vespertiliondae) in northeastern Kansas. *The American Midland Naturalist,* 75**,** 168–198.

PISTOLE, D. H. 1988. A survey of helminth parasites of chiropterans from Indiana. *Proceedings of the Helminthological Society of Washington,* 55**,** 270–274.

POULIN, R. 1997. Species richness of parasite assemblages: Evolution and patterns. *Annual Review of Ecology & Systematics,* 28**,** 341–358.

POULIN, R. 2007. *Evolutionary ecology of parasites.* Princeton University Press, Princeton.

POULIN, R. & GEORGE-NASCIMENTO, M. 2007. The scaling of total parasite biomass with host body mass. *International Journal for Parasitology,* 37**,** 359–364.

PROCHEŞ, Ş. & COWLING, R. M. 2006. Insect diversity in Cape fynbos and neighbouring South African vegetation. *Global Ecology & Biogeography,* 15**,** 445–451.

PROCHEŞ, Ş. & COWLING, R. M. 2007. Do insect distributions fit our biomes? *South African Journal of Science***,** 258–261.

PROCHEŞ, Ş., FOREST, F., VELDTMAN, R., CHOWN, S. L., COWLING, R. M., JOHNSON, S. D., RICHARDSON, D. M. & SAVOLAINEN, V. 2009. Dissecting the plant-insect diversity relationship in the Cape. *Molecular Phylogenetics and Evolution,* 51**,** 94–99.

RAINEY, W. E., PIERSON, E. D., ELMQVIST, T. & COX, P. A. 1995. The role of flying foxes (Pteropodidae) in oceanic island ecosystems of the Pacific. *Ecology, evolution and behaviour of bats.* Clarendon, Oxford.

RIGBY, M. C., HECHINGER, R. F. & STEVENS, L. 2002. Why should parasite resistance be costly? *Trends in Parasitology,* 18**,** 116–120.

RUBENSTEIN, D. I. & HOHMANN, M. E. 1989. Parasites and social behavior of island feral horses. *Oikos,* 55**,** 312–320.

RUTHERFORD, M. C. & WESTFALL, R. H. 1986. Biomes of Southern Africa - an objective categorization. *Memoirs of the Botanical Survey of South Africa,* 54**,** 1–98.

RUTHERFORD, M. C. & WESTFALL, R. H. 1994. Biomes of southern Africa: an objective characterization. *Memoirs of the Botanical Survey of South Africa,* 63.

SALZET, M., CAPRON, A. & STEFANO, G. B. 2000. Molecular crosstalk in host–parasite relationships: schistosome– and leech–host interactions. *Parasitology Today,* 16**,** 536–540.

SAOUD, M. F. A. & RAMADAN, M. M. 1976. Studies on the helminth parasites of bats in Egypt and the factors influencing their occurence with particular reference to digenetic Trematodes. *Zeitschrift für Parasitenkunde,* 51**,** 37–47.

SAOUD, M. F. A. & RAMADAN, M. M. 1977a. A review of the trematode genus *Anchitrema* Looss, 1899 (Dicrocoeliidae), with a redescription of *Anchitrema sanguineum* (Sonsino, 1894) and *Anchitrema longiformis* n. sp. from some Egyptian bats. *Parasitology Research,* 54**,** 61–67.

SAOUD, M. F. A. & RAMADAN, M. M. 1977b. Studies on digenetic trematodes of the genus *Prosthodendrium* Dollfus, 1931 from some Egyptian bats. 1. Trematodes of the subgenus *Prosthodendrium* Doolfus 1931*. Folia Parasitologica (Praha)*, 24**,** 249–259.

SCHOEMAN, M. C. & JACOBS, D. S. 2003. Support for the allotonic frequency hypothesis in an insectivorous bat community. *Oecologia,* 134**,** 154–162.

SENEVIRATNE, S. S., FERNANDO, H. C. & UDAGAMA-RANDENIYA, P. V. 2009. Host specificity in bat ectoparasites: A natural experiment. *International Journal for Parasitology,* 39.

