Host-parasite interactions of two sympatric small mammals from South Africa

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DECLARATION

I, **Dina Mustafa Fagir,** declare that the thesis, which I hereby submit for the degree of PhD Zoology at the University of Pretoria, is my own work and has not been submitted by me for a degree at this or any other tertiary institution.

SIGNATURE: ……………………………....

DATE: ………………………………………

DEDICATION

To my parents ..

Mama Zaza and Jedo Mustafa

To my brother ..

Mohammed

To my Godfather ..

El-Amin El-Rayah

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SUMMARY

Patterns of ectoparasite burden among hosts can be linked to differences in abiotic (i.e. climatic conditions) and biotic (i.e. host characteristics) factors. Although this is well documented for small mammals in the northern hemisphere, similar data for southern Africa, particularly South Africa, is scant. In addition, interspecific interactions in parasite communities may contribute to the distribution of parasites across a host population, however, they are not fully understood due to a lack of studies investigating more than one parasite species. Also, by definition parasites are detrimental to their hosts, reducing host fitness either directly by feeding off the host or indirectly by causing the host to initiate energetically expensive behavioural or immune defences.

The Namaqua rock mouse (*Micaelamys namaquensis*) and the eastern rock sengi (*Elephantulus myurus*) are two sympatric small mammals widely distributed throughout southern Africa, however they have divergent life-history traits. Despite their large geographical distribution there are no systematic studies of the parasite community of *M. namaquensis* and those on *E. myurus* are largely limited to their ticks. The present study aimed to close this gap in our knowledge by firstly assessing the ectoparasite community of *M. namaquensis* and *E. myurus* and furthermore identifying the main parasite species exploiting each host. In addition, I evaluated the effects of abiotic and biotic factors on parasite burden for these two species. In order to assess the contributions of interspecific interactions within the ectoparasite community on parasite distribution I furthermore manipulated the ectoparasite community of sengis using Frontline® to reduce the abundance of fleas and ticks over a period of two years and documented the effect of this treatment on the ectoparasite population dynamic as well

as the body condition index (BCI) of sengis. During the initial assessment a total of 43,900 ectoparasites were collected from both hosts, however, the two hosts sustained very different ectoparasitic burdens. While Namaqua rock mice harboured 23 ectoparasite species, sengis only sustained ten. The ectoparasite community of rock mice was dominated by three species of flea (*Xenopsylla brasiliensis*, *Epirimia aganippes* and *Chiastopsylla godfreyi*) and two species of tick (*Rhipicephalus distinctus* and *Haemaphysalis* spp.) whereas in sengis it was four species of tick (*R. warburtoni/arnoldi*, *R. distinctus*, *Rhipicentor nuttalli* and *Ixodes* spp.). In addition, both hosts sustained large numbers of unidentified ectoparasites. All ectoparasite species exhibited seasonal peaks in abundance coinciding with the warm/wet season probably as a result of favourable climatic conditions during spring and summer. Direct host effects on parasite abundance were observed for the rodent, while there was only weak evidence of a sex bias in parasite burden probably as a result of the contrasting mating systems (promiscuous vs. monogamous).

I observed few direct effects of Frontline® on the parasite burden or BCI in sengis. However, over the study period the abundance of the *Rhipicephalus warburtoni/arnoldi* decreased significantly, while the opposite was true for chiggers suggesting that the treatment was indeed effective and that there might be a competitive interaction between these two species. The lack of similar effects in the other three common ectoparasites might be a result of their low abundances. Although I found no direct effects of any of the main parasite species on sengi BCI, the decrease in tick abundance coincided with an increase in the BCI in sengis suggesting that ticks may have substantial fitness costs for these afrotheres. The present study highlighted the complexity of interspecific interactions within a parasite community on small mammal populations as well as the role such interactions may play in generating the patterns of parasite distribution across their host population.

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CHAPTER ONE

GENERAL INTRODUCTION

Host-parasite interactions

Despite the importance of parasites in wildlife populations, the effects of parasites remain underestimated compared to predation and competition (Irvine 2006; Dunn *et al.* 2013). Parasites are entirely dependent on their hosts to obtain their nutritional requirements and to provide space for living and mating (Kim 1985). As a result, parasites may have dramatic effects on their host's fitness being detrimental to host survival and reproductive output (Combes 2001; Hillegass *et al.* 2008). The resulting interactions between hosts and parasites are complex, as on the one hand hosts attempt to decrease parasite loads, and on the other hand parasites are dependent on the host for their own survival (Morand and Krasnov 2006). In turn, adaptations employed by the host to reduce parasite burdens such as raising an immunological response or increased grooming can be energetically costly and reduce host body condition (Delahay *et al.* 1995; Goüy de Bellocq *et al.* 2006).

Many studies investigating parasite patterns suggest that parasite populations fluctuate both spatially and temporally due to differences in host exposure and susceptibility to parasitic infestations (Wilson *et al.* 2002; Poulin 2007; Bordes *et al.* 2010). Due to the close relationship between parasites and their host it is predicted that changes in host population dynamics and behaviour will have dramatic effects on parasite diversity and their population dynamics. Furthermore, environmental conditions (e.g. temperature and rainfall) as well as parasite life-history traits will influence the relationship between the host and parasite (Wilson *et al.* 2002; Morand and Krasnov. 2006).

Abiotic and biotic factors affecting parasite burden

Parasite loads can be affected by a group of factors that can be divided into environmental (abiotic) factors and host/parasite (biotic) factors (Wilson *et al.* 2002; Poulin 2007; Mostowy and Engelstädter 2011; Renwick and Lambin 2013). They often vary with abiotic factors such as temperature, rainfall and humidity (Weil *et al.* 2006; Poulin 2007). Changes in environmental conditions may have dramatic effects on the abundance and diversity of parasites, which ultimately affects host-parasite dynamics (Kutz *et al.* 2009). Seasonal patterns in parasite loads may also be linked to the relationship of these parasites with their hosts and the specific environmental needs of parasites on and off their hosts (Combes 2001; Krasnov *et al.* 2007). Seasonal patterns are particularly common in ectoparasites (Krasnov 2008). Unlike free-living species, parasites, in particular ectoparasites, experience a "dual" environment (Krasnov *et al.* 2015). This environment is represented by: first, the host that provides parasites with nutrients and a place for living and mating. Second, this environment is also represented by environmental conditionns (i.e. abiotic factors) (Krasnov *et al.* 2015). This is true for ectoparasites that are strongly affected by the off-host life cycle (i.e. ticks, mites and fleas), while lice complete their entire life cycle on their host (Oguge *et al.* 2009, Midgley *et al.* 2003; Krasnov *et al.* 2007, 2015). Ectoparasite taxa that have developmental stages that live off the host are suggested to be more susceptible to seasonal effects (Vinarski *et al.*, 2007; Krasnov 2008, Krasnov *et al.* 2015). For example, seasonal variations in tick burdens can be expected to be pronounced as they spend most of their life cycles off-host (e.g. in the vegetation, Lareschi and Krasnov

2010). In contrast, lice are permanent parasites that never leave the host; therefore seasonal changes are expected to be weak (Kim 2006; Marshall 1981). Fleas and mites also spend part of their life on the host and the rest in the nest of the host (Matthee and Krasnov 2009; Maher and Timm 2014).

Among biotic effects host sex appears to be an important factor modulating parasite burden and sex-biased parasitism has been observed across a wide range of animal taxa (Schalk and Forbes 1997, Moore and Wilson 2002, Duneau and Ebert 2012; Krasnov *et al.* 2012; Kiffner *et al.* 2013, 2014). Many parasitological studies indicate that parasites tend to infest males more heavily than females (Poulin 1996; Zuk and McKean 1996; McCurdy *et al.* 1998; Perkins *et al.* 2003, 2008; Ferrari *et al.* 2004, 2007; Poulin and George-Nascimento 2007; Krasnov *et al.* 2012). Both sexes aim to maximize their fitness, but they tend to use different strategies to achieve this. For example, female mammals usually invest more energy in their immune defences to secure better survival and ultimately fitness. In contrast, males aim to invest more energy in increasing mating rates by making themselves more attractive to females, which is thought to inhibit their own immune responses and parasite defences (Bateman 1948; Trivers 1972; Hamilton and Zuk 1982; Folstad and Karter 1992; Queller 1997; Moore and Wilson 2002; Rolff 2002; Hawlena *et al.* 2005; Grzybek *et al.* 2015). For example, sexual size dimorphism is considered one cause of sex-biased parasitism. This is because larger males may achieve greater mating rates as they may compete more successfully with other males and also be more attractive to females. In addition, the larger size of males might offer a larger target for parasites (Shine 1989; Moore and Wilson 2002; Rolff 2002). Moreover, behavioural differences between the sexes may also contribute to sex-biases in parasite burden; e.g. males tend to have larger home range sizes and higher rates of mobility than females, which increases their chances of encountering parasites (Moore and Wilson 2002; Morand *et al.* 2004; Lane *et al.* 2009). Another possible cause of male-biased parasitism is linked to a reduction in immunocompetence in males, which is thought to be caused by the immunosuppressive properties of the steroid hormone testosterone (Klein 2000; Beagley and Gockel 2003; Harrison *et al.* 2010). While elevated testosterone levels are thought to enhance the expression of male sexual traits, it has been suggested that they may have a negative effect on the immune system (Hamilton and Zuk 1982; Zuk 1990; Roberts *et al.* 2004). Although the role of testosterone as a cause for male-biased parasitism is still debated (Grzybek *et al.* 2015), many studies suggested that interactions between metabolism, growth and reproduction are likely to be involved in sex-biased parasitism (Owens 2002; Bordes *et al.* 2012).

Effects of parasitism on host body condition

Body condition is a measure of the energetic reserves a host has and they are usually stored as fat (Schulte-Hostedde *et al.* 2001). Although differences in host body mass associated with parasitic infestations have been reported in mammals (Moore and Wilson 2002), the common cause for the presence or absence of these patterns has not yet been determined (Le Coeur *et al.* 2015). For instance, a study investigating flea infestation among nine rodent species found that host body mass and sex patterns were not consistent among species despite the fact that these patterns are common determinants of parasite aggregation (Kiffner *et al.* 2013). Parasite activities may incur a cost on the fitness of the host by reducing energy intake or cause secondary symptoms at bite sites (Forbes *et al.* 2000; Chapman *et al.* 2007). In addition, behavioural and physiological responses employed by the host to reduce parasite burdens such as raising an immunological response or increased grooming can be energetically costly and reduce host body condition (Delahay *et al.* 1995; Goüy de Bellocq *et al.* 2006). Host-parasite relationships are inherently shaped by two main forces (Bize *et al.* 2008): first, parasitic infestations are limited by several host life-characteristics such as host body temperature, skin thickness and grooming behaviour (Elliot *et al.* 2002) as well as the amount of high quality resources parasites can extract from the host body (Lehane 2005). Second, immunocompetence which is one of the most important host characteristics for determining parasite resistance (Wakelin 1996). Therefore, parasites are thought to attack hosts that are in poor condition and which are immunodeficient (Roberts *et al.* 2004). Hosts with poor body condition have fewer resources to allocate to costly immune defences (Alonso-Alvarez and Tella 2001; Martin *et al.* 2006). However, although energetic costs associated with parasitism have been shown for some species, negative effects on host body mass are not always apparent and mechanisms that lead to this phenomenon are still unknown (Scantlebury *et al.* 2007; Patterson *et al.* 2015).

Ectoparasites of small mammals

Small mammals belonging to families such as the Muridae, Soricidae, Macroscelididae and Cricetidae are major components of many terrestrial ecosystems (Dickman 1999; Morand and Krasnov 2006). They often occur in large numbers and harbour a great diversity of parasites (Dickman 1999; Morand and Krasnov 2006). Among mammals, small mammals are by far the most common hosts for about 74% of all known flea species (Makundi and Kilonzo 1994). In addition, the importance of small mammals as hosts of immature stages of ticks is well known (Norval 1979; Fourie *et al.* 1992, 2005; Harrison *et al.* 2011, 2012, 2013). The ectoparasite fauna of small mammals of the northern hemisphere is well studied (LoGiudice *et al.* 2003; Morand and Krasnov 2006;

Randolph *et al.* 2006; Laudisoit *et al.* 2009; Kiffner *et al.* 2011; Mfune *et al.* 2013). In contrast, although there is a large number of incidental reports on the ectoparasite fauna of rodents occurring in different parts of Africa (e.g. Fagir and El-Rayah 2009; Laudisoit *et al.* 2009; Yonas *et al.* 2011), such studies are limited for South Africa and are often descriptive (De Graaff 1981; Fourie *et al.* 1992; Horak *et al.* 2005) or only considering a single parasite taxon (Matthee *et al.* 2007; Harrison *et al.* 2011, 2012). Therefore, little is known about which parasites may potentially infest many small mammal hosts.

On the African continent, there have been a considerable number of studies investigating the effects of climatic conditions and host characteristics on parasites, but most of these studies are descriptive, or focused on one parasite taxon. For example, there are few studies from North and East Africa investigating ectoparasite species such as fleas and tick species as well as their role as vectors for zoonotic diseases (Schwan 1986; Soliman *et al.* 2001; Fagir and El-Rayah 2009; Oguge *et al.* 2009; Yonas *et al.* 2011; Billeter *et al.* 2014). As for the Southern African sub-region, there are few studies investigating small mammals and their ectoparasite species, in particularly ticks (e.g. Fourie *et al.* 1992, 2002, 2005; Horak *et al.* 1999, 2002, 2005; Makundi and Kilonzo 1994; Shangula 1998; Njunwa *et al.* 1989; Eiseb 2002; Laudisoit *et al.* 2009; Zimba *et al.* 2011). All of these studies focus on grassland species while there is a much greater host species diversity and density in other habitat types (e.g. Krasnov *et al.* 2010; Matthee and Krasnov 2009; Matthee *et al.* 2007).

The present study aims to fill this gap in our knowledge and focus on two rock-dwelling, sympatric small mammal species that differ vastly in their life-history traits (e.g. diet, mode of reproduction, social system etc.). Therefore, my study will contribute to elucidating further what host traits might affect parasite burden in the same habitat. The present study was carried out to investigate ectoparasite fauna of two widely distributed small mammal species, namely the Namaqua rock mouse (*Micaelamys namaquensis*, previously named *Aethomys namaquensis*, Muridae: Murinae) and the eastern rock sengi or elephant shrew (*Elephantulus myurus*, Macroscelidea: Macroscelididae). In addition to providing the first exhaustive assessment of the ectoparasite species infesting *M. namaquensis* and *E. myurus* it evaluates the possible contributions of abiotic and biotic factors to parasite burden and assesses possible fitness implications of the ectoparasite burden for sengis.

Study species

In the present study, I investigated the host-parasite system of two small mammal species from South Africa namely, the Namaqua rock mouse (*M. namaquensis*) and eastern rock sengis (*E. myurus*). The two study species were chosen for the study because they are the most common small mammal species inhabiting the study area (Fagir *et al.* 2014). Both species co-inhabit the same habitat, i.e. rocky outcrops throughout southern Africa. However, the two species have different life-history traits.

***Namaqua rock mouse* (Micaelamys namaquensis)**

The Namaqua rock mouse is a widely distributed rodent species in the southern African sub-region, extending from southern central Africa through the sub-region of South Africa (south of the Zambezi/Cunene River, Angola, Zambia, Malawi and northern Mozambique) (Chimimba *et al.* 1999; Skinner and Chimimba 2005). It is a nocturnal, medium sized murid (53±15g) and inhabits rocky outcrops or hillside habitats. It has been reported to be omnivorous and granivorous (Woodall and Mackie 1987; Kerley *et* *al.* 1990; Monadjem 1997). Rock mice have been shown to be well adapted to hot, arid environments (Buffenstein 1984). The Namaqua rock mouse is a well-studied species with regards to its taxonomy and reproductive physiology (Chimimba and Dippenaar 1994; Chimimba 1998, 2001; Chimimba *et al.* 1999; Fleming and Nicolson 2004; Meyer and Brandl 2005; Muteka *et al.* 2006a, b; Relton *et al.* 2013). In the eastern parts of South Africa it has been reported that *M. namaquensis* breeds in the rainy warmer months (i.e. summer), from September to May, with a peak between March and April, while in the western coastal areas it breeds during winter (Fleming and Nicholson 2004, Muteka *et al.* 2006a). The average litter size is 3.1 - 3.6 young and they are weaned by 21 - 28 days (Neal 1990; Skinner and Chimimba 2005). In contrast, our current knowledge of the ectoparasite fauna infesting *M. namaquensis* is limited and ambiguous. Very few parasitological studies have been conducted on the species and the focus has been on their ticks (e.g. Fourie *et al.* 1992; Braack *et al.* 1996; Harrison *et al.* 2012). Older records by De Graaff (1981) indicated a diverse array of ectoparasites including 34 flea species from four families namely, Pulicidae, Hystrichopsyllidae, Leptopsyllidae and Chimaeropsyllidae; 12 mite species from two families namely Laelaptidae and Trombiculidae and 26 tick species from three families (Ixodidae, Argasidae and Nuttalliellidae). No louse species were reported by De Graaff (1981), but three species of lice from two families (Hoplopleuridae and Polyplacidae) were reported by Durden and Musser (1994). However, for most of these parasites little or no information is available regarding their sampling locality or number of host individuals sampled and only a single study has sampled the same host population on more than one occasion (Fourie *et al.* 1992).

Eastern rock sengi (Elephantulus myurus)

Eastern rock sengis belong to the order Macroscelidea, an ancient monophyletic group comprising 19 species within four genera (Dumbacher *et al.* 2012, 2014). Like rock mice they are widely distributed throughout the southern African sub-region, from Mozambique north of the Zambezi River throughout the southern and eastern parts of Zimbabwe, eastern Botswana, wide parts of northeast South Africa and western Swaziland (Skinner and Chimimba 2005). Like Namaqua rock mice, eastern rock sengis are restricted to rocky habitats. However, unlike rock mice they are monogamous, territorial and insectivorous and are reported to be active during the warmer hours of the day (Skinner and Chimimba 2005). Their breeding season occurs during the warm, wet summer (September to March) (Medger *et al.* 2012). On average sengis have 3 litters per season, with 1-2 precocial young (Neal 1982; Ribble and Perrin 2005). Eastern rock sengis are hosts to a variety of macroparasites, particularly the immature stages of ixodid ticks (Fourie *et al.* 1995; Harrison *et al.* 2011, Fourie *et al.* 1992, 1995, 2005; Horak *et al.* 2011; Harrison *et al.* 2013). In comparison, the knowledge of other ectoparasite taxa harboured by eastern rock sengis is limited (Fourie *et al.* 1995).

Study objectives

The present study aimed to investigate the ectoparasite fauna exploiting these two sympatric small mammal species and factors affecting the distribution of these ectoparasites within their host populations. The study was carried out in Ezemvelo Nature Reserve, in Gauteng, South Africa. Sampling the Namaqua rock mouse and eastern rock sengi as well as their ectoparasite communities provided the opportunity to test several hypotheses of ectoparasite community organization and assembly within a polygamous (rodent) and monogamous (sengi) host system which inhabit the same habitat (i.e. rocky outcrops) but different niches and one host is an insectivore (sengi) and the other an omnivore (rodent). Firstly, due to the lack of knowledge about the ectoparasite communities infesting the Namaqua rock mouse and sengis, I aimed to carry out the first comprehensive assessment of the ectoparasite community exploiting two sympatric small mammal species with different life-history traits and identify the parasite species most likely to affect host population dynamic (either because of their prevalence or abundance, or both). Secondly, because of known host-parasite relationships, we predicted that ectoparasite community would be sensitive to changes in climatic conditions (abiotic factors) as well as differences between host sexes (biotic factors); therefore I aimed to evaluate the contributions of abiotic and biotic factors on parasite burdens. In addition, I initiated an experiment to investigate the response of the ectoparasite assembly infesting sengis to a targeted anti-parasite treatment over an extended period (three years), using Frontline® to treat animals against fleas and ticks. Finally, I investigated the costs of parasitism measured as body condition to the host.

Outline of thesis

Following the introduction in **Chapter one**, there are three data chapters and a final chapter comprising the main discussion and conclusions. The experimental chapters have been written as individual stand-alone papers and are published in three journals. Thus, there is some overlap between the chapters especially in the materials and methods sections. The chapters are:

Chapter two: I investigated the ectoparasite species associated with the Namaqua rock mouse and provide an extensive list of the ectoparasite species infesting *M. namaquensis*. In addition, I identify the main parasite species and investigated how abiotic and biotic factors affect the parasite burdens in this species (Published as: Fagir *et al.* 2014, *Parasites & Vectors*, 7, 366).

Chapter three: I aimed to record ectoparasite species diversity, prevalence and abundance of the eastern rock sengi. Thus, I conducted an extensive review of the ectoparasite species found on sengis and identified the main parasite taxa parasitizing sengis. Furthermore, I evaluated the effect of seasonality (abiotic factors) and host sex (biotic factors) on parasite loads (Published as: Fagir *et al.* 2015, *African Zoology*, 50 (2), pp. 109-117).

Chapter four: I aimed to investigate the long-term dynamic of the ectoparasite community of sengis as well as the effect of parasitism on host body condition (Published as: Lutermann *et al.* 2015, *International Journal for Parasitology: Parasites and Wildlife*, 4 (1), pp. 148-158).

Chapter five: General discussion and conclusions.

REFERENCES

ALONSO-ALVAREZ, C. & TELLA, J. L. 2001. Effects of experimental food restriction and body-mass changes on the avian T-cell-mediated immune response. *Canadian Journal of Zoology,* 79**,** 101-105.

BATEMAN, A. J. 1948. Intra-sexual selection in Drosophila. *Heredity,* 2**,** 349-368.

BEAGLEY, K. W. & GOCKEL, C. M. 2003. Regulation of innate and adaptive immunity by the female sex hormones oestradiol and progesterone. *FEMS Immunology & Medical Microbiology,* 38**,** 13-22.

BILLETER, S. A., BORCHERT, J. N., ATIKU, L. A., MPANGA, J. T., GAGE, K. L. & KOSOY, M. Y. 2014. Bartonella species in invasive rats and indigenous rodents from Uganda. *Vector-Borne and Zoonotic Diseases,* 14**,** 182-188.

BIZE, P., JEANNERET, C., KLOPFENSTEIN, A. & ROULIN, A. 2008. What makes a host profitable? Parasites balance host nutritive resources against immunity. *American Naturalist,* 171**,** 107-118.

BORDES, F., MORAND, S., KRASNOV, B. R. & POULIN, R. 2010. Parasite diversity and latitudinal gradients in terrestrial mammals. *The Biogeography of Host-Parasite Interactions***,** 89-98.

BORDES, F., PONLET, N., DE BELLOCQ, J. G., RIBAS, A., KRASNOV, B. R. & MORAND, S. 2012. Is there sex-biased resistance and tolerance in Mediterranean wood mouse (*Apodemus sylvaticus*) populations facing multiple helminth infections? *Oecologia,* 170**,** 123-135.

BRAACK, L., HORAK, I. G., JORDAAN, L. C., SEGERMAN, J. & LOUW, J. 1996. The comparative host status of red veld rats (*Aethomys chrysophilus*) and bushveld gerbils (*Tatera leucogaster*) for epifaunal arthropods in the southern Kruger National Park, South Africa. *The Onderstepoort journal of veterinary research,* 63**,** 149-158.

BUFFENSTEIN, R. 1984. The importance of microhabitat in thermoregulation and thermal conductance in two Namib rodents—a crevice dweller, *Aethomys namaquensis*, and a burrow dweller, *Gerbillurus paeba*. *Journal of Thermal Biology,* 9**,** 235-241.

CHAPMAN, C. A., SAJ, T. L. & SNAITH, T. V. 2007. Temporal dynamics of nutrition, parasitism, and stress in colobus monkeys: implications for population regulation and conservation. *American Journal of Physical Anthropology,* 134**,** 240-250.

CHIMIMBA, C. 1998. A taxonomic synthesis of southern African *Aethomys* (Rodentia: Muridae) with a key to species. *Mammalia,* 62**,** 427-438.

CHIMIMBA, C. 2001. Infraspecific morphometric variation in *Aethomys namaquensis* (Rodentia: Muridae) from southern Africa. *Journal of Zoology,* 253**,** 191-210.

CHIMIMBA, C. & DIPPENAAR, N. 1994. Non-geographic variation in *Aethomys chrysophilus* (De Winton, 1897) and A. namaquensis (A. Smith, 1834)(Rodentia: Muridae) from southern Africa. *South African Journal of Zoology,* 29**,** 107-107.

CHIMIMBA, C. T., DIPPENAAR, N. J. & ROBINSON, T. J. 1999. Morphometric and morphological delineation of southern African species of *Aethomys* (Rodentia: Muridae). *Biological Journal of the Linnean Society,* 67**,** 501-527.

COMBES, C. 2001. *Parasitism: the ecology and evolution of intimate interactions,* Chicago & London, University of Chicago Press.

DE GRAAFF, G. 1981. *The rodents of Southern Africa: notes on their identification, distribution, ecology, and taxonomy*, Butterworth-Heinemann, Durban, South Africa, 267p.

DELAHAY, R., SPEAKMAN, J. & MOSS, R. 1995. The energetic consequences of parasitism: effects of a developing infection of Trichostrongylus tenuis (Nematoda) on red grouse (*Lagopus lagopus scoticus*) energy balance, body weight and condition. *Parasitology,* 110**,** 473-482.

DICKMAN, C. R. 1999. Rodent-ecosystem relationships: a review. *Ecologically-based management of rodent pests. ACIAR Monograph***,** 113-133.

DUMBACHER, J. P., RATHBUN, G. B., OSBORNE, T. O., GRIFFIN, M. & EISEB, S. J. 2014. A new species of round-eared sengi (genus *Macroscelides*) from Namibia. *Journal of Mammalogy,* 95**,** 443-454.

DUMBACHER, J. P., RATHBUN, G. B., SMIT, H. A. & EISEB, S. J. 2012. Phylogeny and Taxonomy of the Round-Eared Sengis or Elephant-Shrews, Genus *Macroscelides* (Mammalia, Afrotheria, Macroscelidea). *Plos One,* 7.

DUNEAU, D. & EBERT, D. 2012. Host Sexual Dimorphism and Parasite Adaptation. *PLoS Biology,* 10**,** e1001271, 1-9.

DUNN, J. C., GOODMAN, S. J., BENTON, T. G. & HAMER, K. C. 2013. Avian blood parasite infection during the non-breeding season: an overlooked issue in declining populations? *BMC ecology,* 13**,** 30.

DURDEN, L. A. & MUSSER, G. G. 1994. The mammalian hosts of the sucking lice (Anoplura) of the world: a host-parasite list. *Bulletin of the Society for Vector Ecology,* 19**,** 130-168.

EISEB, S. 2002. Fleas (Insecta: Siphonaptera) of small mammals occurring at Gellapost and Nabaos, Keetmanshoop District in Southern Namibia.*MSc thesis, Department of Biological Sciences, University of Zimbabwe, Harare.*

ELLIOT, S. L., BLANFORD, S. & THOMAS, M. B. 2002. Host–pathogen interactions in a varying environment: temperature, behavioural fever and fitness. *Proceedings of the Royal Society of London B: Biological Sciences,* 269**,** 1599-1607.

FAGIR, D. M. & EL-RAYAH, E.-A. 2009. Parasites of the Nile rat in rural and urban regions of Sudan. *Integrative Zoology,* 4**,** 179-187.

FAGIR, D. M., UECKERMANN, E. A., HORAK, I. G., BENNETT, N. C. & LUTERMANN, H. 2014. The Namaqua rock mouse (*Micaelamys namaquensis*) as a potential reservoir and host of arthropod vectors of diseases of medical and veterinary importance in South Africa. *Parasites & Vectors,* 7, p. 366.

FERRARI, N., CATTADORI, I. M., NESPEREIRA, J., RIZZOLI, A. & HUDSON, P. J. 2004. The role of host sex in parasite dynamics: field experiments on the yellownecked mouse *Apodemus flavicollis*. *Ecology Letters,* 7**,** 88-94.

FERRARI, N., ROSA, R., PUGLIESE, A. & HUDSON, P. J. 2007. The role of sex in parasite dynamics: model simulations on transmission of *Heligmosomoides polygyrus* in populations of yellow-necked mice, *Apodemus flavicollis*. *International Journal for Parasitology,* 37**,** 341-349.

FLEMING, P. & NICOLSON, S. 2004. Sex differences in space use, body condition and survivorship during the breeding season in the Namaqua rock mouse, *Aethomys namaquensis*. *African Zoology,* 39**,** 123-132.

FOLSTAD, I. & KARTER, A. J. 1992. Parasites, bright males, and the immunocompetence handicap. *American Naturalist***,** 603-622.

FORBES, A., HUCKLE, C., GIBB, M., ROOK, A. & NUTHALL, R. 2000. Evaluation of the effects of nematode parasitism on grazing behaviour, herbage intake and growth in young grazing cattle. *Veterinary parasitology,* 90**,** 111-118.

FOURIE, L., HORAK, I. & VAN DEN HEEVER, J. 1992. relative host status of rock elephant shrews *Elephantulus myurus* and Namaqua rock mice *Aethomys namaquensis* for economically important ticks. *South African journal of zoology= Suid-Afrikaanse tydskrif vir dierkunde*.

FOURIE, L., HORAK, I. & WOODALL, P. 2005. Elephant shrews as hosts of immature ixodid ticks. *Onderstepoort Journal of Veterinary Research,* 72**,** p. 293-301.

FOURIE, L., HORAK, I. G., KOK, D. & VAN ZYL, W. 2002. Hosts, seasonal occurrence and life cycle of *Rhipicentor nuttalli* (Acari: Ixodidae). *The Onderstepoort journal of veterinary research,* 69**,** 177.

FOURIE, L., TOIT, J. D., KOK, D. & HORAK, I. 1995. Arthropod parasites of elephantshrews, with particular reference to ticks. *Mammal Review,* 25**,** 31-37.

GOÜY DE BELLOCQ, J., KRASNOV, B., KHOKHLOVA, I., GHAZARYAN, L. & PINSHOW, B. 2006. Immunocompetence and flea parasitism of a desert rodent. *Functional Ecology,* 20**,** 637-646.

GRZYBEK, M., BAJER, A., BEHNKE-BOROWCZYK, J., AL-SARRAF, M. & BEHNKE, J. M. 2015. Female host sex-biased parasitism with the rodent stomach nematode *Mastophorus muris* in wild bank voles (*Myodes glareolus*). *Parasitology Research,* 114**,** 523-33.

HAMILTON, W. D. & ZUK, M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science,* 218**,** 384-387.

HARRISON, A., BASTOS, A. D., MEDGER, K. & BENNETT, N. C. 2013. Eastern rock sengis as reservoir hosts of *Anaplasma bovis* in South Africa. *Ticks and tick-borne diseases* 4**,** 503-5.

HARRISON, A. & BENNETT, N. C. 2012. The importance of the aggregation of ticks on small mammal hosts for the establishment and persistence of tick-borne pathogens: an investigation using the R(0) model. *Parasitology,* 139**,** 1605-13.

HARRISON, A., BOWN, K. J. & HORAK, I. G. 2011. Detection of *Anaplasma bovis* in an undescribed tick species collected from the eastern rock sengi *Elephantulus myurus*. *Journal of Parasitology,* 97**,** 1012-6.

HARRISON, A., SCANTLEBURY, M. & MONTGOMERY, W. 2010. Body mass and sexbiased parasitism in wood mice *Apodemus sylvaticus*. *Oikos,* 119**,** 1099-1104.

HAWLENA, H., ABRAMSKY, Z. & KRASNOV, B. R. 2005. Age-biased parasitism and density-dependent distribution of fleas (Siphonaptera) on a desert rodent. *Oecologia,* 146**,** 200-8.

HILLEGASS, M. A., WATERMAN, J. M. & ROTH, J. D. 2008. The influence of sex and sociality on parasite loads in an African ground squirrel. *Behavioral Ecology,* 19**,** 1006-1011.

HORAK, I., CHAPARRO, F., BEAUCOURNU, J. & LOUW, J. 1999. Parasites of domestic and wild animals in South Africa. XXXVI. Arthropod parasites of yellow mongooses, *Cynictis penicillata* (G. Cuvier, 1829). *Onderstepoort Journal of Veterinary Research,* 66**,** 33-38.

HORAK, I., FOURIE, L. & BRAACK, L. 2005. Small mammals as hosts of immature ixodid ticks. *Onderstepoort Journal of Veterinary Research,* 72, p. 255-261.

HORAK, I. G., CAMICAS, J.-L. & KEIRANS, J. E. 2002. The Argasidae, Ixodidae and Nuttalliellidae (Acari: Ixodida): a world list of valid tick names. *Experimental & applied acarology,* 28, 27-54.

HORAK, I. G., WELMAN, S., HALLAM, S. L., LUTERMANN, H. & MZILIKAZI, N. 2011. Ticks of four-toed elephant shrews and Southern African hedgehogs. *Onderstepoort J Vet Res,* 78, 243.

IRVINE, R. 2006. Parasites and the dynamics of wild mammal populations. *Animal Science,* 82, 775-781.

KERLEY, G., KNIGHT, M. & ERASMUS, T. 1990. Small mammal microhabitat use and diet in the southern Kalahari, South Africa. *S. AFR. J. WILDL. RES./S.-AFR. NATURNAV.,* 20, 123-126.

KIFFNER, C., STANKO, M., MORAND, S., KHOKHLOVA, I. S., SHENBROT, G. I., LAUDISOIT, A., LEIRS, H., HAWLENA, H. & KRASNOV, B. R. 2013. Sex-biased parasitism is not universal: evidence from rodent-flea associations from three biomes. *Oecologia,* 173, 1009-22.

KIFFNER, C., STANKO, M., MORAND, S., KHOKHLOVA, I. S., SHENBROT, G. I., LAUDISOIT, A., LEIRS, H., HAWLENA, H. & KRASNOV, B. R. 2014. Variable effects of host characteristics on species richness of flea infracommunities in rodents from three continents. *Parasitology research,* 113, 2777-2788.

KIFFNER, C., VOR, T., HAGEDORN, P., NIEDRIG, M. & RUEHE, F. 2011. Factors affecting patterns of tick parasitism on forest rodents in tick-borne encephalitis risk areas, Germany. *Parasitology Research,* 108, 323-335.

KIM, K. C. 1985. *Coevolution of parasitic arthropods and mammals,* New York, USA, John Wiley & Sons.

KIM, K. C. 2006. Blood-sucking lice (Anoplura) of small mammals: True parasites. *Micromammals and Macroparasites.* Springer.

KLEIN, S. 2000. The effects of hormones on sex differences in infection: from genes to behavior. *Neuroscience & Biobehavioral Reviews,* 24, 627-638.

KRASNOV, B. R. 2008. Life Cycles. *Functional and Evolutionary Ecology of Fleas: A Model for Ecological Parasitology.* UK: Cambridge

KRASNOV, B. R., BORDES, F., KHOKHLOVA, I. S. & MORAND, S. 2012. Gender-biased parasitism in small mammals: patterns, mechanisms, consequences. *mammalia,* 76, 1-13.

KRASNOV, B. R., MATTHEE, S., LARESCHI, M., KORALLOVINARSKAYA, N. P. & VINARSKI, M. V. 2010. Cooccurrence of ectoparasites on rodent hosts: null model analyses of data from three continents. *Oikos,* 119, 120-128.

KRASNOV, B. R., SHENBROT, G. I., KHOKHLOVA, I. S. & POULIN, R. 2007. Geographical variation in the ‘bottomup’control of diversity: fleas and their small mammalian hosts. *Global Ecology and Biogeography,* 16, 179-186.

KRASNOV, B. R., SHENBROT, G. I., KHOKHLOVA, I. S., STANKO, M., MORAND, S. & MOUILLOT, D. 2015. Assembly rules of ectoparasite communities across scales: combining patterns of abiotic factors, host composition, geographic space, phylogeny and traits. *Ecography,* 38, 184-197.

KUTZ, S. J., JENKINS, E. J., VEITCH, A. M., DUCROCQ, J., POLLEY, L., ELKIN, B. & LAIR, S. 2009. The Arctic as a model for anticipating, preventing, and mitigating climate change impacts on host-parasite interactions. *Veterinary Parasitology,* 163**,** 217-228.

LANE, J. E., BOUTIN, S., GUNN, M. R. & COLTMAN, D. W. 2009. Sexually selected behaviour: red squirrel males search for reproductive success. *Journal of Animal Ecology,* 78**,** 296-304.

LARESCHI, M. & KRASNOV, B. R. 2010. Determinants of ectoparasite assemblage structure on rodent hosts from South American marshlands: the effect of host species, locality and season. *Medical and Veterinary Entomology,* 24**,** 284-292.

LAUDISOIT, A., LEIRS, H., MAKUNDI, R. & KRASNOV, B. R. 2009. Seasonal and habitat dependence of fleas parasitic on small mammals in Tanzania. *Integrative Zoology,* 4**,** 196-212.

LE COEUR, C., ROBERT, A., PISANU, B. & CHAPUIS, J. L. 2015. Seasonal variation in infestations by ixodids on Siberian chipmunks: effects of host age, sex, and birth season. *Parasitolgy Research,* 114**,** 2069-78.

LEHANE, M. J. 2005. *The biology of blood-sucking in insects*, Cambridge University Press.

LOGIUDICE, K., OSTFELD, R. S., SCHMIDT, K. A. & KEESING, F. 2003. The ecology of infectious disease: effects of host diversity and community composition on Lyme disease risk. *Proc Natl Acad Sci U S A,* 100**,** 567-71.

MAHER, S. P. & TIMM, R. M. 2014. Patterns of host and flea communities along an elevational gradient in Colorado. *Canadian Journal of Zoology,* 92**,** 433-442.

MAKUNDI, R. & KILONZO, B. 1994. Seasonal dynamics of rodent fleas and its implication on control strategies in Lushoto district, northeastern Tanzania. *Journal of Applied Entomology,* 118**,** 165-171.

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

MARTIN, L., HAN, P., LEWITTES, J., KUHLMAN, J., KLASING, K. & WIKELSKI, M. 2006. Phytohemagglutinininduced skin swelling in birds: histological support for a classic immunoecological technique. *Functional Ecology,* 20**,** 290-299.

MATTHEE, S., HORAK, I. G., BEAUCOURNU, J.-C., DURDEN, L. A., UECKERMANN, E. A. & MCGEOCH, M. A. 2007. Epifaunistic arthropod parasites of the four-striped mouse, *Rhabdomys pumilio*, in the Western Cape Province, South Africa. *Journal of Parasitology,* 93**,** 47-59.

MATTHEE, S. & KRASNOV, B. R. 2009. Searching for generality in the patterns of parasite abundance and distribution: ectoparasites of a South African rodent, *Rhabdomys pumilio*. *International Journal of Parasitology,* 39**,** 781-8.

MCCURDY, D. G., SHUTLER, D., MULLIE, A. & FORBES, M. R. 1998. Sex-biased parasitism of avian hosts: relations to blood parasite taxon and mating system. *Oikos***,** 303-312.

MEDGER, K., CHIMIMBA, C. T., BENNETT, N. C. & KITCHENER, A. 2012. Seasonal reproduction in the eastern rock elephant-shrew: influenced by rainfall and ambient temperature? *Journal of Zoology,* 288**,** 283-293.

MEYER, J. & BRANDL, R. 2005. Nesting sites, nest density of *Aethomys namaquensis* (Rodentia, Muridae) in the Thornveld savannah of South Africa. *Mammalian Biology-Zeitschrift für Säugetierkunde,* 70**,** 126-129.

MFUNE, J., KANGOMBE, F. & EISEB, S. 2013. Host specificity, prevalence and intensity of infestation of fleas (Order Siphonaptera) of small mammals atselected sites in the city of Windhoek, Namibia.

MIDGLEY, G., HANNAH, L., MILLAR, D., THUILLER, W. & BOOTH, A. 2003. Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biological Conservation,* 112**,** 87-97.

MONADJEM, A. 1997. Stomach contents of 19 species of small mammals from Swaziland. *South African Journal of Zoology,* 32**,** 23-26.

MOORE, S. L. & WILSON, K. 2002. Parasites as a viability cost of sexual selection in natural populations of Mammals. *Science,* 297**,** 2015-2018.

MORAND, S., DE BELLOCQ, J. G., STANKO, M. & MIKLISOVÁ, D. 2004. Is sex-biased ectoparasitism related to sexual size dimorphism in small mammals of Central Europe? *Parasitology,* 129**,** 505-510.

MORAND, S. & KRASNOV, B. R. E. 2006. *Micromammals and Macroparasites: From Evolutionary Ecology to Management*, Tokyo: Springer-Verlag, Japan.