SHANNON, C. E. & WEAVER, W. 1949. *The mathematical theory of communication.* University of Illinois Press, Urbana.

SHEELER-GORDON, L. L. & OWEN, R. D. 1999. Host tracking or resource tracking? The case of *Periglischrus* wing mites (Acarina: Spinturnicidae) of leaf-nosed bats (Chiroptera: Phyllostomidae) from Michoacan, Mexico. *Acta Zoologica Mexicana (Neuva Serie),* 76**,** 85–102.

SILVESTRE, A., CHARTIER, C., SUAVÉ, C. & CABARET J. 2000. Relationship between helminth species diversity, intensity of infection and breeding management in dairy goats. *Veterinary Parasitology*, 94, 91-105.

SĬMKOVÁ, A., OTTOVÁ, E. & MORAND, S. 2006. MHC variability, life traitsand parasite diversity of European cyprinid fish. *Evolutionary Ecology,* 20**,** 465–467.

SIMMONS, N. B., SEYMOUR, K. L., HABERSETZER, J. & GUNNELL, G. F. 2008. Primitive early Eocene bat from Wyoming and the evolution of flight and echolocation. *Nature,* 451**,** 818–821.

SKINNER, J. D. & SMITHERS, R. H. N. 1990. *The mammals of the southern African subregion.* University of Pretoria Press, Pretoria.

SKRJABIN, K. L., N. P. SHIKHOBALOVA, R. S. SCHULZ, T. I. POPOVA, S. N. BOEV, AND S. L. DELYAMURE. 1952. Key to parasitic nematodes. Vol. III Strongylata, K. I. Skrjabin (ed.). (English translation by Israel Program for Science Translations 1961, Jerusalem.)

SKRJABIN, K. I., SHIKHOBALOVA, N. P. & SCHULTZ, R. S. 1954. Essentials of nematodology. Trichostrongylids of animals and man. *Israel Program for Scientific Translations, Jerusalem, Israel, and the United States Department of Agriculture, Washington, D.C.,* 3**,** 1–704.

SPEAKMAN, J. R. & RACEY, P.A. 1986. The influence of body condition on sexual development of male brown long-eared bats (*Plecotus auritus*) in the wild. *Journal of Zoology, London*, 210, 515–525.

STOFFBERG, S., JACOBS, D. S. & MILLER-BUTTERWORTH, C. M. 2004. Field identification of two morphologically similar bats, *Miniopterus schreibersii natalensis* and *Miniopterus fraterculus* (Chiroptera: Vespertilionidae). *African Zoology,* 39**,** 47–53.

SURES, B. & STREIT, B. 2001. Parasites and climate synchronize red grouse populations. *Parasitology*, 123, 185-191.

TAYLOR, P. J. 2000. *Bats of southern Africa.* University of Natal Press, Pietermaritzburg.

TEELING, E. C., SCALLY, M., KAO, D. J., ROMAGNOLI, M. L., SPRINGER, M. S. & STANHOPE, M. J. 2000. Molecular evidence regarding the origin of echolocation and flight in bats. *Nature,* 403**,** 188.

TELLO, J. S., STEVENS, R. D. & DICK, C. W. 2008. Patterns of species co-occurrence and density compensation: a test for interspecific competition in bat ectoparasite infracommunities. *Oikos,* 117**,** 693–702.

TER HOFSTEDE, H. M. & FENTON, M. B. 2005. Relationships between roost preferences, ectoparasite density, and grooming behaviour of neotropical bats. *Journal of Zoology,* 266**,** 333–340.

TER HOFSTEDE, H. M., FENTON, M. B. & WHITAKER JR, J. O. 2004. Host and host-site specificity of bat flies (Diptera: Streblidae and Nycteribiidae) on Neotropical bats (Chiroptera). *Canadian Journal of Zoology,* 82**,** 616–626.