MOSTOWY, R. & ENGELSTÄDTER, J. 2011. The impact of environmental change on host–parasite coevolutionary dynamics. *Proceedings of the Royal Society of London B: Biological Sciences,* 278**,** 2283-2292.

MUTEKA, S., CHIMIMBA, C. & BENNETT, N. 2006b. Reproductive photoresponsiveness in *Aethomys ineptus* and *A. namaquensis* (Rodentia: Muridae) from southern Africa. *Journal of Zoology,* 268**,** 225-231.

MUTEKA, S. P., CHIMIMBA, C. T. & BENNETT, N. C. 2006a. Reproductive seasonality in *Aethomys namaquensis* (Rodentia: Muridae) from southern Africa. *Journal of mammalogy,* 87**,** 67-74.

NEAL, B. 1982. Reproductive Ecology of the Rufous Elephant-Shrew, *Elephantulus rufescens* (Macroscelididae), in Kenya. *Z. SAUTIERKD.,* 47**,** 65-71.

NEAL, B. 1990. Observations on the early post-natal growth and development of *Tatera leucogaster*, *Aethomys chrysophilus* and *A. namaquensis* from Zimbabwe, with a review of the pre-and post-natal growth and development of African muroid rodents. *Mammalia,* 54**,** 245-270.

NJUNWA, K., MWAIKO, G., KILONZO, B. & MHINA, J. 1989. Seasonal patterns of rodents, fleas and plague status in the Western Usambara Mountains, Tanzania. *Medical and veterinary entomology,* 3**,** 17-22.

NORVAL, R. 1979. The limiting effect of host availability for the immature stages on population growth in economically important ixodid ticks. *The Journal of parasitology,* 65**,** 285-287.

OGUGE, N., DURDEN, L., KEIRANS, J., BALAMI, H. & SCHWAN, T. 2009. Ectoparasites (sucking lice, fleas and ticks) of small mammals in southeastern Kenya. *Medical and veterinary entomology,* 23**,** 387-392.

OWENS, I. P. 2002. Sex differences in mortality rate. *SCIENCE-NEW YORK THEN WASHINGTON-***,** 2008-2008.

PATTERSON, J. E. H., NEUHAUS, P., KUTZ, S. J. & RUCKSTUHL, K. E. 2015. Patterns of ectoparasitism in North American red squirrels (*Tamiasciurus hudsonicus*): Sex-biases, seasonality, age, and effects on male body condition. *International journal for parasitology. Parasites and wildlife,* 4**,** 301-6.

PERKINS, S. E., CATTADORI, I. M., TAGLIAPIETRA, V., RIZZOLI, A. P. & HUDSON, P. J. 2003. Empirical evidence for key hosts in persistence of a tick-borne disease. *International journal for parasitology,* 33**,** 909-917.

PERKINS, S. E., FERRARI, M. & HUDSON, P. 2008. The effects of social structure and sex-biased transmission on macroparasite infection. *Parasitology,* 135**,** 1561-1569.

POULIN, R. 1996. Sexual inequalities in helminth infections: a cost of being a male? *American Naturalist***,** 287-295.

POULIN, R. 2007. Are there general laws in parasite ecology? *Parasitology,* 134**,** 763-76.

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

QUELLER, D. C. 1997. Why do females care more than males? *Proceedings of the Royal Society of London B: Biological Sciences,* 264**,** 1555-1557.

RANDOLPH, S. E., ASOKLIENE, L., AVSIC-ZUPANC, T., BORMANE, A., BURRI, C., GERN, L., GOLOVLJOVA, I., HUBALEK, Z., KNAP, N., KONDRUSIK, M., KUPCA, A., PEJCOCH, M., VASILENKO, V. & ZYGUTIENE, M. 2008. Variable spikes in tick-borne encephalitis incidence in 2006 independent of variable tick abundance but related to weather. *Parasites & Vectors,* 1**,** 44.

RELTON, C., BENNETT, N. C. & MEDGER, K. 2013. The mode of ovulation in the Namaqua rock mouse, *Micaelamys namaquensis*. *Canadian Journal of Zoology,* 91**,** 829-836.

RENWICK, A. R. & LAMBIN, X. 2013. Host-parasite interactions in a fragmented landscape. *International Journal of Parasitology,* 43**,** 27-35.

RIBBLE, D. O. & PERRIN, M. R. 2005. Social organization of the eastern rock elephant-shrew (*Elephantulus myurus*): the evidence for mate guarding. *Belgian Journal of Zoology,* 135**,** 167.

ROBERTS, M. L., BUCHANAN, K. L. & EVANS, M. 2004. Testing the immunocompetence handicap hypothesis: a review of the evidence. *Animal behaviour,* 68**,** 227-239.

ROLFF, J. 2002. Bateman's principle and immunity. *Proceedings of the Royal Society of London B: Biological Sciences,* 269**,** 867-872.

SCANTLEBURY, M., WATERMAN, J., HILLEGASS, M., SPEAKMAN, J. & BENNETT, N. 2007. Energetic costs of parasitism in the Cape ground squirrel *Xerus inauris*. *Proceedings of the Royal Society of London B: Biological Sciences,* 274**,** 2169-2177.

SCHALK, G. & FORBES, M. R. 1997. Male biases in parasitism of mammals: effects of study type, host age, and parasite taxon. *Oikos***,** 67-74.

SCHULTE-HOSTEDDE, A., MILLAR, J. & HICKLING, G. 2001. Evaluating body condition in small mammals. *Canadian Journal of Zoology,* 79**,** 1021-1029.

SCHWAN, T. G. 1986. Seasonal abundance of fleas (Siphonaptera) on grassland rodents in Lake Nakuru National Park, Kenya, and potential for plague transmission. *Bulletin of entomological research,* 76**,** 633-648.

SHANGULA, K. 1998. Successful plague control in Namibia. *South African Medical Journal88***,** 1428-1430.

SHINE, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology***,** 419-461.

SKINNER, J. D. & CHIMIMBA, C. T. 2005. *The mammals of the southern African subregion. 3rd revised edition*.

SOLIMAN, S., MAIN, A. J., MARZOUK, A. S. & MONTASSER, A. A. 2001. Seasonal studies on commensal rats and their ectoparasites in a rural area of Egypt: The relationship of ectoparasites to the species, locality, and relative abundance of the host. *Journal of Parasitology,* 87**,** 545-553.

TRIVERS, R. 1972. Parental investment and sexual selection. *Sexual Selection & the Descent of Man, Aldine de Gruyter, New York***,** 136-179.

WAKELIN, D. 1996. *Immunity to parasites: how parasitic infections are controlled*, Cambridge University Press.

WEIL, Z. M., MARTIN II, L. B. & NELSON, R. J. 2006. Interactions among immune, endocrine, and behavioural response to infection. *Micromammals and Macroparasites.* Springer.

WILSON, K., BJØRNSTAD, O., DOBSON, A., MERLER, S., POGLAYEN, G., RANDOLPH, S., READ, A. & SKORPING, A. 2002. Heterogeneities in macroparasite infections: patterns and processes. *The ecology of wildlife diseases***,** 6-44.

WOODALL, P. & MACKIE, R. 1987. Caecal size and function in the rock elephant shrew *Elephantulus myurus* (Insectivora, Macroscelididae) and the Namaqua rock mouse *Aethomys namaquensis* (Rodentia, Muridae). *Comparative Biochemistry and Physiology Part A: Physiology,* 87**,** 311-314.

YONAS, M., WELEGERIMA, K., LAUDISOIT, A., BAUER, H., GEBREHIWOT, K., DECKERS, S., KATAKWEBA, A., MAKUNDI, R. & LEIRS, H. 2011. Preliminary investigation on rodent–ectoparasite associations in the highlands of Tigray, Northern Ethiopia: implications for potential zoonoses. *Integrative zoology,* 6**,** 366-374.

ZIMBA, M., PFUKENYI, D., LOVERIDGE, J. & MUKARATIRWA, S. 2011. Seasonal abundance of plague vector *Xenopsylla brasiliensis* from rodents captured in three habitat types of periurban suburbs of Harare, Zimbabwe. *Vector-Borne and Zoonotic Diseases,* 11**,** 1187-1192.

ZUK, M. 1990. Reproductive strategies and disease susceptibility: an evolutionary viewpoint. *Parasitology today,* 6**,** 231-233.

ZUK, M. & MCKEAN, K. A. 1996. Sex differences in parasite infections: patterns and processes. *International journal for parasitology,* 26**,** 1009-1024.

CHAPTER TWO

ECTOPARASITE SPECIES ASSOCIATED WITH THE NAMAQUA ROCK MOUSE (*Micaelamys namaquensis*) IN SOUTH AFRICA[1]

SUMMARY

The current study aimed to assess the ectoparasite community of the Namaqua rock mouse (*Micaelamys namaquensis*), a rodent species widely distributed throughout the southern African sub-region. The ectoparasite species diversity, prevalence and abundance were recorded. In addition, we investigated the effect of season and host sex on the main ectoparasite taxa. A total of 6,725 ectoparasites representing four taxa were collected from 216 mice. Fleas and immature ticks were the most prevalent parasites recovered followed by mites and lice. At the same time, mites were the most abundant taxon recovered. The most prevalent and abundant ectoparasite species were: *Xenopsylla brasiliensis* (flea), *Hoplopleura patersoni* (louse), chiggers and *Androlaelaps rhabdomysi* (mites) as well as *Rhipicephalus distinctus* and *Haemaphysalis* spp. (ticks). All ectoparasite taxa exhibited seasonal peaks in abundance coinciding with the warm/wet season. In addition, sex-biased parasitism was observed for lice, mites as well as ticks. Our results suggest that abiotic factors have significant effects on the abundance and diversity of parasites. In addition, host behaviour and reproductive investment may play a role in parasite abundance patterns.

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INTRODUCTION

The prevalence and/or abundance of parasites within a single host or in a host population often undergoes cyclical fluctuations dependent on the seasons and/or the host population dynamics (Lass and Ebert 2006; Luis *et al*. 2010). Changes in environmental conditions can have dramatic effects on the abundance and diversity of parasites, which ultimately affects the host-parasite dynamics (Kutz *et al.* 2009). Seasonal patterns are particularly common in ectoparasites (Krasnov 2008). Ectoparasite taxa that have developmental stages that live off the host are suggested to be more susceptible to seasonal effects (Vinarski *et al.*, 2007; Krasnov 2008). For example, lice are permanent parasites that never leave the host, therefore seasonal changes are expected to be weak (Kim 2006; Marshall 1981). In contrast, seasonal variation in tick burdens is expected to be more pronounced as they spend most of their life cycles off-host (e.g. in the vegetation, Lareschi and Krasnov 2010). Fleas and mites also spend part of their life on the host and the rest in the nest of the host (Matthee and Krasnov 2009). Therefore, seasonal variation is expected to be more pronounced in fleas, mites and ticks, than in lice (Sonenshine 1993; Matthee and Krasnov 2009). It has been suggested that fluctuations in environmental conditions may affect parasite abundances directly as well as indirectly through seasonal effects on hosts (Altizer *et al.* 2006; Martin *et al.* 2008). For instance, host densities can increase during the breeding season, due to changes in host social behaviour and contact rates between individuals, variation in host exposure to infective/immature stages of parasites in the environment, rates of births and mortality of hosts as well as changes in the host immune defences (Gillett 1974; Gremillion-Smith and Woolf 1988; Dobson and Carper 1992; Krasnov *et al.*, 2002; Altizer *et al.* 2006).

Sex-biased parasitism has been observed across a wide range of animal taxa (Schalk and Forbes 1997, Moore and Wilson 2002). Many parasitological studies have indicated that parasites tend to infest males more heavily than females (Poulin 1996; Poulin and George-Nascimento 2007; Zuk and McKean 1996; McCurdy *et al.* 1998; Ferrari *et al.* 2004). Both sexes aim to maximize their fitness, but they tend to use different strategies to achieve this. For example, female mammals usually invest more energy in their immune defences to secure better survival and ultimately fitness. In contrast, males aim to invest more energy in increasing mating rates with females by making themselves more attractive to females, which may compromise their own immune responses and parasite defences (Hamilton and Zuk 1982; Folstad and Karter 1992; Bateman 1948; Trivers 1972). For example, sexual size dimorphism is considered one cause of sex-biased parasitism and larger males may achieve greater mating rates and may be more successful in competing with other males and also be more attractive to females. In addition, the larger size of males might offer a larger target for parasites (Shine 1989; Rolff 2002, Moore and Wilson 2002). Moreover, behavioural differences between sexes may also contribute towards sex-biases; e.g. males tend to have larger home range sizes and higher rates of mobility than females, which could increase their chances of encountering parasites (Morand *et al.* 2004).

Another possible cause of male sex-bias is linked to a reduction in immunocompetence to parasitic infestations in males, which is thought to be caused by the immunosuppressive properties of steroid hormones and in particular testosterone (Klein 2000; Beagley and Gockel 2003; Harrison *et al.* 2010). The increase in testosterone levels is known to help with expression of male sexual traits during mating season, but at the same time it may compromise the immune system (Hamilton and Zuk 1982; Zuk 1990; Roberts *et al.* 2004).

Unlike in the southern hemisphere, the ectoparasite fauna of small mammals (particularly rodents) in the northern hemisphere is well studied (LoGiudice *et al.* 2003; Morand and Krasnov 2006; Randolph *et al.* 2008; Laudisoit *et al.* 2009; Kiffner *et al.* 2011 a, b; Mfune *et al.* 2013). Although there is a large number of incidental reports on the ectoparasite fauna of rodents occurring in different parts of Africa (e.g. Fagir and El-Rayah 2009; Laudisoit *et al.* 2009; Yonas *et al.* 2011), such studies are limited for South Africa and are often descriptive (De Graaff 1981; Fourie *et al.* 1992; Horak *et al.* 2005) or only considering a single parasite taxon (Harrison *et al.* 2011, 2012). Therefore, little is known about which parasites may potentially infest many endemic rodent hosts. Hence, the present study was carried out to investigate the ectoparasite fauna of a murid species, namely the Namaqua rock mouse, *Micaelamys namaquensis* (previously named *Aethomys namaquensis*). This rodent is widely distributed in the southern African sub-region, extending from southern central Africa through the sub-region of South Africa (south of the Zambezi/Cunene River, Angola, Zambia, Malawi and northern Mozambique (Chimimba *et al.* 1999; Skinner and Chimimba 2005). It is a nocturnal, medium sized murid (53±15g). Rock mice are thought to live communally in small colonies and to rocky outcrops or hillside habitats. *Micaelamys namaquensis* has been reported to be omnivorous as well as granivorous (Woodall and Mackie 1987; Kerley *et al.* 1990; Monadjem 1997). Rock mice have been shown to be well adapted to hot, arid environments (Buffenstein 1984). In the eastern parts of South Africa it has been reported that *M. namaquensis* breeds in the rainy warmer months (i.e. summer), from September to May, with peak between March and April, while in the western coastal areas it breeds during winter (Fleming and Nicholson 2004, Muteka *et al.* 2006a). The average litter size is 3.1 - 3.6 young which are weaned by 21 - 28 days (Neal 1990; Skinner and Smithers 1990). The Namaqua rock mouse is a well-studied species with regards to its taxonomy and reproductive physiology (Chimimba and Dippenaar 1994; Chimimba 1998, 2001; Chimimba *et al.* 1999; Fleming and Nicolson 2004; Meyer and Brandl 2005; Muteka *et al.* 2006a, b; Relton *et al.* 2013). In contrast, the current knowledge of the ectoparasite fauna infesting *M. namaquensis* is limited and ambiguous. Very few parasitological studies have been conducted on the species and the focus has been predominantly on their tick parasites (e.g. Fourie *et al.* 1992; Braack *et al.* 1996; Harrison *et al.* 2012). Older records by De Graaff (1981) indicated a diverse array of ectoparasites including 34 flea species from four families namely, Pulicidae, Hystrichopsyllidae, Leptopsyllidae and Chimaeropsyllidae; 12 species of mites from two families namely (Laelaptidae and Trombiculidae) and 26 species of ticks from three families (Ixodidae, Argasidae and Nuttalliellidae). No louse species were recorded by De Graaff (1981), but three species of lice from two families (Hoplopleuridae and Polyplacidae) were reported by Durden and Musser (1994). However, for most of these parasites little or no information is available regarding their sampling locality or number of host individuals sampled and only a single study has sampled the same host population on more than one occasion (Fourie *et al.* 1992). Consequently, the aim of the current study was to:

- Carry out the first comprehensive assessment of the ectoparasite community parasitising *M. namaquensis* in a single locality.
- Identify the most important ectoparasite species sustained by *M. namaquensis*.

- Investigate the contributions of abiotic (i.e. season) and biotic factors (i.e. host sex) on the distribution of ectoparasite taxa among hosts.

MATERIALS AND METHODS

Animals were sampled at Telperion/Ezemvelo Nature Reserve (25° 41' S, 28° 56' E) at the border between the Gauteng and Mpumalanga Provinces, South Africa, using 72 live-Sherman traps (H. B. Sherman Traps, Inc., Tallahassee, Florida) per plot on 16 plots (8 rocky outcrops and 8 grasslands). Sampling took place five times between April 2010 and April 2011 to cover all seasons (April/May 2010, July/August 2010, October/November 2010; January/February 2011, April/May 2011). During the first trip sampling was limited to five rocky outcrops and one grassland plot. In addition, during the last trip mice were exclusively sampled from rocky outcrops (8 plots). Traps were baited with a mixture of peanut butter and oats and set over night in four parallel straight lines, approximately 10 m apart. Each trap line consisted of 18 traps placed about 10 m apart. Traps were set for four consecutive nights and checked around dawn. To limit trap related deaths as a result of environmental exposure, traps were closed during the day and bedding was provided in the traps during winter.

Animals were removed from the traps using Ziplock® bags and then restrained by hand and the sex of each individual was recorded. Each individual was checked carefully by back-combing the fur for the presence of ectoparasites. In addition, ear margins, legs and the base of the tail were also checked for the presence of ectoparasites. Ectoparasites were removed using fine tweezers and stored in 70% ethanol for later counting and identification to species level. All mice captured were marked with ear notches and subsequently released at their site of capture. For the current study only the first capture of an individual during a capture period was included. Fleas and lice were identified by Dina M. Fagir with the help of an expert taxonomist (Eddie D. Green) using the morphological key of Segerman (1995) and Ledger (1980), respectively. Mites were identified by Eddie A. Ueckermann using Krantz and Walter (2009) and ticks were identified to species or species group by Ivan G. Horak using descriptions provided by Walker *et al.* (2000). For microscopic examination, fleas, lice and mites were cleared and mounted following the techniques described in Krantz and Walter (2009), Ledger (1980) and Segerman (1995), respectively.

Prevalence and mean abundance (as defined by Bush *et al.* 1997) were calculated for the four higher taxa (i.e. fleas, lice, mites and ticks) and for individual parasite species. None of the data collected were normally distributed (Kolmogorov-Smirnov test: $P < 0.001$). Hence, the effect of season, i.e. April 2010 (autumn), July 2010 (winter), October 2010 (spring), January 2011 (summer) and April 2011 (autumn) and host sex on variation in prevalence and abundance of ectoparasites were investigated using generalized linear models (GLMs). A model with a binomial distribution with a logit-link function was selected for prevalence data and a negative-binomial distribution with a log-link function for abundance data. Post-hoc analyses were done with pairwise comparisons using the least significant difference (LSD). Only comparisons between consecutive trips for season and between the sexes during the same month were considered. Due to the low prevalence and/or abundance of some of the parasite species encountered (see results section) these analyses were carried out at a taxon level. All statistical analyses were conducted in IBM SPSS version 21 (IBM SPSS Statistics 21.Ink 2013).

RESULTS

A total of 216 mice of which 120 males (55.6%) and 96 females (44.4%) were captured and examined for ectoparasites (Table 1). From these a total of 6,725 ectoparasites from four taxa were collected (Table 2). Fleas and immature ticks were the most prevalent parasites recovered followed by mites and lice (Table 2). In contrast, mites were the most abundant taxon recovered (Table 2).

Table 1 Summary of the number of *M. namaquensis* captured per trip.

Season	No. of animals	Males	Females
April 2010	79	42	37
July 2010	19	8	11
October 2010	48	29	19
January 2011	46	25	21
April 2011	24	16	8

Table 2 Summary of the parasite groups found on *M. namaquensis* and their infestation parameters.