THEWISSEN, J. G. M. & BABCOCK, S. 1992. The origin of flight in bats. *Bioscience,* 42**,** 340–345.

THOMAS, A.J. 2011. *Factors affecting the emergence times of seven sympatric insectivorous bat species*. Unpublished Masters Thesis, University of Cape Town, Cape Town.

TOMPKINS, D. M. & CLAYTON, D. A. 1999. Host resources govern the specificity of swiftlet lice: size matters. *Journal of Animal Ecology,* 68**,** 489–500.

TORCHIN, M. E., LAFFERTY, K. D. & KURIS, A. M. 2001. Release from parasites as natural enemies: Increased performance of a globally introduced marine crab. *Biological Invasions,* 3**,** 333–345.

UBELAKER, J. E. 1970. Some observations on ecto- and endoparasites of Chiroptera. *In:* SLAUGHTER, B. H. & WALTON, D. W. (eds.) *About bats.* Southern Methodist University Press, Dallas.

UBELAKER, J. E., SPECIAN, R. D. & DUSZYNSKI, D. W. 1977. Endoparasites. *In:* BAKER, R. J., JR, J. K. J. & CARTER, D. C. (eds.) *Biology of bats of the New World Family Phyllostomatidae. Part II.* Texas: Special Publications of the Museum of Texas Tech University, Lubbock.

UCHIKAWA, K. 1985. Mites of the genus *Calcarmyobia* (Acarina, Myobiidae) with information on the taxonomy of their host bats of the genus *Miniopterus* (Chiroptera, Miniopteridae). *Bulletin of the Brittish Museum of Natural History (Zoology),* 48**,** 15–25.

UCHIKAWA, K., ZHANG, M., O'CONNOR, B. M. & KLOMPEN, H. 1994. Contribution of the taxonomy of the genus *Spinturnix* (Acari: Spinturnicidae), with the erection of a new genus, *Emballonuria*. *Folia Parasitologica,* 41**,** 287–304.

VAN DER MERWE, M. 1973. Aspects of the social behaviour of the Natal clinging bat, *Miniopterus schreibersii natalensis* (A. Smith, 1834). *Mammalia,* 37**,** 379–389.

WEGNER, K. M., REUSCH, T. B. H. & KALBE, M. 2003. Multiple parasites are driving major histocompatibility complex polymorphism in the wild. *Journal of Evolutionary Biology,* 16**,** 224–232.

WENZEL, R. L., TIPTON, V. J. & KIEWLICZ, A. 1966. The streblid batflies of Panama (Diptera Calypterae: Streblidae). *Ectoparasites of Panama.* Field Museum of Natural History, Chicago.

WHITAKER JR, J. O. 1988. Collecting and preserving ectoparasites for ecological study. *In:* KUNZ, T. H. (ed.) *Ecological and behavioral methods for the study of bats.* Smithsonian, Washington D.C.

WHITAKER JR, J. O. & MUMFORD, R. E. 1978. Foods and ectoparasites of bats from Kenya, East Africa. *Journal of Mammalogy,* 59**,** 632–634.

WILSON, D. E. 1989. Bats. *In:* LIETH, H. & WERGER, M. J. A. (eds.) *Tropical rain forest ecosystems. Biogeographical and ecological studies.* Elsevier, Amsterdam.

YAMAGUTI, S. 1961. *Systema Helminthum: the nematodes of vertebrates.* Interscience Publishers, Inc., John Wiley & Sons, New York.

YAMAGUTI, S. 1971. *Synopsis of digenetic trematodes of vertebrates*. Keigaku Publishing Co., Tokyo.