Taxon	Total no. of parasites	Prevalence (%)	Mean abundance (±SE)
Fleas	1072	78.2	4.96 (±0.42)
Lice	508	21.3	2.35 (±0.77)
Mites	3301	53.7	15.28 (±3.23)
Ticks	1744	78.2	8.07 (±1.34)

Ectoparasite species

A total of five species of flea representing four genera (*Xenopsylla, Chiastopsylla, Epirimia* and *Dinopsyllus*) were collected (Table 3). With a prevalence of 61.2% and a mean of 2.74±0.30 individuals, *Xenopsylla brasiliensis* was the most prevalent and abundant flea species (Table 3). The prevalence and abundance of *Chiastopsylla* *godfreyi* and *Epirimia aganippes* were substantially lower, but with 28.7% and 26.9% these two flea species were still quite common (Table 3). In contrast, *Dinopsyllus ellobius* and *Demeillonia granti* only occurred at a low prevalence and abundance (Table 3). Although *X. brasiliensis*, *C. godfreyi* and *E. aganippes* were the most prevalent flea species they only occurred at low abundances (Table 3).

A total of three species of lice were recovered of which *Hoplopleura patersoni* was the most prevalent and abundant species (Table 3). However, the prevalence of *H. aethomydis* was not much lower, while both prevalence and abundance of *Polyplax praomydis* was substantially lower than that of both *Hoplopleura* spp. (Table 3). Despite their high abundance both *Hoplopleura* spp. only occurred at low abundances.

A total of six mite species and one family were collected (Table 3). Unidentified trombiculid (chigger) mites were the most prevalent and abundant mites followed by *Androlaelaps rhabdomysi.* Unlike the previous two taxa, trombiculid mites and *A. rhabdomysi*, occurred at a high prevalence and abundance (Table 3). A total of 46 specimens of *Laelaps* species (we were unable to identify them to the species level) were found, consisting of five nymphs and 41 adults. Hence, they are referred to as *Laelaps* spp. The remaining species occurred at substantially lower prevalences and abundances (Table 3).

A total of eight tick species were recovered of which *Rhipicephalus distinctus* was the most prevalent and abundant tick species, followed by *Haemaphysalis* spp. (Table 3). The larvae and nymphs of *Rhipicephalus warburtoni* and *Rhipicephalus arnoldi* closely resemble each other, thus we have chosen to pool the immature ticks of both species together and refer to them as *Rhipicephalus warburtoni/arnoldi.* The same procedure was followed with the larvae and nymphs of *Haemaphysalis* (*Rhipistoma*) spp. and

Ixodes spp. Unlike the two prevalent species of tick all the remaining tick species occurred at substantially lower prevalences and abundances (Table 3).

Influence of season and host sex on ectoparasite distribution

Fleas

Both total flea prevalence and abundance varied significantly with season (Table 4). Post-hoc analyses revealed that flea prevalence was significantly greater in October 2010 (98%) compared to January 2011 (63%, LSD: $P < 0.0001$, Figure 1a), while it did not differ significantly for any of the remaining comparisons of consecutive seasons ($P \geq 0.224$). The flea abundance was significantly higher in October 2010 (7.93±1.24) compared to January 2011 (2.48±0.43, LSD: $P < 0.0001$) and July 2010 (4.41±1.13, $P = 0.037$, Figure 1b). Host sex and the interaction between season and sex had no significant effect on either flea prevalence or abundance (Table 4).

Table 3 Summary of the ectoparasite species found on Namaqua rock mice and their infestation parameters.

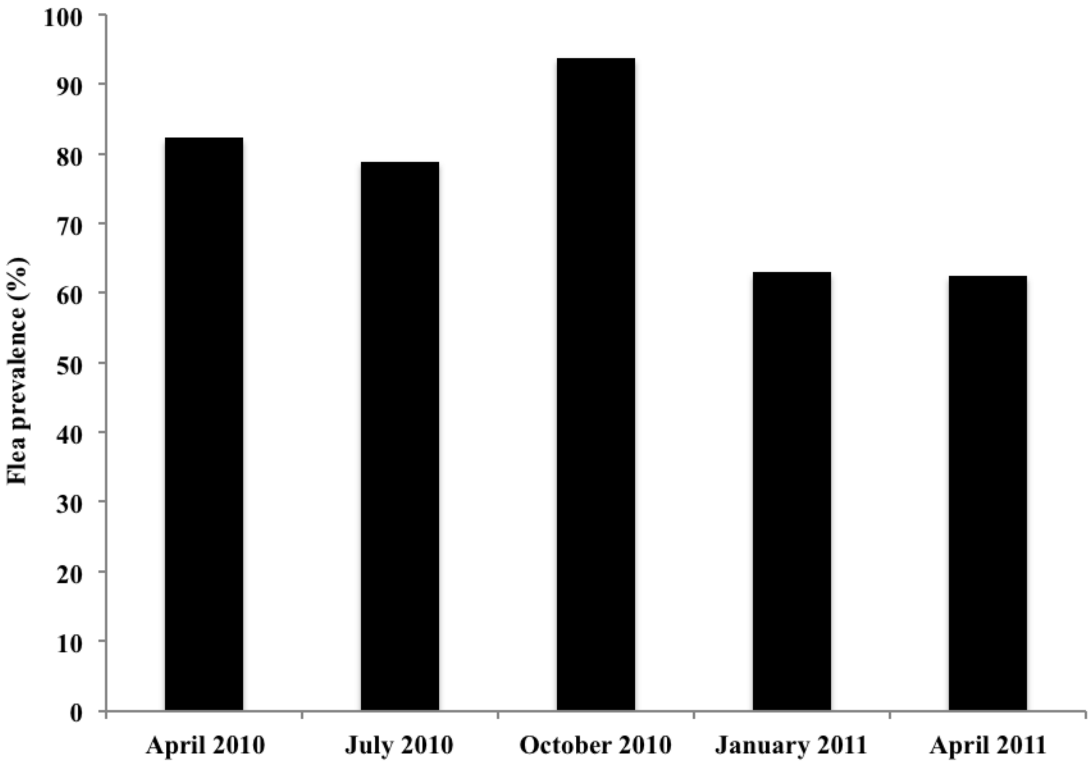
Species		**Larva**	**Nymph**	**Male**	**Female**	**Total**	**Prevalence (%)**	**Mean abundance (±SE)**
Fleas	*Xenopsylla brasiliensis*	-	-	351	240	591	61.2%	2.74 (±0.29)
	Chiastopsylla godfreyi	-	-	75	113	188	28.7%	0.87 (±0.15)
	Epirimia aganippes	-	-	91	127	218	26.9%	1.01 (±0.17)
	Dinopsyllus ellobius	-	-	18	0	18	6.0%	0.08 (±0.02)
	Demeillonia granti	-	-	1	0	1	0.5%	0.00 (±0.01)
Lice	*Hoplopleura patersoni*	-	-	162	31	193	16.2%	0.89 (±0.27)
	Hoplopleura aethomydis	-	-	10	101	111	12.0%	0.51 (±0.20)
	Polyplax praomydis	-	-	14	7	21	5.1%	0.10 (±0.03)
Mites	Trombiculidae (chiggers)	3001	-	-	-	3001	25.9%	13.89 (±3.23)
	Androlaelaps rhabdomysi	-	84	33	63	180	20.4%	0.83 (±0.23)
	Laelaps spp.	0	5	11	30	46	5.6%	0.21 (±0.13)
	Laelaps roubaudi	0	0	4	27	31	3.7%	0.14 (±0.08)
	Androlaelaps zuluensis	0	0	0	32	32	0.5%	0.15 (±0.14)
	Laelaps simillimus	0	0	0	2	2	0.5%	0.01 (±0.01)
	Androlaelaps marshalli	0	1	0	0	1	0.5%	0.00 (±(0.01)
Ticks	*Rhipicephalus distinctus*	956	306	-	-	1262	67.1%	5.84 (±1.05)
	Haemaphysalis spp.	382	67	-	-	449	23.3%	2.08 (±0.63)
	Rhipicephalus warburtoni/arnoldi	16	3	-	-	19	5.1%	0.09 (±0.02)
	Rhipicephalus evertsi evertsi	4	0	-	-	4	1.9%	0.02 (±0.01)
	Rhipicephalus decoloratus	3	0	-	-	3	1.4%	0.01 (±0.01)
	Ixodes spp.	4	0	-	-	5	1.4%	0.02 (±0.01)
	Rhipicephalus appendiculatus	1	1	-	-	2	0.9%	0.01 (±0.01)
	Rhipicephalus spp.	2	0	-	-	2	0.9%	0.01 (±0.01)

Table 4 Results of the GLMs for total ectoparasite prevalence and abundance of Namaqua rock mice.

Parasite groups	**Factors**	**Prevalence**			**Abundance**		
		Wald χ^2	**df**	**p**	**Wald χ^2**	**df**	**p**
Fleas	**Season**	12.312	4	0.015*	30.642	4	<0.0001*
	Sex	0.075	1	0.785	0.016	1	0.900
	Season x sex	2.631	4	0.621	4.214	4	0.378
Lice	**Season**	6.123	4	0.190	178.256	4	<0.0001*
	Sex	0.000	1	1.000	32.491	1	<0.0001*
	Season x sex	2.764	4	0.598	14.596	2	<0.001*
Mites	**Season**	29.674	4	0.000*	400.066	4	0.000*
	Sex	1.390	1	0.238	5.330	1	0.021*
	Season x sex	4.540	4	0.338	1.673	4	0.796
Ticks	**Season**	9.065	4	0.059*	166.435	4	0.000*
	Sex	0.000	1	0.999	5.284	1	0.022*
	Season x sex	0.628	4	0.960	13.432	4	0.009*

*indicates significant results.

a.



b.

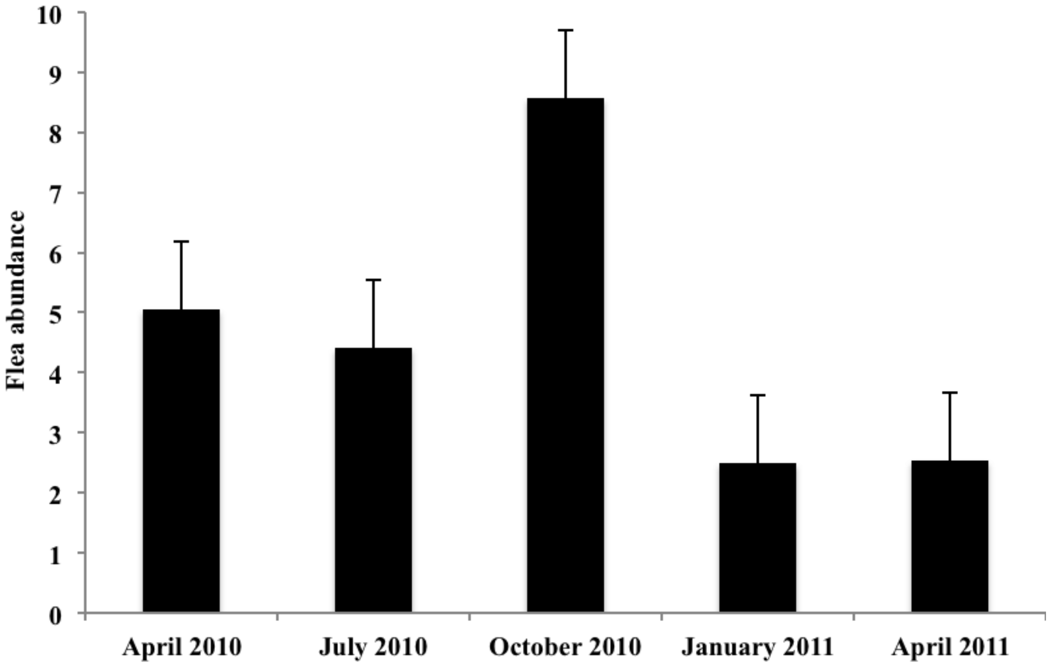


Figure 1 Seasonal variation in a. prevalence and b. abundance of fleas on *M. namaquensis*. Displayed are means ± SE.

Lice

Of all mice captured the highest individual burden was 133 lice. The louse prevalence did not vary significantly with any of the factors considered (Table 4). Conversely, the louse abundance varied significantly with all factors considered (Table 4). Post-hoc analysis showed that louse abundance was significantly higher during October 2010 (4.96±0.36) compared to July 2010 (0.00±0.48) and January 2011 (0.97±0.15, $P < 0.0001$ for both). In contrast, it was significantly lower in January 2011 (0.97±0.15) compared to April 2011 (1.91±0.44, LSD: $P = 0.042$), but did not significantly differ between April 2010 (0.00±0.00) and July 2010 (0.0±0.48, LSD: $P = 1.000$). Males harboured significantly more lice (2.85±1.26) than did the females (1.73±0.72). Comparisons of louse abundance between sexes within the same season showed that males had significantly more lice than females in both October 2010 and April 2011 ($P < 0.0001$ for both), while in July 2010 females had significantly more lice than males ($P < 0.0001$, Figure 2). None of the remaining comparisons were significant ($P \geq 0.317$). Post-hoc comparisons for the sexes considered separately across different seasons showed that the louse abundance of males was significantly greater in October 2010 than in July 2010 and January 2011 ($P < 0.0001$ for both), and April 2011 than in January 2011 ($P < 0.0001$, Figure 2). None of the remaining comparisons for males were significant ($P \geq 0.317$). Females had significantly more lice in July 2010 than in April 2010 and October 2010 ($P < 0.0001$ for both), and October 2010 than January 2011 ($P < 0.0001$, Figure 2). None of the remaining comparisons for females were significant ($P \geq 0.422$).

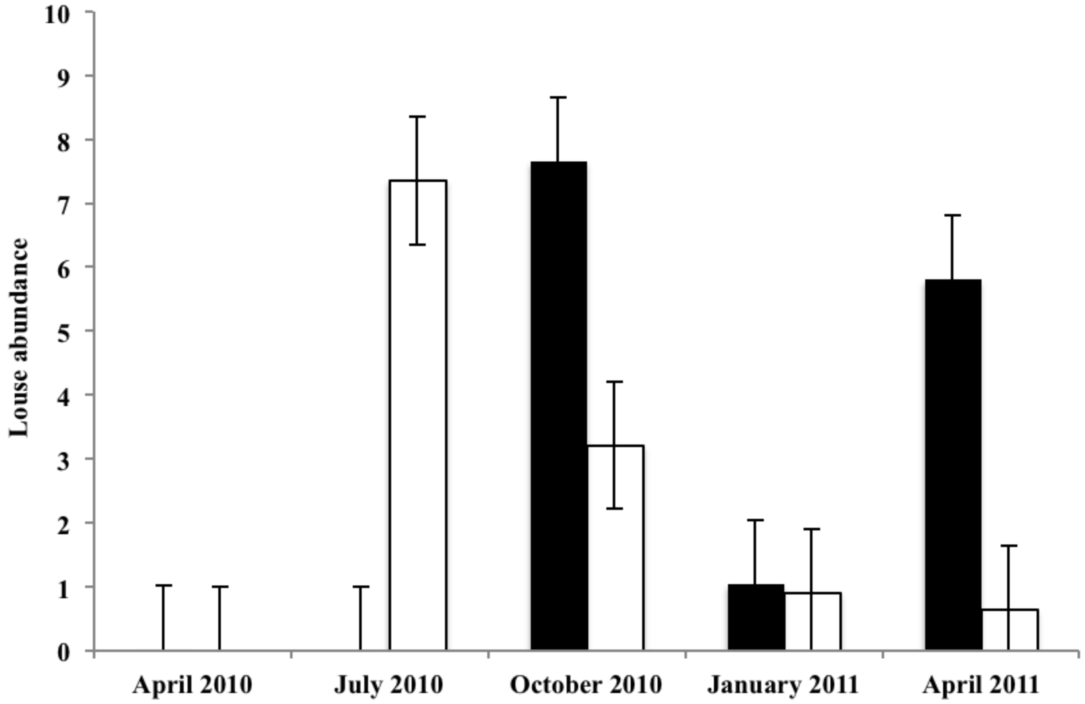


Figure 2 Variation in the abundance of lice with season and sex in *M. namaquensis*. Displayed are means ± SE, black bars represent males and white bars represent females.

Mites

The highest individual mite burden observed was 404 mites. Both total mite prevalence and abundance varied significantly with season (Table 3). Post-hoc analyses showed that mite prevalence was significantly lower in April 2010 (31%) than July 2010 (56%, LSD: P = 0.045), while it was significantly higher in January 2011 (95%) compared to October 2010 (47%, LSD: P = 0.0001) and April 2011 (66%, LSD: P = 0.034, Figure 3a). Neither sex nor the interaction between season and sex had a significant effect on mite prevalence (Table 4).

The mite abundance was significantly affected by season (Table. 4). It was significantly higher in January 2011 compared to October 2010 and April 2011 (LSD: P = 0.0001, Figure 3b). In addition, the abundance of mites was significantly greater in July 2010 than in April 2010 (LSD: P = 0.006) and October 2010 (LSD: P = 0.010, Figure 3b). Females had significantly more mites (20.38±6.35) than on males (11.21±2.79). The interaction between season and sex was not significant (Table 4).

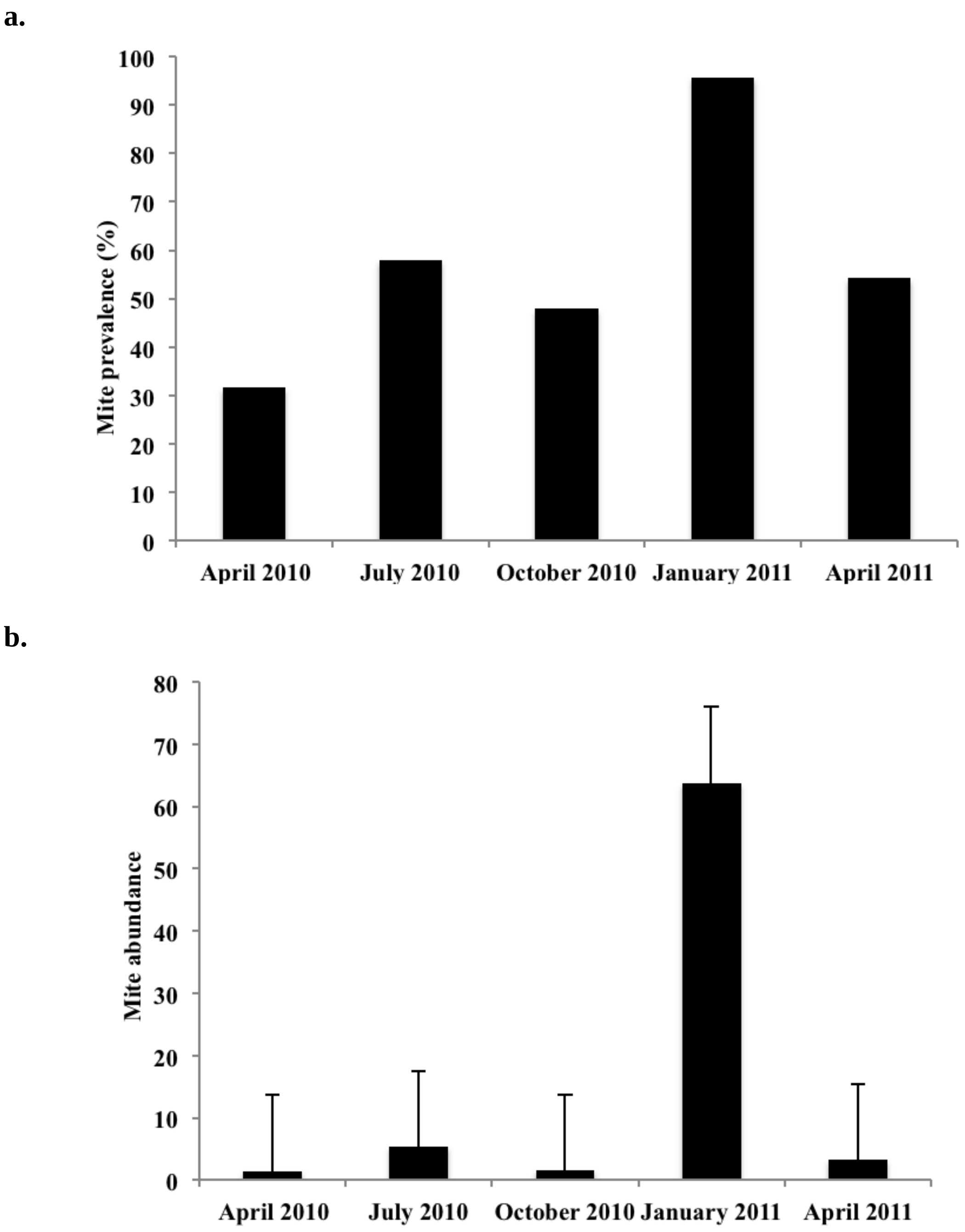


Figure 3 Seasonal **v**ariations in a. prevalence and b. abundance of mites on *M. namaquensis*. Displayed are means ± SE.

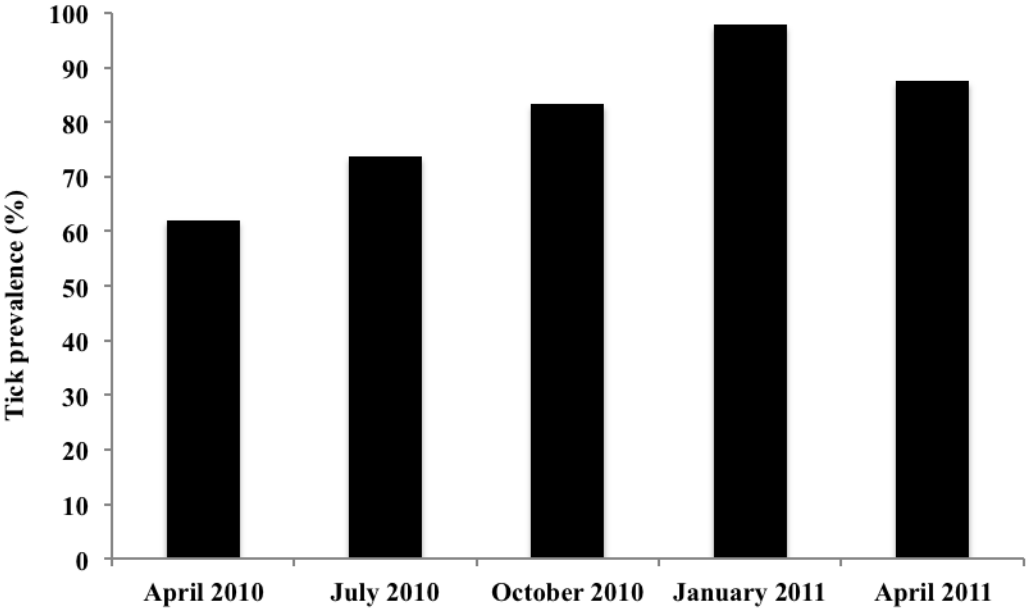
Ticks

A total of 78.2% of mice were infested with ticks. The tick prevalence varied significantly with season (Table 4). Post-hoc analyses revealed that the tick prevalence was significantly greater in January 2011 than in October 2010 (LSD: P = 0.004, Figure 4a), but not any other consecutive seasons (P ≥ 0.096). None of the other factors considered had any significant effect on the total tick prevalence (Table 4).

The tick abundance varied significantly with all factors considered (Table 4). Post-hoc analyses showed that tick numbers were significantly higher in January 2011 (21.34±3.23) compared to October 2010 (7.64±1.20) and April 2011 (6.38±1.50, LSD: P = 0.0001 for both) and significantly lower in July 2010 (3.20±0.85) compared to October 2010 (7.64±1.20, LSD: P = 0.003). Furthermore, in April 2010 (1.45±0.22), tick abundance was lower than in July 2010 (3.20±0.85, LSD: P = 0.047, Figure 4b). Tick numbers were significantly greater for males (6.69±0.78) when compared to females (4.45±0.60).

The interaction between season and sex was significant (Table 4). Post-hoc analyses showed that males sustained significantly higher tick abundance than females in April 2010 (LSD: P = 0.002, Figure 4b). None of the remaining comparisons between the sexes were significant (P ≥ 0.106). In addition, results of comparisons of the same sex across different seasons showed that males had higher tick numbers in January 2011 than in October 2010 (LSD: P = 0.01, Figure 4b). None of the pairwise comparisons for males between the remaining seasons were significant (P ≥ 0.064). Among females, tick abundance was significantly higher in January 2011 compared to October 2010 (LSD: P = 0.001) and April 2011 (LSD: P = 0.0001), and significantly lower in July 2010 compared to October 2010 (LSD: P = 0.016, Figure 4b). None of the remaining comparisons were significant (P ≥ 0.104).

a.



b.

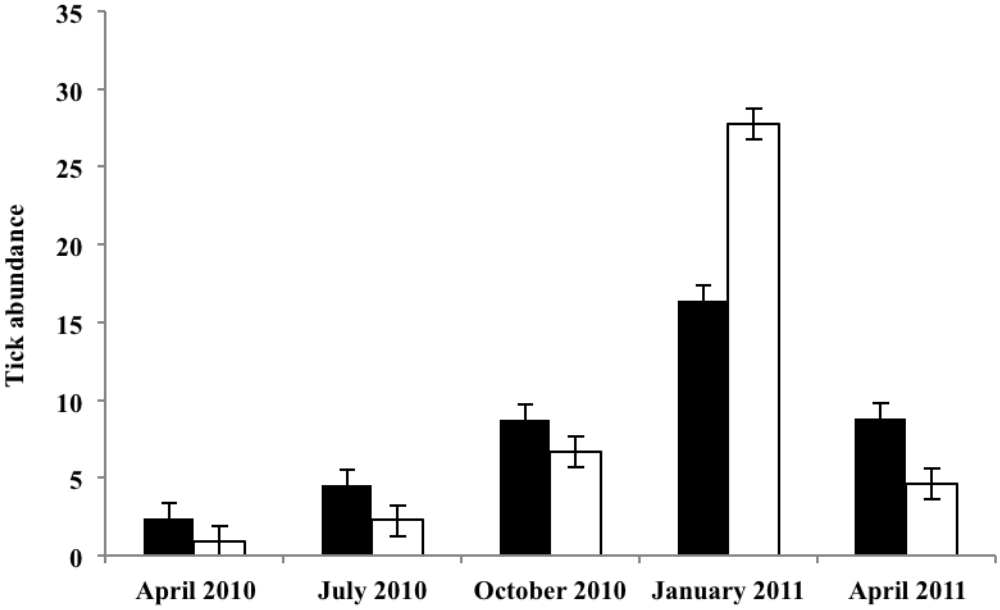


Figure 4 Seasonal variations in: a. prevalence; b. abundance of ticks on *M. namaquensis*. Displayed are means ± SE, black bars represent males and white bars represent females.

DISCUSSION

The current study aimed to assess the ectoparasite community harboured by *Micaelamys namaquensis* and identify the most important species. In addition, we investigated the impact of abiotic and biotic factors on ectoparasite distribution in the study species. Our study is the first long-term assessment of ectoparasite burdens of *M. namaquensis* from a single locality and provides novel data on the ectoparasite species found on the rock mouse in South Africa. We recorded a great diversity of ectoparasites, which consisted of 23 species from four taxa. A previous review by De Graaff (1981) lists an impressive numbers of ectoparasite species collected from *M. namaquensis* in the southern African sub-region including 34 species of fleas, two families of mites namely Laelaptidae and Trombiculidae, 13 species of tick species and no louse species. The present study found five species of fleas, six species and one family (Trombiculidae) of mites, as well as eight species of ticks. In comparison to De Graaff (1981) records, this diversity appears low. However, it is worth stressing that De Graaff's records were accumulated across the entire geographical distribution of the study species. Hence the number of ectoparasite species recorded in the present study is remarkably large since it stems from a single locality. The present study makes a valuable contribution in regards of reporting a new host as well as new locality records of three species of lice (*H. patersoni*, *H. aethomydis* and *P. praomydis*) and two species of mites (*A. rhabdomysi* and *L. roubaudi*).

The results of the current study show that fleas and ticks were the most prevalent ectoparasite taxa infesting *M. namaquensis* followed by mites. Five flea species were recorded of which *Xenopsylla brasiliensis* (Siphonaptera: Pulicidae), *Chiastopsylla godfreyi* (Siphonaptera: Chimaeropsyllidae) and *Epirimia aganippes* (Siphonaptera:

Chimaeropsyllidae) were the most prevalent. Although these three flea species were the most prevalent they only occur at low abundances. Most of the species of flea collected occur throughout South Africa (Segerman 1995). *Praomys natalensis* (Rodentia: Muridae), *Aethomys chrysophilus* (Rodentia: Muridae) and *M. namaquensis* (Rodentia: Muridae) are the main natural hosts of *X. brasiliensis* (Segerman 1995), which suggests that *X. brasiliensis* has a low host specificity, while *Chiastopsylla godfreyi* and *Epirimia aganippes* are reported to be host-specific for *M. namaquensis* (Segerman 1995; Braack *et al.* 1996; Mfune *et al.* 2013). In addition, two species of flea were also reported in the present study, namely *Demeillonia granti* (Siphonaptera: Chimaeropsyllidae) and *Dinopsyllus ellobius* **(**Siphonaptera**:** Hystrichopsyllidae). Both species occurred at low prevalence and abundance. This may be explained by the fact that *D. granti* is host-specific for sengis, while *D. ellobius* prefers hosts such as gerbils (*Tatera* spp., Rodentia: Muridae), multimammate mice (*P. natalensis*) and four striped mice (*Rhabdomys pumilio*, Rodentia: Muridae , Fourie *et al.* 1995; Segerman 1995).

Little is known about the louse species collected in the present study. Of the three louse species recorded *Hoplopleura* spp. were the most prevalent, but both species occurred at low abundance. The low louse abundance may be attributed to low host density in the study area, high temperatures and low humidity affecting the survival of lice (Cooke 1984; Cooke and Skewes 1988). In addition, lice are highly host specific and it is known for some louse species to infest two or more closely related host species (Durden and Musser 1994). All louse species collected in the present study have been previously reported for *M. namaquensis* and the closely related red veld rat (*Aethomys chrysophilus*, Ledger 1980; Braack *et al.* 1996), which suggests that these louse species may be specific for the genera *Aethomys* and *Micaelamys*.

A total of seven mite species were collected. By far the most prevalent and abundant mites recorded in the current study were Trombiculid larvae (chiggers). The identity of the chigger larvae collected in the present study is uncertain mainly because of lack of taxonomic expertise in South Africa. Trombiculid mites are a diverse group in the Acari and only the larval stages are parasitic on a wide range of small mammals and birds (Ewing 1944). Chiggers are known for their low host specificity and have been reported by other researchers, e.g. van der Mescht (2011) found high infestations of trombiculid larvae on *R. pumilio* in the Western Cape Province, South Africa. Matthee *et al* (2007) also reported chigger mites on *R. pumilio.* The second common species of mite (*A. rhabdomysi*) has been previously collected from *R. pumilio* in the Western Cape (Matthee *et al.* 2007; Matthee and Ueckermann 2008; van der Mescht 2011). The remaining mite species occurred at low abundance and have been reported before for a number of other rodent species (Zumpt 1961).

Several species of ticks have been collected in the present study, with exception of *R. distinctus* and *Haemaphysalis* spp. all these occurred at low prevalence and abundance. This is possibly due to the host preference of most of these ticks. With the exception of *R. warburtoni* and *R. arnoldi* most of the *Rhipicephalus* spp. collected are known to prefer hosts living in grassland habitats rather than rocky outcrops. Eastern rock sengis are also known to be the preferred host for *R. warburtoni, R. arnoldi* and *Ixodes* (Horak *et al.* 2005; Harrison *et al.* 2011, 2012; Fagir *et al.* 2015).

In the current study, fleas along with ticks were the most prevalent ectoparasite taxa, but fleas and lice occurred at low abundances in comparison to mites and ticks. This may be attributed to the low host densities in the study area as well as the host specificity for the fleas and lice compared to ticks and mites. With the exception of lice the prevalence of all parasite taxa showed seasonal variations in prevalence and abundance. Previous reports of seasonal patterns by Braack *et al.* (1996) recorded the highest infestation with *X. brasiliensis* on *Aethomys chrysophilus* during November and December. In the same study, high numbers of lice were recorded from May to July. This contrasts with our results, which indicated that louse abundance was significantly higher in October. However, the sample sizes in Braack *et al.* (1996) were low (Kruger National Park, Mpumalanga Province). Seasonal peaks in prevalence and abundance of ectoparasite species usually coincide with the wet season (from September to May, Benoit and Denlinger 2010). In the present study we recorded this peak for fleas in spring, while for mites and ticks it was in summer. Given that most fleas and mites (but not chiggers) spend part of their life cycle in the host's nest while ticks usually spend their time off the host in the surrounding environment, the difference between fleas and mites is unexpected. Chiggers are more environmentally dependent; they quest from the environment like ticks while the other species occur in the nest. This behaviour would then account for the patterns observed in the present study.

Seasonal variation in ectoparasite burdens may be linked to changes in environmental conditions (e.g. temperature and rainfall) as well as changes in host physiology and/or activities (Weil *et al.* 2006). Ectoparasite taxa differ with regards to their association with hosts, therefore they react differently to changes in abiotic and biotic conditions (Midgley *et al.* 2003). Thus, fleas and mites may be able to respond quickly to changes in the environment (i.e. rainfall) as well as changes in host immunity as a result of reproductive activity and the breeding season, which starts in September for *M. namaquensis* in the study area (Muteka *et al.* 2006a). Both flea prevalence and abundance exhibited seasonal variation; more fleas were collected in October compared to other seasons. Seasonal patterns in rodent flea abundances have been reported by many studies. For instance, van der Mescht *et al*. (2011) reported a high abundance of fleas on *R. pumilio* during winter in South Africa, while in Zimbabwe Zimba *et al.* (2011) reported high flea indices during the hot-dry season. In other African countries such as Kenya (Schwan 1986) and Tanzania (Makundi and Kilonzo 1994) seasonal patterns of prevalence and abundance of fleas on rodents have also been reported. Seasonal patterns in the distribution of fleas have been reported in other parts of the world as well e.g. Hawaii (Kartman and Lonergan 1955), Vietnam (Olson 1969), and Taiwan (Murrel and Cates, 1970) and the United States of America (Smith 1955; Layne 1963). Seasonal patterns in flea abundance were reported to be common in areas with pronounced seasonality in environmental conditions (e.g. temperature and rainfall, Makundi and Kilonzo 1994). In Tanzania a rapid decline in the abundance of fleas was reported in April and May and Makundi & Kilonzo (1994) suggested that this was due the heavy rains in February and March. A similar observation was reported in Vietnam and Sri Lanka (Hirst 1927; Olson 1969). Hirst (1927) stated that humid conditions and moisture on ground surface and burrows are very important factors affecting fleas breeding.

Very little is known regarding seasonal patterns in the populations of mites in South Africa. In southern Africa, many taxonomic studies have been conducted on mites harboured by rodents (e.g. Zumpt 1961; Horak *et al.* 1987; Braack *et al.* 1996), but few researchers have investigated seasonal variations in both their prevalence and abundance (Braack *et al.* 1996). The high prevalence and abundance of chiggers recorded in the present study may be explained by the fact that chiggers do not reside in the host burrow. Therefore, they might be more affected by climate conditions. Hence these seasonal patterns could be expected to be more similar to those of ticks than those of fleas.

With the exception of fleas, all other ectoparasite taxa showed sex-biased patterns. Louse and tick burdens were higher in males, while the numbers of mites were greater in females. The sex-biased patterns of ticks might be attributed to differences between host sexes as well as differences in parasite life cycles. For instance, the movement of males and their interactions with surrounding environment and multiple potential mates may expose males to greater numbers of ticks (Waterman 1995). In addition, different reproductive strategies of males and females may lead to several differences in their physiology, morphology and behaviour (Mooring *et al.* 1996; Rolff 2002). For instance, males tend to have larger body sizes and larger home ranges, which help males to find, compete and attract potential mating females (Deviche and Cortez 2005). However, these male-mating strategies may increase their vulnerability to infestations by parasites (i.e. ticks) (Moore and Wilson 2002; Rolff 2002). In contrast, sex-biased patterns of infestation may coincide with the reproductive investment (i.e. pregnancy and lactation) as well as the sedentary life-style of female rock mice that makes them better targets for chiggers that are not very mobile.

In conclusion, *Micaelamys namaquensis* harboured 23 species of ectoparasites from four taxa in the study area with fleas and ticks being the most important ones with regards to prevalence while mites were the most abundant. All ectoparasite taxa exhibited seasonal peaks in abundance coinciding with the warm and wet period of the year. In addition, sex-biased patterns of infestation were recorded for lice, mites and ticks. Results suggest that these patterns may be attributed to differences in abiotic factors, i.e. climatic conditions such as temperature and rainfall, and biotic factors, i.e.

host characteristics such as reproductive activity and differences in males’ and females’ behaviour.

REFERENCES

ALTIZER, S., DOBSON, A., HOSSEINI, P., HUDSON, P., PASCUAL, M. & ROHANI, P. 2006. Seasonality and the dynamics of infectious diseases. *Ecology letters,* 9**,** 467-484.

BATEMAN, A. J. 1948. Intra-sexual selection in Drosophila. *Heredity,* 2**,** 349-368.

BEAGLEY, K. W. & GOCKEL, C. M. 2003. Regulation of innate and adaptive immunity by the female sex hormones oestradiol and progesterone. *FEMS Immunology & Medical Microbiology,* 38**,** 13-22.

BENOIT, J. B. & DENLINGER, D. L. 2010. Meeting the challenges of on-host and off-host water balance in blood-feeding arthropods. *Journal of Insect Physiology,* 56**,** 1366-76.

BRAACK, L., HORAK, I. G., JORDAAN, L. C., SEGERMAN, J. & LOUW, J. 1996. The comparative host status of red veld rats (*Aethomys chrysophilus*) and bushveld gerbils (*Tatera leucogaster*) for epifaunal arthropods in the southern Kruger National Park, South Africa. *The Onderstepoort journal of veterinary research,* 63**,** 149-158.

BUFFENSTEIN, R. 1984. The importance of microhabitat in thermoregulation and thermal conductance in two Namib rodents—a crevice dweller, *Aethomys namaquensis*, and a burrow dweller, *Gerbillurus paeba*. *Journal of Thermal Biology,* 9**,** 235-241.

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***,** 575-583.

CHIMIMBA, C. 1998. A taxonomic synthesis of southern African *Aethomys* (Rodentia: Muridae) with a key to species. *Mammalia,* 62**,** 427-438.

CHIMIMBA, C. 2001. Infraspecific morphometric variation in *Aethomys namaquensis* (Rodentia: Muridae) from southern Africa. *Journal of Zoology,* 253**,** 191-210.

CHIMIMBA, C. & DIPPENAAR, N. 1994. Non-geographic variation in *Aethomys chrysophilus* (De Winton, 1897) and *A. namaquensis* (A. Smith, 1834) (Rodentia: Muridae) from Southern Africa. *South African Journal of Zoology,* 29**,** 107-107.

CHIMIMBA, C. T., DIPPENAAR, N. J. & ROBINSON, T. J. 1999. Morphometric and morphological delineation of southern African species of *Aethomys* (Rodentia: Muridae). *Biological Journal of the Linnean Society,* 67**,** 501-527.

COOKE, B. 1984. Factors Limiting the Distribution of the European Rabbit Flea, *Spilopsyllus Cuniculi* (Dale)(Siphonaptera), in Inland South Australia. *Australian Journal of Zoology,* 32**,** 493-506.

COOKE, B. & SKEWES, M. 1988. The Effects of Temperature and Humidity on the Survival and Development of the European Rabbit Flea, *Spilopsyllus-Cuniculi* (Dale). *Australian journal of zoology,* 36**,** 649-659.

DE GRAAFF, G. 1981. *The rodents of Southern Africa: notes on their identification, distribution, ecology, and taxonomy*, Butterworth-Heinemann, Durban, South Africa, 267p.

DEVICHE, P. & CORTEZ, L. 2005. Androgen control of immunocompetence in the male house finch, *Carpodacus mexicanus* Müller. *The Journal of experimental biology,* 208**,** 1287-1295.

DOBSON, A. & CARPER, R. 1992. Global warming and potential changes in host-parasite and disease-vector relationships.

DURDEN, L. A. & MUSSER, G. G. 1994. The mammalian hosts of the sucking lice (Anoplura) of the world: a host-parasite list. *Bulletin of the Society for Vector Ecology,* 19**,** 130-168.

EWING, H. 1944. The trombiculid mites (chigger mites) and their relation to disease. *The Journal of Parasitology,* 30**,** 339-365.

FAGIR, D. M. & EL-RAYAH, E.-A. 2009. Parasites of the Nile rat in rural and urban regions of Sudan. *Integrative Zoology,* 4**,** 179-187.