APPENDICES:

Table 7: Ectoparasite species collected from *Miniopterus natalensis* hosts, South Africa

Biome	Sample Site	Order	Family	Genus	Species	No. of Ectoparasites
Albany Thicket	Table Farm	Acari	Ixodidae	*Ixodes*	*simplex*	22
			Laelapiade	*Ichoronyssus*	*miniopteri*	12
			Macronyssidae	*Macronyssus*	sp. A	2
					sp. B	5
					sp. C	20
			Spinturnicidae	*Spinturnix*	*semilunaris*	18
		Diptera	Nycteribiidae	*Nycteribia*	*schmidlii*	36
				Penicillidia	*fulvida*	3
		Siphonaptera	Ischnopsyllidae	*Oxyparius*	*isomalus*	4
Albany Thicket Total						**122**
Fynbos	De Hoop Nature Reserve	Acari	Ixodidae	*Ixodes*	*simplex*	5
			Laelapiade	*Ichoronyssus*	*miniopteri*	42
			Macronyssidae	*Macronyssus*	sp. B	24
			Spinturnicidae	*Spinturnix*	*semilunaris*	20
		Diptera	Streblidae	*Ascodipteron*	sp. A	3
			Nycteribiidae	*Nycteribia*	*schmidlii*	16
				Penicillidia	*fulvida*	3
Fynbos Total						**113**
Grassland	Sudwala Caves	Acari	Ixodidae	*Ixodes*	*simplex*	12
			Laelapiade	*Ichoronyssus*	*miniopteri*	2
			Macronyssidae	*Macronyssus*	sp. A	4
					sp. B	4
					sp. C	25

Table 7 (cont.): Ectoparasite species collected from *Miniopterus natalensis* hosts, South Africa

					sp. D	1
					sp. F	1
			Myobiidae	*Calcarmyobia*	*rhinolophia*	1
			Spinturnicidae	*Spinturnix*	*semilunaris*	3
		Diptera	Streblidae	*Ascodipteron*	sp. A	11
			Nycteribiidae	*Nycteribia*	*schmidlii*	35
Grassland Total						**99**
Nama Karoo	Vanderkloof Dam	Acari	Laelapiade	*Ichoronyssus*	*miniopteri*	12
			Macronyssidae	*Macronyssus*	sp. A	2
					sp. B	1
					sp. C	16
			Myobiidae	*Calcarmyobia*	*rhinolophia*	1
			Spinturnicidae	*Spinturnix*	*semilunaris*	3
		Diptera	Nycteribiidae	*Nycteribia*	*schmidlii*	14
				Penicillidia	*fulvida*	1
		Siphonaptera	Ischnopsyllidae	*Oxyparius*	*isomalus*	12
Nama Karoo Total						**62**
Savanna	Koegelbeen Sinkhole	Acari	Ixodidae	*Ixodes*	*simplex*	2
			Laelapiade	*Ichoronyssus*	*miniopteri*	5
			Macronyssidae	*Macronyssus*	sp. A	2
					sp. B	13
					sp. C	19
			Spinturnicidae	*Spinturnix*	*semilunaris*	11
		Diptera	Nycteribiidae	*Nycteribia*	*schmidlii*	39
				Penicillidia	*fulvida*	2
			Streblidae	*Ascodipteron*	sp. A	2
				Brachytarsina	sp. A	1
		Siphonaptera	Ischnopsyllidae	*Oxyparius*	*isomalus*	21

Table 7 (cont.): Ectoparasite species collected from *Miniopterus natalensis* hosts, South Africa

	Koegelbeen Sinkhole Total					**117**
	Shongweni Dam	Acari	Laelapiade	*Ichoronyssus*	*miniopteri*	5
			Macronyssidae	*Macronyssus*	sp. B	4
					sp. C	4
					sp. E	1
			Myobiidae	*Calcarmyobia*	*rhinolophia*	1
			Spinturnicidae	*Spinturnix*	*semilunaris*	10
		Diptera	Streblidae	*Ascodipteron*	sp. A	4
			Nycteribiidae	*Nycteribia*	*schmidlii*	58
				Penicillidia	*fulvida*	1
	Shongweni Dam Total					**88**
Savanna Total						**205**
Succulent Karoo	Steenkampskraal Mine	Acari	Macronyssidae	*Macronyssus*	sp. C	1
			Spinturnicidae	*Spinturnix*	*semilunaris*	1
		Diptera	Nycteribiidae	*Nycteribia*	*schmidlii*	4
		Siphonaptera	Ischnopsyllidae	*Oxyparius*	*isomalus*	3
Succulent Karoo Total						**9**
Grand Total						**610**

sp. = *species*

Table 8: Endoparasite species collected from *Miniopterus natalensis* hosts, South Africa