FAGIR, D. M., HORAK, I. G., UECKERMANN, E. A., BENNETT, N. C. & LUTERMANN, H. 2015. Ectoparasite diversity in the eastern rock sengis (*Elephantulus myurus*): the effect of seasonality and host sex. *African Zoology,* 50**,** 109-117.

FERRARI, N., CATTADORI, I. M., NESPEREIRA, J., RIZZOLI, A. & HUDSON, P. J. 2004. The role of host sex in parasite dynamics: field experiments on the yellownecked mouse *Apodemus flavicollis*. *Ecology Letters,* 7**,** 88-94.

FLEMING, P. & NICOLSON, S. 2004. Sex differences in space use, body condition and survivorship during the breeding season in the Namaqua rock mouse, *Aethomys namaquensis*. *African Zoology,* 39**,** 123-132.

FOLSTAD, I. & KARTER, A. J. 1992. Parasites, bright males, and the immunocompetence handicap. *American Naturalist***,** 603-622.

FOURIE, L., HORAK, I. & VAN DEN HEEVER, J. 1992. Relative host status of rock elephant shrews *Elephantulus myurus* and Namaqua rock mice *Aethomys namaquensis* for economically important ticks. *South African journal of zoology= Suid-Afrikaanse tydskrif vir dierkunde*.

FOURIE, L., TOIT, J. D., KOK, D. & HORAK, I. 1995. Arthropod parasites of elephantshrews, with particular reference to ticks. *Mammal Review,* 25**,** 31-37.

GILLETT, J. 1974. Direct and indirect influences of temperature on the transmission of parasites from insects to man. Symposium.

GREMILLION-SMITH, C. & WOOLF, A. 1988. Epizootiology of skunk rabies in North America. *Journal of wildlife diseases,* 24**,** 620-626.

HAMILTON, W. D. & ZUK, M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science,* 218**,** 384-387.

HARRISON, A. & BENNETT, N. C. 2012. The importance of the aggregation of ticks on small mammal hosts for the establishment and persistence of tick-borne pathogens: an investigation using the R(0) model. *Parasitology,* 139**,** 1605-13.

HARRISON, A., BOWN, K. J. & HORAK, I. G. 2011. Detection of *Anaplasma bovis* in an undescribed tick species collected from the eastern rock sengi *Elephantulus myurus*. *Journal of Parasitology,* 97**,** 1012-6.

HARRISON, A., ROBB, G. N., BENNETT, N. C. & HORAK, I. G. 2012. Differential feeding success of two paralysis-inducing ticks, *Rhipicephalus warburtoni* and *Ixodes rubicundus* on sympatric small mammal species, *Elephantulus myurus* and *Micaelamys namaquensis*. *Veterinary Parasitology,* 188**,** 346-54.

HARRISON, A., SCANTLEBURY, M. & MONTGOMERY, W. 2010. Body mass and sexbiased parasitism in wood mice *Apodemus sylvaticus*. *Oikos,* 119**,** 1099-1104.

HIRST, L. F. 1927. Rat-flea surveys and their use as a guide to plague preventive measures. *Transactions of the Royal Society of Tropical Medicine and Hygiene,* 21**,** 87-108.

HORAK, I., FOURIE, L. & BRAACK, L. 2005. Small mammals as hosts of immature ixodid ticks. *Onderstepoort Journal of Veterinary Research,* 72**,** p. 255-261.

HORAK, I. G., GUILLARMOD, A. J., MOOLMAN, L. & DE VOS, V. 1987. Parasites of domestic and wild animals in South Africa. XXII. Ixodid ticks on domestic dogs and on wild carnivores. *The Onderstepoort journal of veterinary research,* 54**,** 573-580.

KARTMAN, L. & LONERGAN, R. P. 1955. Wild-rodent-flea control in rural areas of an enzootic plague region in Hawaii: A preliminary investigation of methods. *Bulletin of the World Health Organization,* 13**,** 49.

KERLEY, G., KNIGHT, M. & ERASMUS, T. 1990. Small mammal microhabitat use and diet in the southern Kalahari, South Africa. *South African. Journal of Wildlife Research,* 20**,** 123-126.

KIFFNER, C., LÖDIGE, C., ALINGS, M., VOR, T. & RÜHE, F. 2011a. Bodymass or sexbiased tick parasitism in roe deer (*Capreolus capreolus*) A GAMLSS approach. *Medical and veterinary entomology,* 25**,** 39-45.

KIFFNER, C., VOR, T., HAGEDORN, P., NIEDRIG, M. & RUEHE, F. 2011b. Factors affecting patterns of tick parasitism on forest rodents in tick-borne encephalitis risk areas, Germany. *Parasitology Research,* 108**,** 323-335.

KIM, K. C. 2006. Blood-sucking lice (Anoplura) of small mammals: True parasites. *Micromammals and Macroparasites.* Springer.

KLEIN, S. 2000. The effects of hormones on sex differences in infection: from genes to behavior. *Neuroscience & Biobehavioral Reviews,* 24**,** 627-638.

KRANTZ, G. & WALTER, D. 2009. A manual of acarology, 3rd. Lubbock, TX: Texas Tech University Press.

KRASNOV, B. R. 2008. Life Cycles. *Functional and Evolutionary Ecology of Fleas: A Model for Ecological Parasitology.* UK: Cambridge

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.

KUTZ, S. J., JENKINS, E. J., VEITCH, A. M., DUCROCQ, J., POLLEY, L., ELKIN, B. & LAIR, S. 2009. The Arctic as a model for anticipating, preventing, and mitigating climate change impacts on host-parasite interactions. *Veterinary Parasitology,* 163**,** 217-228.

LARESCHI, M. & KRASNOV, B. R. 2010. Determinants of ectoparasite assemblage structure on rodent hosts from South American marshlands: the effect of host species, locality and season. *Medical and Veterinary Entomology,* 24**,** 284-292.

LASS, S. & EBERT, D. 2006. Apparent seasonality of parasite dynamics: analysis of cyclic prevalence patterns. *Proceedings of the Royal Society of London B: Biological Sciences,* 273**,** 199-206.

LAUDISOIT, A., LEIRS, H., MAKUNDI, R. & KRASNOV, B. R. 2009. Seasonal and habitat dependence of fleas parasitic on small mammals in Tanzania. *Integrative Zoolology,* 4**,** 196-212.

LAYNE, J. N. 1963. Study of the parasite of the Florida mouse, *Peromyscus floridanus*, in relation to host and environmental factors. *Tulane Studies in Zoology,* 11**,** 1-27.

LEDGER, J. A. 1980. *The arthropod parasites of vertebrates in Africa south of the Sahara. Volume IV. Phthiraptera (Insecta),* South African Institute for Medical Research.

LOGIUDICE, K., OSTFELD, R. S., SCHMIDT, K. A. & KEESING, F. 2003. The ecology of infectious disease: effects of host diversity and community composition on Lyme disease risk. *Proc Natl Acad Sci U S A,* 100**,** 567-71.

LUIS, A. D., DOUGLASS, R. J., MILLS, J. N. & BJØRNSTAD, O. N. 2010. The effect of seasonality, density and climate on the population dynamics of Montana deer mice, important reservoir hosts for Sin Nombre hantavirus. *Journal of Animal Ecology,* 79**,** 462-470.

MAKUNDI, R. & KILONZO, B. 1994. Seasonal dynamics of rodent fleas and its implication on control strategies in Lushoto district, northeastern Tanzania. *Journal of Applied Entomology,* 118**,** 165-171.

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

MARTIN, L. B., WEIL, Z. M. & NELSON, R. J. 2008. Seasonal changes in vertebrate immune activity: mediation by physiological trade-offs. *Philosophical Transactions of the Royal Society of London B: Biological Sciences,* 363**,** 321-39.

MATTHEE, S., HORAK, I. G., BEAUCOURNU, J.-C., DURDEN, L. A., UECKERMANN, E. A. & MCGEOCH, M. A. 2007. Epifaunistic arthropod parasites of the four-striped mouse, *Rhabdomys pumilio*, in the Western Cape Province, South Africa. *Journal of Parasitology,* 93**,** 47-59.

MATTHEE, S. & KRASNOV, B. R. 2009. Searching for generality in the patterns of parasite abundance and distribution: ectoparasites of a South African rodent, *Rhabdomys pumilio*. *International Journal of Parasitology,* 39**,** 781-8.

MATTHEE, S. & UECKERMANN, E. A. 2008. Ectoparasites of rodents in Southern Africa: a new species of *Androlaelaps* Berlese, 1903 (Acari: Parasitiformes: Laelapidae) from *Rhabdomys pumilio* (Sparrman) (Rodentia: Muridae). *Systematic Parasitology,* 70**,** 185-90.

MCCURDY, D. G., SHUTLER, D., MULLIE, A. & FORBES, M. R. 1998. Sex-biased parasitism of avian hosts: relations to blood parasite taxon and mating system. *Oikos***,** 303-312.

MEYER, J. & BRANDL, R. 2005. Nesting sites, nest density of *Aethomys namaquensis* (Rodentia, Muridae) in the Thornveld savannah of South Africa. *Mammalian Biology-Zeitschrift für Säugetierkunde,* 70**,** 126-129.

MFUNE, J., KANGOMBE, F. & EISEB, S. 2013. Host specificity, prevalence and intensity of infestation of fleas (Order Siphonaptera) of small mammals atselected sites in the city of Windhoek, Namibia.

MIDGLEY, G., HANNAH, L., MILLAR, D., THUILLER, W. & BOOTH, A. 2003. Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biological Conservation,* 112**,** 87-97.

MONADJEM, A. 1997. Stomach contents of 19 species of small mammals from Swaziland. *South African Journal of Zoology,* 32**,** 23-26.

MOORE, S. L. & WILSON, K. 2002. Parasites as a viability cost of sexual selection in natural populations of Mammals. *Science,* 297**,** 2015-2018.

MOORING, M. S., MCKENZIE, A. A. & HART, B. L. 1996. Role of sex and breeding status in grooming and total tick load of impala. *Behavioral Ecology and Sociobiology,* 39**,** 259-266.

MORAND, S., DE BELLOCQ, J. G., STANKO, M. & MIKLISOVÁ, D. 2004. Is sex-biased ectoparasitism related to sexual size dimorphism in small mammals of Central Europe? *Parasitology*, 129**,** 505-510.

MORAND, S. & KRASNOV, B. R. E. 2006. *Micromammals and Macroparasites: From Evolutionary Ecology to Management*, Tokyo: Springer-Verlag, Japan.

MURREL, K. & CATES, M. 1970. Seasonal periodicity of ectoparasites of *Rattus rattus* l'anezumi temminck from Taiwan. *Journal of medical entomology, 7(3), pp.367-370.*

MUTEKA, S., CHIMIMBA, C. & BENNETT, N. 2006b. Reproductive photoresponsiveness in *Aethomys ineptus* and *A. namaquensis* (Rodentia: Muridae) from southern Africa. *Journal of Zoology*, 268**,** 225-231.

MUTEKA, S. P., CHIMIMBA, C. T. & BENNETT, N. C. 2006a. Reproductive seasonality in *Aethomys namaquensis* (Rodentia: Muridae) from Southern Africa. *Journal of mammalogy*, 87**,** 67-74.

NEAL, B. 1990. Observations on the early post-natal growth and development of *Tatera leucogaster*, *Aethomys chrysophilus* and *A. namaquensis* from Zimbabwe, with a review of the pre-and post-natal growth and development of African muroid rodents. *Mammalia*, 54**,** 245-270.

OLSON, W. 1969. Rat-flea indices, rainfall, and plague outbreaks in Vietnam, with emphasis on the Pleiku area. *The American journal of tropical medicine and hygiene*, 18**,** 621-628.

POULIN, R. 1996. Sexual inequalities in helminth infections: a cost of being a male? *American Naturalist***,** 287-295.

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

RANDOLPH, S. E., ASOKLIENE, L., AVSIC-ZUPANC, T., BORMANE, A., BURRI, C., GERN, L., GOLOVLJOVA, I., HUBALEK, Z., KNAP, N., KONDRUSIK, M., KUPCA, A., PEJCOCH, M., VASILENKO, V. & ZYGUTIENE, M. 2008. Variable spikes in tick-borne encephalitis incidence in 2006 independent of variable tick abundance but related to weather. *Parasites and Vectors*, 1**,** 44.

RELTON, C., BENNETT, N. C. & MEDGER, K. 2013. The mode of ovulation in the Namaqua rock mouse, *Micaelamys namaquensis*. *Canadian Journal of Zoology*, 91**,** 829-836.

ROBERTS, M. L., BUCHANAN, K. L. & EVANS, M. 2004. Testing the immunocompetence handicap hypothesis: a review of the evidence. *Animal behaviour*, 68**,** 227-239.

ROLFF, J. 2002. Bateman's principle and immunity. *Proceedings of the Royal Society of London B: Biological Sciences*, 269**,** 867-872.

SCHALK, G. & FORBES, M. R. 1997. Male biases in parasitism of mammals: effects of study type, host age, and parasite taxon. *Oikos***,** 67-74.

SCHWAN, T. G. 1986. Seasonal abundance of fleas (Siphonaptera) on grassland rodents in Lake Nakuru National Park, Kenya, and potential for plague transmission. *Bulletin of entomological research*, 76**,** 633-648.

SEGERMAN, J. 1995. *Siphonaptera of southern Africa: handbook for the identification of fleas*, South African Institute for Medical Research.

SHINE, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology***,** 419-461.

SKINNER, J. & SMITHERS, R. 1990. The mammals of the South African subregion. *University of Pretoria, Pretoria*.

SKINNER, J. D. & CHIMIMBA, C. T. 2005. *The mammals of the southern African subregion. 3rd revised edition*.

SMITH, W. W. 1955. Relation of certain environmental factors to the abundance and distribution of house mouse ectoparasites in Mississippi. *Transactions of the American Microscopical Society***,** 170-175.

SONENSHINE, D. 1993. *Biology of ticks, vol. II*, Oxford University Press, New York, NY.

TRIVERS, R. 1972. Parental investment and sexual selection. *Sexual Selection & the Descent of Man, Aldine de Gruyter, New York***,** 136-179.

VAN DER MESCHT, L. 2011. *Ectoparasite assemblage of the four-striped mouse, Rhabdomys pumilio: the effect of anthropogenic habitat transformation and temporal variation.* University of Stellenbosch.

VINARSKI, M. V., KORALLO, N. P., KRASNOV, B. R., SHENBROT, G. I. & POULIN, R. 2007. Decay of similarity of gamasid mite assemblages parasitic on Palaearctic small mammals: geographic distance, host-species composition or environment. *Journal of Biogeography,* 34**,** 1691-1700.

WALKER, J. B., KEIRANS, J. E. & HORAK, I. G. 2000. *The genus Rhipicephalus (Acari, Ixodidae): a guide to the brown ticks of the world*, Cambridge University Press.

WATERMAN, J. M. 1995. The social organization of the Cape ground squirrel (*Xerus inauris*; Rodentia: Sciuridae). *Ethology,* 101**,** 130-147.

WEIL, Z. M., MARTIN II, L. B. & NELSON, R. J. 2006. Interactions among immune, endocrine, and behavioural response to infection. *Micromammals and Macroparasites.* Springer.

WOODALL, P. & MACKIE, R. 1987. Caecal size and function in the rock elephant shrew *Elephantulus myurus* (Insectivora, Macroscelididae) and the Namaqua rock mouse *Aethomys namaquensis* (Rodentia, Muridae). *Comparative Biochemistry and Physiology Part A: Physiology,* 87**,** 311-314.

YONAS, M., WELEGERIMA, K., LAUDISOIT, A., BAUER, H., GEBREHIWOT, K., DECKERS, S., KATAKWEBA, A., MAKUNDI, R. & LEIRS, H. 2011. Preliminary investigation on rodent–ectoparasite associations in the highlands of Tigray, Northern Ethiopia: implications for potential zoonoses. *Integrative zoology,* 6**,** 366-374.

ZIMBA, M., PFUKENYI, D., LOVERIDGE, J. & MUKARATIRWA, S. 2011b. Seasonal abundance of plague vector *Xenopsylla brasiliensis* from rodents captured in three habitat types of periurban suburbs of Harare, Zimbabwe. *Vector-Borne and Zoonotic Diseases,* 11**,** 1187-1192.

ZUK, M. 1990. Reproductive strategies and disease susceptibility: an evolutionary viewpoint. *Parasitology today,* 6**,** 231-233.

ZUK, M. & MCKEAN, K. A. 1996. Sex differences in parasite infections: patterns and processes. *International journal for parasitology,* 26**,** 1009-1024.

ZUMPT, F. 1961. The arthropod parasites of vertebrates in Africa south of the Sahara. Vol. I (Chelicerata). *Publications of the South African Institute for Medical Research. South African Institute for Medical Research, Johannesburg, South Africa,* 457.

CHAPTER THREE

ECTOPARASITE BURDENS IN THE EASTERN ROCK SENGI (*Elephantulus myurus*): THE EFFECT OF SEASONALITY AND HOST SEX[2]

SUMMARY

The eastern rock sengi (*Elephantulus myurus*) is an insectivore that is well known for its capacity to harbour large burdens of ticks of veterinary importance. The present study aimed to investigate all ectoparasite species infesting sengis from a previously unstudied locality (Ezemvelo Nature Reserve, Gauteng, South Africa) to record ectoparasite species diversity, prevalence and abundance, as well as the effects of season and host sex on ectoparasite loads. A total of 81 sengis were examined for the presence of ticks, mites, fleas and lice from April 2010 until April 2011. The parasite assemblage comprised 9 species of ticks, a single family of mites, one species of louse and two species of flea. The immature stages of ixodid ticks and mites (chiggers) were the most numerous ectoparasites recovered, lice and fleas were also collected from the sengis. The prevalence and abundance varied with season and host sex for the abundance of ticks (peak was in October 2010) and the mite (peak was in January 2011). Furthermore, there were significant differences in parasites' abundance within sex over season, which may be linked to the host behaviour as well as to the life cycles of the parasites.

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INTRODUCTION

Several studies have been conducted to record the parasite species of medical and economic importance infesting small mammal in South Africa (e.g. Fourie *et al.* 1992, 2005; Horak *et al.* 1993; Lutermann *et al.* 2012a, b). However, the majority of such studies have been conducted in anthropogenically-transformed habitats and there is still an essential need for basic research to investigate the factors that affect the prevalence and abundance of ectoparasite burdens on these hosts in their natural habitat.

In general, parasites show aggregated or over-dispersed patterns of distribution on their hosts (i.e. they parasitise a few host individuals, while most host individuals have only a few or no parasites, Boag *et al.* 2001; Krasnov *et al.* 2002, 2006). Parasite aggregation can be affected by a group of factors that can be divided into environmental (abiotic) and host/parasite (biotic) factors (Wilson *et al.* 2002; Poulin 2007). Parasite burdens often vary with season and abiotic factors such as temperature, rainfall and humidity can affect parasite burdens (Weil *et al.* 2006; Poulin 2007). Seasonal patterns in parasite loads are also linked to their relationship with their hosts and the specific environmental needs of parasites on and off their hosts. Ectoparasite taxa may respond differently to seasonal changes due to the fact that they differ in their host associations (Krasnov and Matthee 2010; Van der Mescht 2011). For instance, lice are closely associated with their hosts, they live, feed, reproduce and die on the host from generation to generation until the host dies (Kim 2006; Marshall 1981). Therefore seasonal patterns in louse burden can be expected to be weak. In contrast, seasonal variation in the number of ticks is expected to be stronger, as ticks spend only limited amount of time of their life on the host for blood meals and the remainder of the time in the vegetation (Lareschi 2006, 2010; Lareschi and Krasnov 2010; Matthee *et al.* 2010; Morand *et al.* 2004).

Seasonal heterogeneities in parasite distributions across their hosts can also be linked to differences between individual hosts in exposure and susceptibility to parasites due to host physiology and/or behaviour (Weil *et al.* 2006; Lutermann *et al.* 2012a). Seasonal variations in temperature, rainfall, energy intake and nutrients may influence the exposure and susceptibility of the host to parasitic infestation (Randolph 2004; Nelson *et al.* 2002; Altizer *et al.* 2006; Martin *et al.* 2008). For example, during cold periods when resources are limited and there is a high thermoregulatory demand, hosts may sustain more parasites (Nelson 2004). Alternatively, seasonal variance in climate variables may lead to an increase in parasite loads during warmer seasons when more energy and nutrients are available to hosts (Lutermann *et al.* 2012a).

Seasonal variation in ectoparasite burdens has been documented in a number of studies carried out in different localities in Africa (Makundi and Kilonzo 1994; Laudisoit *et al.* 2009). Several such studies have investigated the seasonal variation of different ectoparasite species infesting small mammals in South Africa (Horak *et al.* 1993; Louw *et al.* 1993, 1995; Braack *et al.* 1996; Anderson and Kok 2003; Fourie *et al.* 2002, 2005; Petney *et al.* 2004; Horak *et al.* 2005; Lutermann *et al.* 2012a, b). However, most of these studies focused on a single parasite taxon (ticks or fleas) and were mainly descriptive.

Sex-bias and in particular male-biased patterns have been recorded from many mammal species (Poulin 1996; Moore and Wilson 2002; Morand *et al.* 2004; Krasnov *et al.* 2005; Hillegass *et al.* 2008). This bias may be due to a number of factors such as morphology (e.g. large size), behaviour (e.g. sex-specific ranging patterns) and/or physiology (e.g. immune system and hormones) (Lutermann *et al.* 2012a). Males of many species tend to be larger than females and may therefore be able to sustain larger parasite burdens than females (Moore and Wilson 2002; Klein 2004; Morand *et al.* 2004; Krasnov *et al.* 2005). They also tend to roam over larger areas searching for possible mates, or defending their territories and are therefore more likely to be exposed to a greater number of parasites (Krasnov *et al.* 2005; Scantlebury *et al.* 2010). However, very few studies have been carried out to investigate and compare sex-biased patterns of parasite species (belonging to the same or different higher taxa) infesting the same host species (Lareschi 2006; Presley and Willig 2008).

Rodents and other sympatric insectivore species carry different species of fleas, lice, mites as well as immature stages of tick species (Harrison *et al.* 2012). The role of rodents as hosts for ectoparasites and carriers of pathogens is well known and documented throughout the world (Sonenshine 1991; Norval 1979; Randolph *et al.* 1999; Bown *et al.* 2003; Karbowiak 2004). However, the role of sympatric insectivore species in harbouring ectoparasites, in particular immature stages of tick species, is still unclear (Harrison *et al.* 2011, 2012). Several studies from Europe (Bown *et al.* 2011) as well as Africa, particularly South Africa (MacLeod 1970; Colbo and MacLeod 1976; Fourie *et al.* 1992, 2005; Horak *et al.* 2011; Harrison *et al.* 2011), have reported tick infestation in both rodents and small insectivores such as shrews (Order Eulipotyphla) and sengis or elephant shrews (Order Macroscelidea). These studies indicated that sengis are highly infested by large numbers of immature stages of different species of tick belonging to 27 species within six genera, but also by other ectoparasite taxa such as fleas and mites (Fourie *et al.* 1992, 1995, 2005; Beaucournu *et al.* 2003; Horak *et al.* 2011; Harrison *et al.* 2011). In addition, sengi tick burden may be 100 times that of the sympatric rodents (Fourie *et al*. 1992; Harrison *et al.* 2012).

The eastern rock sengi (*Elephantulus myurus*) belongs to the order Macroscelidea, an ancient monophyletic group comprising 19 species within four genera that are widely distributed throughout the southern African sub-region, from Mozambique north of the Zambezi River throughout the southern and eastern parts of Zimbabwe, eastern Botswana, wide parts of northeast South Africa and western Swaziland (Skinner and Chimimba 2005, Dumbacher *et al.* 2012, 2014). Eastern rock sengis are restricted to rocky habitats, monogamous, terrestrial and insectivorous (Skinner and Chimimba 2005). Their breeding season occurs during the warm, wet summer (September to March) (Medger *et al.* 2012). Eastern rock sengis are hosts to a variety of macroparasites, particularly the immature stages of ixodid ticks (Fourie *et al.* 1995; Harrison *et al.* 2011). In comparison, the knowledge of other ectoparasite taxa harboured by eastern rock sengis is largely unknown (Fourie *et al.* 1992, 1995, 2005; Horak *et al.* 2011; Harrison *et al.* 2013).

The present study aimed to:

- Determine all species of ectoparasites infesting eastern rock sengis over an extended period.
- Identify the parasite species most likely to affect host population dynamics (either because of their prevalence or abundance or both).
- Assess the patterns of prevalence and abundance of ectoparasite species infesting eastern rock sengis with regards to season and host sex.

MATERIALS AND METHODS

Study area and capture plots

Eastern rock sengis were sampled at Telperion/Ezemvelo Nature Reserve (25° 41’ S, 28° 56’ E) located on the border between Gauteng and Mpumalanga Provinces, South Africa. The reserve is approximately 11000 ha in size and the vegetation cover is described as highveld grassland and savannah with large rocky outcrops that occur throughout the reserve (Swanepoel 2006). Sampling took place five times from April 2010 until May 2011 to cover all seasons (April/May 2010, July/August 2010, October/November 2010; January/February 2011, April/May 2011). Sixteen plots comprising eight rocky outcrops and eight grasslands were selected for the study. However, this procedure was changed during the first trip (April 2010) where sampling took place from only five rocky outcrops and one grassland plot. In addition, during the last trip (April 2011) sengis were only sampled from rocky outcrops (8 plots).

Host species and trapping protocol

Animals were collected using 72 Live-Sherman traps (H. B. Sherman Traps, Inc., Tallahassee, Florida) baited with a mixture of peanut butter and oats to attract animals. Traps were set in each plot in four parallel straight lines approximately 10 m apart and each line consisted of 18 traps with10 m between traps. Traps were set overnight for four consecutive nights. They were opened in the late afternoon (around 18:00), checked early each morning (around 05:00) and kept closed during the day. To limit trap related deaths as a result of environmental exposure, bedding was provided in the traps during winter.

Laboratory procedure

Captured animals were transferred to a field laboratory and processed immediately. Animals were removed from the traps using Ziplock® bags and then restrained by hand and the sex of each individual was recorded. Each individual was checked carefully for ectoparasites with particular attention to the ear margins, legs and the base of the tail where ticks and mites aggregated (D. M. Fagir, personal observation). The rest of the body was searched by back-combing the fur for the presence of fleas and lice. Ectoparasites were removed using fine tweezers and stored in 70% ethanol for later counting of parasites and their individual identification to the species level. All sengis captured were marked with ear notches and subsequently released at their site of capture. For the current study only the first capture of an individual during a capture period was included. Ticks were identified to species whenever possible by Ivan G. Horak using descriptions provided by Walker *et al.* (2000). Mites were identified to family level by Eddie A. Ueckermann using Krantz and Walter (2009). Lice and fleas were identified by Dina M. Fagir with the help of an expert taxonomist using the morphological key of Ledger (1980) and Segerman (1995), respectively. For microscopic examination, mites, lice and fleas were mounted following the techniques described in Krantz and Walter (2009), Ledger (1980) and Segerman (1995), respectively. The developmental stages were recorded for all parasite species encountered and parasites were counted.

Data analysis

Following Bush *et al.* (1997), parasite prevalence was defined as the number of hosts infested with one or more individuals of a particular parasite species divided by the total number of hosts examined for that parasite species and mean abundance was the total number of parasites of a particular species infesting each host divided by the total number of hosts sampled. None of the data were normally distributed (Kolmogorov-Smirnov10 test: $P < 0.001$). Therefore, the effect of seasonality, i.e. April 2010 (autumn), July 2010 (winter), October 2010 (spring), January 2011 (summer), April 2011 (autumn) on variation of prevalence and abundance of the different ectoparasite species was investigated using generalized linear models (GLMs). A model with a binomial distribution with logit-link function was selected for prevalence data while a negative-binomial distribution log-link function was chosen for abundance data. Data were analysed at higher taxon level as well as at species level. Only the most prevalent parasite species (>15%) were analysed in depth while for the remainder only descriptive statistics are provided. Post-hoc analyses were done with pairwise comparisons using the least significant difference (LSD). In order to avoid excessive post-hoc results only comparisons between consecutive trips for season and only either between consecutive months separately for each sex or between the sexes during the same month were reported. Different developmental stages of parasite species (i.e. larva, nymph, male, female) were pooled for analysis. All statistical analyses were conducted in IBM SPSS version 21 (IBM SPSS Statistics 21.Ink 2013).

RESULTS

A total of 81 individual sengis of which 44 were males (54.3%) and 37 females (45.7%) were examined for ectoparasites. The numbers of hosts caught per trip are displayed in Table 1. Immature ticks (98.8%) represented by far the largest proportion of ectoparasites recovered, followed by mites, lice and fleas (Table 2).

Table 1 Summary of host individuals caught per trip.

Season	**Males**	**Females**
April 2010	13	10
July 2010	9	2
October 2010	7	10
January 2011	8	8
April 2011	7	7

Table 2 Summary of the parasite groups found on eastern rock sengis and their infestation parameters.

Taxon	**Total no. of parasites**	**Prevalence (%)**	**Mean abundance (±SE)**
Ticks	25497	98.8	314.78 (±24)
Mites	11584	63.0	143.01 (±33.02)
Lice	62	9.9	0.77 (±0.41)
Fleas	32	8.6	0.41 (±0.21)

Ticks

A total of 11 species of ixodid tick, representing four genera (*Rhipicephalus*, *Rhipicentor*, *Haemaphysalis* and *Ixodes*) were collected (Table 3). Large numbers of larvae and nymphs of ticks belonging to the *Rhipicephalus pravus* group (Walker *et al.* 2000) were collected. Some engorged nymphs from this group were allowed to moult and gave rise to the adults of two tick species namely: *Rhipicephalus warburtoni* and *Rhipicephalus arnoldi*. The larvae and nymphs of these two species so closely resemble each other that it would have required individual specimens to be mounted on glass slides and examined under a light microscope to determine their separate identities, a procedure which was not practical considering the thousands of immature ticks involved (see results) and that many of these were semi-engorged or engorged. We have therefore chosen to pool these immature ticks as *R. warburtoni/ arnoldi*. In addition, the larvae and nymphs of two *Haemaphysalis* species (*Haemaphysalis elliptica* and *Haemaphysalis* sp.) were also present. As both of these species belong to the subgenus *Rhipistoma* we have chosen to identify them as *Haemaphysalis* (*Rhipistoma*) spp. The same procedure has been followed with the larvae and nymphs of the two *Ixodes* species (*Ixodes cavipalpus* and *Ixodes* sp.) that were recovered.

The total tick prevalence did not vary significantly with season or host sex, nor was the interaction between season and sex significant (Table 4). In contrast, tick abundance varied significantly with season (Table 4, Figure 1). Post-hoc analyses showed that overall tick abundance was significantly higher in spring 2010 than in winter 2010 (LSD: $P = 0.018$) and summer 2011 (LSD: $P = 0.016$). Tick abundance was higher in autumn 2010 than in winter 2010, but not significantly so (LSD: $P = 0.056$). None of the remaining comparisons were significant ($P \geq 0.113$). Host sex and interaction between season and sex had no significant effect on total tick abundance (Table 4).

Table 3 Summary of the ectoparasite species found and their infection parameters in eastern rock sengis.

	Species	**Total no. of larvae**	**Total no. of nymphs**	**Total no. of males**	**Total no. of females**	**Total numbers**	**Total prevalence (%)**	**Total mean abundance (±SE)**
Ticks	*Rhipicephalus appendiculatus*	635	19	-	-	654	2.5%	8.07 (±8.06)
	Rhipicephalus warburtoni/R. arnoldi	21896	2325	-	-	24309	97.5%	300.11 **(**± 23.82**)**
	Rhipicephalus arnoldi[*]	0	23	-	-	23	4.9%	0.28 **(**± 0.17**)**
	Rhipicephalus warburtoni[*]	0	42	-	-	42	4.9%	0.52 **(**± 0.30**)**
	Rhipicephalus distinctus	29	25	-	-	54	27.2%	0.67 **(**± 0.25**)**
	Rhipicephalus decoloratus	2	0	-	-	2	2.5%	0.02 **(**± 0.01**)**
	Rhipicephalus evertsi evertsi	7	0	-	-	7	6.2%	0.09 **(**± 0.04**)**
	Rhipicentor spp.	2	31	-	-	33	17.3%	0.41 **(**± 0.13**)**
	Haemaphysalis (*Rhipistoma*) spp.	9	2	-	-	11	9.9%	0.14 **(**± 0.05**)**
	Ixodes spp.	435	14	-	-	449	44.4%	5.54 **(**± 1.91**)**
Mites	Trombiculidae larvae (Chiggers)	11584	-	-	-	11584	63.0%	143.01 (±33.01)
Lice	*Neolinognathus elephantuli*	-	-	21	41	62	9.9%	0.77 (±0.41)
Fleas	*Xenopsylla brasiliensis*	-	-	1	2	3	3.7%	0.04 (±0.02)
	Demeillonia granti	-	-	5	24	29	3.7%	0.36 (±0.21)

[*] Engorged nymphs were allowed to moult and gave rise to the adult ticks.

Table 4 Results of the GLMs for total tick and mite prevalence and abundance of eastern rock sengis.

Parasite groups	**Factors**	**Prevalence**			**Abundance**		
		Wald χ^2	**df**	**P**	**Wald χ^2**	**df**	**P**
Ticks	**Season**	-	-	-	11.259	4	0.024*
	Sex	-	-	-	1.100	1	0.294
	Season x sex	-	-	-	0.989	4	0.911
Mites	**Season**	6.035	4	0.197	215.067	4	0.000*
	Sex	0.000	1	1.000	2.438	1	0.118
	Season x sex	0.334	4	0.988	16.284	4	0.003*

* indicates significant results.

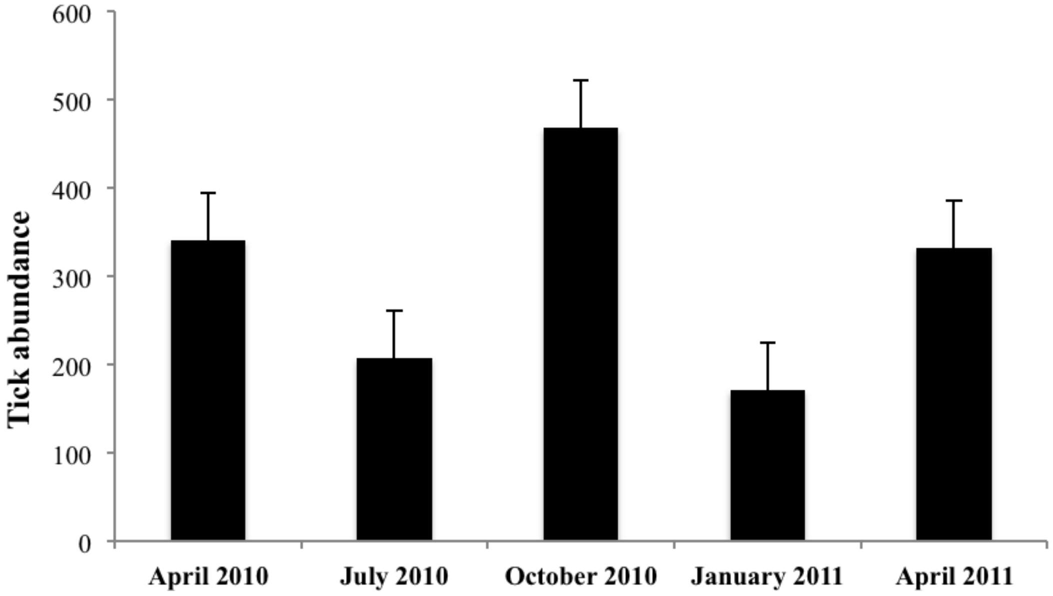

Figure 1 Seasonal variation in overall tick abundance in eastern rock sengi (*Elephantulus myurus*). Displayed are means ± standard error (SE).

The *R. warburtoni/ arnoldi* grouping was the most prevalent and abundant tick species, followed by *Ixodes* spp. and *R. distinctus* as the second and third most prevalent ticks on sengis (>15% therefore their prevalence and abundance were investigated in-depth analyses, Table 4).

R. warburtoni/ arnoldi had a prevalence of 97.5% and this high prevalence precluded any meaningful statistical analysis. In contrast, the abundance of *R. warburtoni/ arnoldi* varied significantly with season (Table 5, Figure 2). Post-hoc analyses revealed that it was significantly greater in spring 2010 compared to winter 2010 (LSD: $P = 0.017$) and summer 2011 (LSD: $P = 0.012$). None of the other pairwise comparisons were significant ($P \geq 0.053$). Neither host sex nor the interaction between season and sex had a significant effect on the *R. warburtoni/ arnoldi* abundance (Table 5).

The prevalence of *Ixodes* spp. varied significantly with season (Table 5 and Figure 3). Post-hoc tests showed that the prevalence of *Ixodes* spp. was significantly greater in autumn 2010 than in winter 2010 (LSD: $P = 0.026$). In addition, the *Ixodes* spp. prevalence was significantly lower in spring 2010 compared to summer (LSD: $P = 0.001$, Figure 3). None of the remaining comparisons between consecutive months were significant ($P \geq 0.338$). Similarly, neither host sex nor the interaction between season and sex was significant (Table 5). The abundance of *Ixodes* spp. varied significantly with season (Table 5, Figure 4). Post-hoc results showed that the abundance of *Ixodes* spp. was significantly higher in autumn 2010 compared to winter 2010 (LSD: $P < 0.0001$). In addition, *Ixodes* spp. abundance was significantly lower in spring 2010 than in summer 2011 (LSD: $P < 0.0001$, Figure 4). No other comparisons between successive seasons were significant ($P \geq 0.077$). The interaction between season and sex was significant (Table 5, Figure 4). Post-hoc results showed that females carried a significantly greater abundance of *Ixodes* spp. in autumn 2010 compared to winter

(LSD: P = 0.006) and in summer compared to autumn 2011 (LSD: P = 0.030, Figure 4). In addition, the abundance of *Ixodes* spp. in females increased significantly from spring to summer (LSD: P = 0.014). Among males *Ixodes* spp. abundance decreased significantly from autumn 2010 to winter (LSD: P = 0.012), but increased significantly from spring to summer (LSD: P = 0.007, Figure 4). None of the remaining comparisons between consecutive months was significant ($P \geq 0.340$) for males nor were any of the comparisons between the sexes in a season significant ($P \geq 0.066$).

None of the factors considered had a significant effect on the prevalence of *R. distinctus* (Table 5). Similarly, the abundance of *R. distinctus* did not vary significantly with season, nor was the interaction between sex and season significant. In contrast, the abundance of *R. distinctus* was significantly greater for females (1.11±3.26) than for males (0.30±0.59, Table 5). Neither the prevalence nor the abundance of *Rhipicentor* spp. was significantly affected by any of the factors considered (Table 5).

Table 5 Results of GLMs for the prevalence and abundance of ectoparasite species.

Parasites	Factors	Prevalence			Abundance		
		Wald χ^2	**df**	**P**	**Wald χ^2**	**df**	**P**
Rhipicephalus warburtoni/ arnoldi	**Season**	-	-	-	12.152	4	0.016*
	Sex	-	-	-	0.795	1	0.372
	Season x sex	-	-	-	1.013	4	0.908
***Ixodes* spp.**	**Season**	11.927	4	0.018*	65.366	4	0.000*
	Sex	0.000	1	1.000	0.824	1	0.364
	Season x sex	1.470	4	0.832	8.789	3	0.032*
Rhipicephalus distinctus	**Season**	4.451	4	0.348	7.162	3	0.067
	Sex	0.000	1	1.000	6.662	1	0.01*
	Season x sex	2.466	4	0.651	0.757	3	0.860
***Rhipicentor* spp.**	**Season**	0.194	4	0.996	4.542	3	0.209
	Sex	0.000	1	1.000	0.573	1	0.449
	Season x sex	0.546	4	0.969	1.251	1	0.263

*indicates significant results.