Biome	Sample Site	Group Reference	Order	Family	Genus	Species	No. of Endoparasites
Albany Thicket	Table Farm	Nematoda	Enoplida	Capillariidae	*Aonchotheca*	sp.	3
			Spirurida	Onchocercidae	*Litomosa*	*chiropterorum*	213
				Physalopteridae	*Physaloptera*	sp.	1
			Strongylida	Molineidae	*Molinostrongylus*	sp. A	2
						sp. B	1
						ornatus	32
		Cestoda	Cyclophyllidea	Hymenolepididae	nd	nd	14
Albany Thicket Total							**266**
Fynbos	De Hoop Nature Reserve	Nematoda	Enoplida	Capillariidae	*Aonchotheca*	sp.	1
			Spirurida	Onchocercidae	*Litomosa*	*chiropterorum*	25
				Physalopteridae	*Physaloptera*	sp.	4
			Strongylida	Molineidae	*Molinostrongylus*	sp. A	3
						ornatus	19
Fynbos Total							**52**
Grassland	Sudwala Caves	Nematoda	Enoplida	Capillariidae	*Aonchotheca*	sp.	13
			Spirurida	Onchocercidae	*Litomosa*	*chiropterorum*	2
			Strongylida	Molineidae	*Molinostrongylus*	sp. A	4
						ornatus	6
		Trematoda	Plagiorchiida	Anchitrematidae	*Anchitrema*	*sanguineum*	1
				Lecithodendriidae	*Paralecithodendrium*	*khalili*	1429
						parvouterus	69
		Cestoda	Cyclophyllidea	Hymenolepididae	nd	nd	8
Grassland Total							**1532**
Nama Karoo	Vanderkloof Dam	Nematoda	Enoplida	Capillariidae	*Aonchotheca*	sp.	2
			Spirurida	Onchocercidae	*Litomosa*	*chiropterorum*	202

Table 8 (cont.): Endoparasite species collected from *Miniopterus natalensis* hosts, South Africa

			Strongylida	Molineidae	*Molinostrongylus*	sp. A	4
Nama Karoo Total							**208**
Savanna	Koegelbeen Sinkhole	Nematoda	Enoplida	Capillariidae	*Aonchotheca*	sp.	21
			Spirurida	Onchocercidae	*Litomosa*	*chiropterorum*	71
			Strongylida	Molineidae	*Molinostrongylus*	sp. A	96
		Trematoda	Plagiorchiida	Lecithodendriidae	*Paralecithodendrium*	*parvouterus*	33
	Koegelbeen Sinkhole Total						**221**
	Shongweni Dam	Nematoda	Enoplida	Capillariidae	nd	nd	2
			Spirurida	Onchocercidae	*Litomosa*	*chiropterorum*	175
		Trematoda	Plagiorchiida	Lecithodendriidae	*Paralecithodendrium*	*khalili*	6
		Cestoda	Cyclophyllidea	Hymenolepididae	nd	nd	5
	Shongweni Dam Total						**188**
Savanna Total							**409**
Succulent Karoo	Steenkampskraal Mine	Nematoda	Spirurida	Onchocercidae	*Litomosa*	*chiropterorum*	15
			Strongylida	Molineidae	*Molinostrongylus*	sp. A	1
	Steenkampskraal Mine Total						16
Succulent Karoo Total							**16**
Grand Total							**2483**

sp. = species
nd = not determined