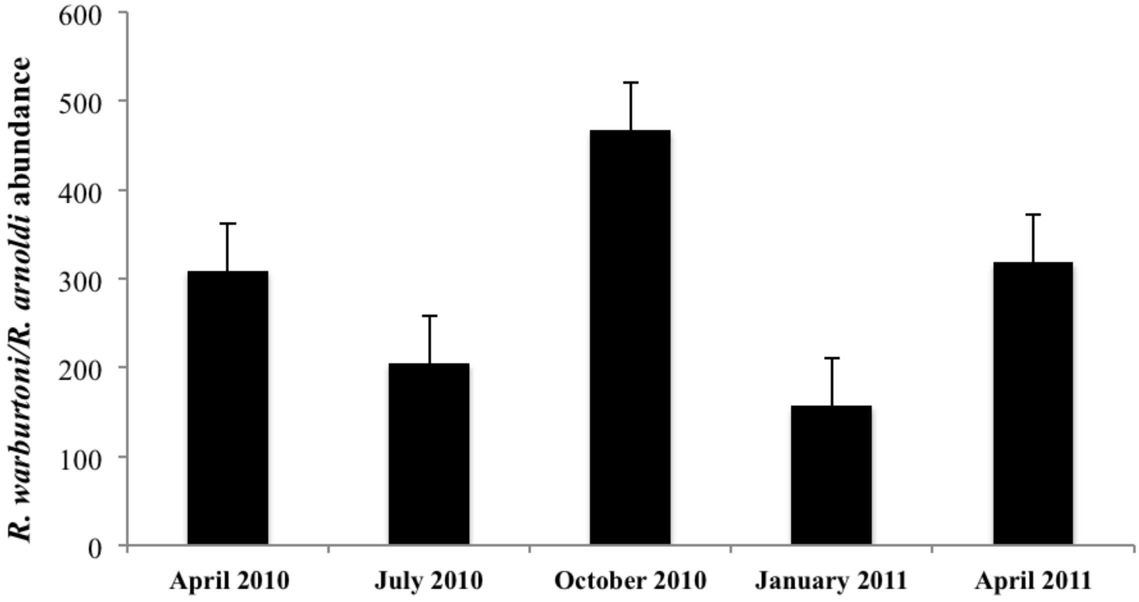

Figure 2 Seasonal variation of abundance of *Rhipicephalus warburtoni/ arnoldi* on eastern rock sengis. Displayed are means ± SE.

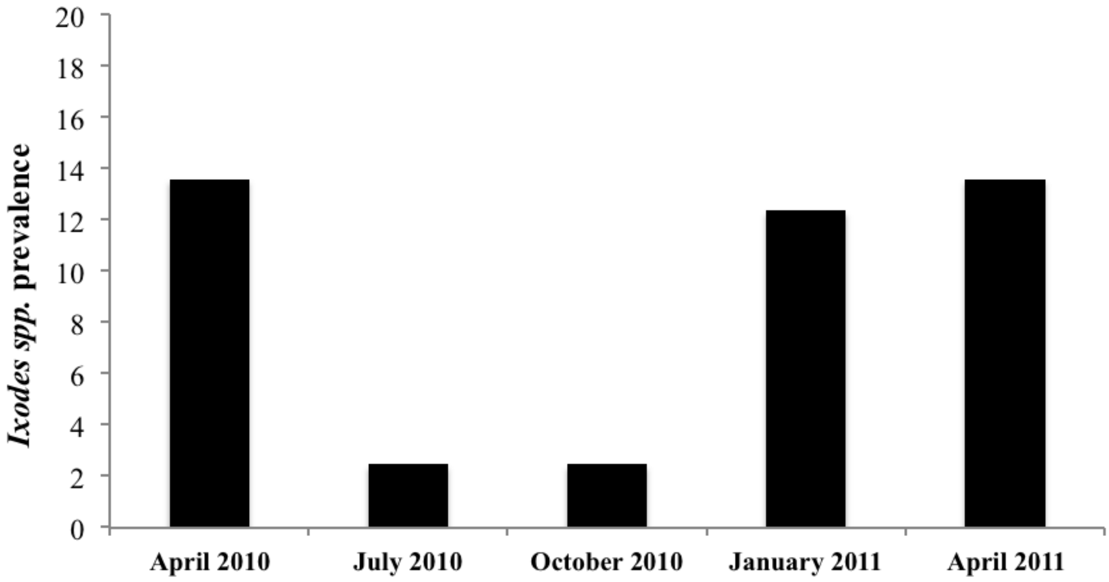

Figure 3 Seasonal variations in the prevalence of *Ixodes* spp. of *E. myurus*.

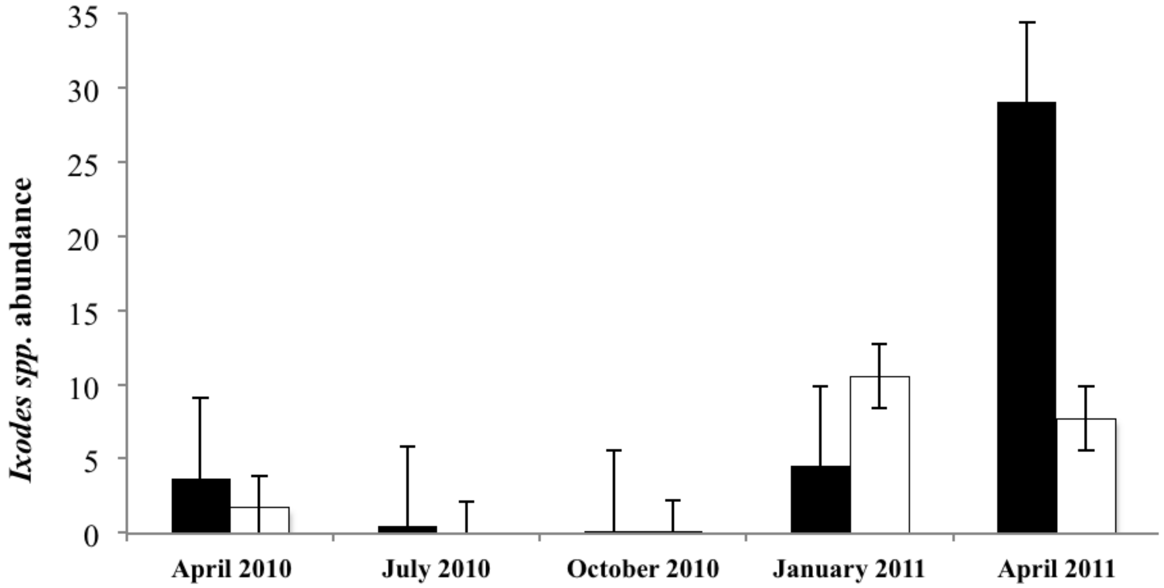

Figure 4 Variation in abundance of *Ixodes* spp. with season and host sex. Displayed are means ± SE, black bars represent males and white bars represent females.

Mites

Only the larval stage (chiggers) of one family of mites (Trombiculidae) was recovered. The prevalence of chiggers did not vary significantly with any of the factors considered (Table 4). In contrast, chigger abundance varied significantly with season. Post-hoc analyses showed that chigger abundance was significantly higher in autumn 2010 than in winter 2010 and significantly lower in spring 2010 compared to summer 2011 ($P < 0.0001$ for both, Figure 5). In addition, the chigger abundance was significantly greater in summer 2011 compared to autumn 2011 (LSD: $P = 0.023$). Host sex had no significant effect on the abundance of chiggers (Table 4). However, the interaction between season and sex was significant (Table 4, Figure 5). Post-hoc results showed that for males the chigger abundance was significantly greater in autumn 2010 than in winter (LSD: $P = 0.002$) and in summer compared to spring (LSD: $P = 0.005$, Figure 5).

Females showed a significant decrease in chigger abundance from winter to spring (LSD: $P = 0.003$) and from summer to autumn 2011 (LSD: $P = 0.036$, Figure 5). In contrast, their chigger abundance increased significantly from spring to summer (LSD: $P = 0.005$, Figure 5). The abundance of chiggers was significantly lower for females compared to males in winter (LSD: $P = 0.004$). None of the remaining pairwise comparisons was significant ($P \geq 0.055$).

Lice

A total of 62 lice were collected and identified as *Neolinognathus elephantuli* (Table 4). Only eight animals (9.9%) were infested with lice and the highest individual burden consisted of 29 lice.

Fleas

A total of 32 fleas belonging to two flea species namely, *Xenopsylla brasiliensis* (n=3) and *Demeillonia granti* (n=29) were found on sengis. Seven animals (8.6%) were infested and the highest individual burden consisted of 11 fleas (Table 3).

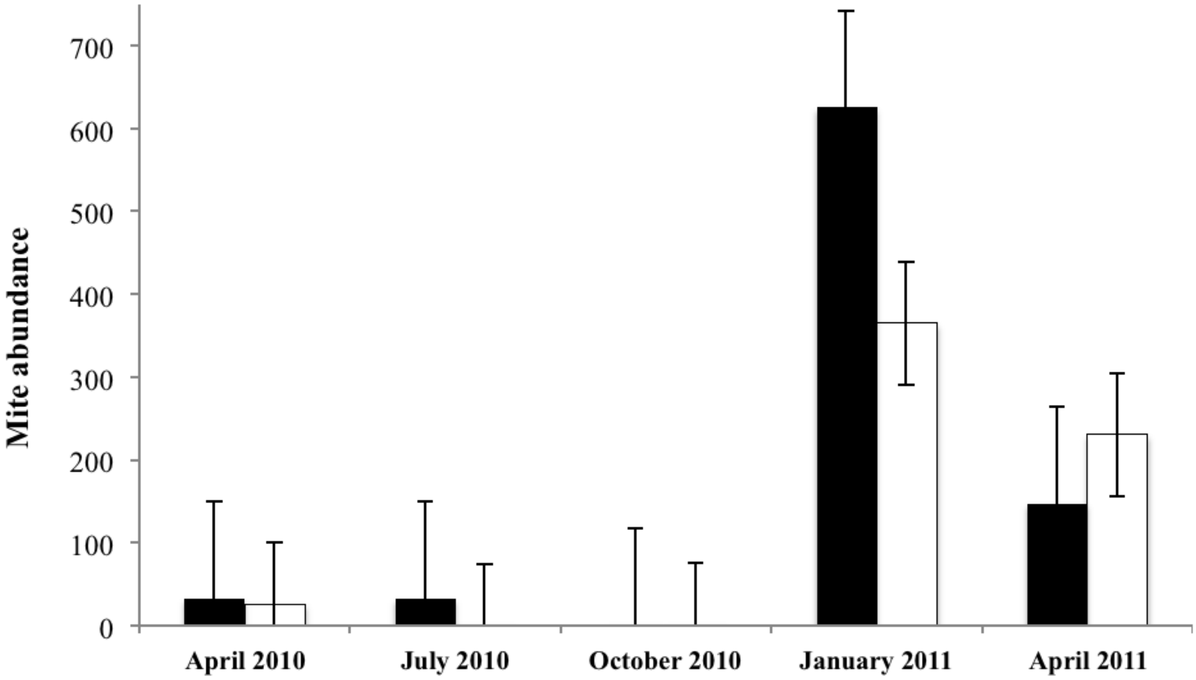

Figure 5 Variation in abundance of chiggers with season and sex in eastern rock sengi (*Elephantulus myurus*). Displayed are means ± SE, black bars represent males and white bars represent females.

DISCUSSION

The present study recorded a high ectoparasite species diversity on the eastern rock sengi (*Elephantulus myurus*). Most of the tick species recovered in the present study have been reported previously by other researchers in South Africa (e.g. Fourie *et al.* 1992, 1995, 2005; Horak *et al.* 2011; Harrison *et al.* 2011, 2012). In addition, Fourie *et al.* (1995) listed a total of two non-tick parasites for the study species, namely: *Ornithonyssus capensis* (Acari: Laelaptidae) and *Neolinognathus elephantuli* (Anoplura: Neolinogathidae). Beaucournu *et al.* (2003) report two flea species (*Demeillonia granti* and *Ctenocephalidae* sp.) for sengis. However, the present study makes a valuable contribution with regards to new parasite records (chiggers) and a new locality record was reported for one species of tick (*R. appendiculatus*).

The eleven tick species recovered from the sengis represent the largest number of species recovered from rock sengis from a single locality. Prior to this, eight tick species had been recovered from Cape rock sengis (*Elephantulus edwardii*) on a farm in the Western Cape Province (Fourie *et al.* 2005). In the present study, the immature stages of *R. warburtoni, R. arnoldi, R. distinctus, Ixodes* spp. and *Rhipicentor* spp. were present. The *R. warburtoni/arnoldi* group were the most prevalent (97.5%) and abundant (300.11±23.827) ticks, while *Ixodes* spp., *R. distinctus* and *Rhipicentor* spp. were also prevalent, however they occurred at low abundances. This is in agreement with the findings of Harrison *et al.* (2011, 2012) and Lutermann *et al.* (2012a, b) from a sengi population in the Limpopo Province 359.9 km north of the study population.

Mites represented by larvae of one family (Trombiculidae) were found on large numbers (63%) of sengis in the present study. The numbers and respective species identity were not determined due to the lack of taxonomic expertise in South Africa.

The Trombiculidae (chiggers) is a large worldwide family; larvae of this family are parasitic, while other life stages (nymphs and adults) are free living in the soil (Baker 1999). Chigger mites (larva stage) are known to cause skin eruptions and itching (Ewing 1944) as well as transmitting scrub typhus (Traub and Wisseman 1974; Roberts and Janovy 2000; Wenge *et al.* 2009). Trombiculidae larvae are distributed worldwide parasitizing a wide range of animals such as cats, dogs, rodents, birds as well as human beings (Baker 1999). Chigger mites have been previously reported from other small rodents in South Africa such as *R. pumilio* and *Otomys irroratus* (Matthee *et al.* 2010).

Only one species of louse was found in the present study, *Neolinognathus elephantuli* (Family: Neolinogathidae). According to Ledger (1980) it is host specific for sengis. Little is known about the geographical distribution, biology and breeding cycle of this louse species. Fourie *et al.* (1995) reported *N. elephantuli* for a number of other sengi e.g. *Elephantulus brachyrhynchus* and *E. myurus* which suggest that this louse might be specific for the sengis suggesting that its distributional range may be largely limited by sengi distribution.

Two species of flea were reported in this study, *Xenopsylla brasiliensis* and *Demeillonia granti.* Little literature is available on geographical distribution and breeding cycles of these two flea species (Segerman 1995). The common host for *X. brasiliensis* is *Rattus rattus,* but previous reports recorded this flea from other small mammals such as the Namaqua rock mouse *Micaelamys namaquensis*, a sympatric species that also shares rocky outcrops (Zumpt 1966; Segerman 1995, see previous chapter), which suggests that the presence of this species of flea in the present study is accidental. The genus *Demeillonia* comprises two species, *Demeillonia granti* and *Demeillonia miriamae*, both species known for their host specificity to sengis.

Demeillonia granti has been reported to infest species such as *Elephantulus rupestris*, *Macroscelides proboscideus*, *E. edwardii*, *E. myurus* as well as *M. namaquensis*, which share the same rocky habitat as the sengis (Zumpt 1966; Segerman 1995; Beaucournu *et al.* 2003).

In the present study immature ticks were present throughout the year (100% prevalence) and the data from seasonal patterns indicated that immature ticks were most abundant during the warm and wet months (April-May and October-November). Chigger mites were also present throughout the year, with clear seasonal patterns as well as differences between sexes during particular seasons. The abundance of *R. warburtoni/arnoldi* was higher in October, and this may be linked to reproductive activity of the host and associated changes in immune responses (Christe *et al.* 2000). Lutermann *et al.* (2012b) found that the abundance of *R. warburtoni* increased on adult male and pregnant female sengis during the breeding season. In addition, seasonal variation in prevalence and/or abundance of tick species may be attributed to their life cycle and climate factors (e.g. temperature, rainfall and humidity). As ticks spend most of their life-time off-host, this can increase the effect of exposure to different abiotic factors such as temperature and rainfall (Needham and Teel 1991; Benoit and Denlinger 2010). Seasonal patterns for Acari have been reported in previous studies, e.g. Lutermann *et al.* (2012a) found that the abundance of *R. warburtoni* increased during cool dry months compared to hot wet months in a sengi population in the Limpopo Province, SA. In the current study, the abundance of *Ixodes* spp. and chiggers was significantly lower in April 2010 than in April 2011. This may be due to the fact that the study area received more rainfall in April 2011 than in April 2010. The remaining two common tick species (*R. distinctus* and *Rhipicentor* spp.) did not show any seasonal patterns in the present study, which may be attributed to their low abundance. As with ticks, mite abundances can be affected by rainfall and increases in temperature (Marshall 1981). In the present study, chigger abundance increased during January. This is in agreement with the findings of Viljoen *et al.* (2011) where mite abundance was also higher in summer. Seasonal patterns in parasite burdens can be attributed to changes in environment factors such as temperature and rainfall as well as differences in host physiology and/or behaviour (Weil *et al.* 2006). Previous studies have indicated that tick and mite abundances are driven by changes in climatic conditions such as temperature and moisture, due to the fact that the climate conditions can affect hatching of eggs, larval and nymph activity and growth as well as the reproductive cycles (Randolph 2004; Marshall 1981). Variance in patterns between parasites taxa may be attributed to the off-host stages of the life cycle in the case of ticks, mites and fleas, while lice complete their entire life cycle on their host (Oguge *et al.* 2009). Ectoparasites differ with respect to their host association; therefore they are expected to react differently to changes in climate conditions (Midgley *et al.* 2003).

In the current study the abundance of three of the five common ectoparasite species showed sex-bias.. *Ixodes* spp., *R. distinctus* and chiggers were male-biased during April (*Ixodes* spp. and *R. distinctus*) and January (chiggers). Male-biases have been reported for *Ixodes rubicundus* in the Free State Province, SA (Fourie *et al.,* 1992). Differences between sexes (female-biased) within season were reported for some of the parasite species. Female-bias is common in flea and lice infestations (Askew 1971; Marshall, 1981). Marshall (1981) reported female bias in 70 and 78% of collections that included 17 species of lice and 108 species of flea, respectively. In South Africa, several studies on small mammals have demonstrated female-biased parasitism for fleas (Horak and

Fourie 1986; Louw *et al*. 1993, 1995; Beaucournu *et al.*, 2003). The female bias in *Ixodes* spp. in the present study is comparable with that in several other members of this genus, and Fourie and Horak (1994) and Horak and Boomker (1998) have recorded similar patterns for *I. rubicundus* and *Ixodes sp.* respectively. Variance in parasite burdens between sexes over season can also be attributed to the host breeding strategies (Krasnov *et al.* 2005). For instance, males tend to roam larger areas searching for potential mates, which can increase their (i.e. males) potential rates to come in contact with other individuals infested with ectoparasites (Fleming and Nicolson 2004).

In conclusion, the current study demonstrates that sengis host a large diversity of ectoparasitic species with ticks representing by far the majority of these parasites. Seasonal variation and sex-biased patterns were recorded for some of the ectoparasite species collected and we hypothesised that these patterns might be linked to climatic conditions, reproductive effort during the breeding seasons and differences in host behaviour between sexes.

REFERENCES

ALTIZER, S., DOBSON, A., HOSSEINI, P., HUDSON, P., PASCUAL, M. & ROHANI, P. 2006. Seasonality and the dynamics of infectious diseases. *Ecology letters,* 9**,** 467-484.

ANDERSON, P. & KOK, O. 2003. Ectoparasites of springhares in the Northern Cape Province, South Africa. *South African Journal of Wildlife Research,* 33**,** p. 23-32.

ASKEW, R. R. 1971. *Parasitic insects*, London: Heinemann Educational Books Ltd., 48 Charles Street, W1X 8AH.

BAKER, A. S. 1999. *Mites and ticks of domestic animals: An identification guide and information source,* The Stationary Office.

BEAUCOURNU, J., HORAK, I. & FOURIE, L. 2003. Fleas of elephant shrews (Mammalia, Macroscelididae), and a new host and locality record for Macroscelidopsylla albertyni De Meillon & Marcus, 1958 (Siphonaptera, Chimaeropsyllidae). *The Onderstepoort journal of veterinary research,* 70**,** 251.

BENOIT, J. B. & DENLINGER, D. L. 2010. Meeting the challenges of on-host and off-host water balance in blood-feeding arthropods. *J Insect Physiol,* 56**,** 1366-76.

BOAG, B., LELLO, J., FENTON, A., TOMPKINS, D. & HUDSON, P. 2001. Patterns of parasite aggregation in the wild European rabbit (Oryctolagus cuniculus). *International journal for parasitology,* 31**,** 1421-1428.

BOWN, K. J., BEGON, M., BENNETT, M., WOLDEHIWET, Z. & OGDEN, N. H. 2003. Seasonal dynamics of Anaplasma phagocytophila in a rodent-tick (Ixodes trianguliceps) system, United Kingdom. *Emerging infectious diseases,* 9**,** 63.

BOWN, K. J., LAMBIN, X., TELFORD, G., HEYDER-BRUCKNER, D., OGDEN, N. H. & BIRTLES, R. J. 2011. The common shrew (Sorex araneus): a neglected host of tick-borne infections? *Vector-Borne and Zoonotic Diseases,* 11**,** 947-953.

BRAACK, L., HORAK, I. G., JORDAAN, L. C., SEGERMAN, J. & LOUW, J. 1996. The comparative host status of red veld rats (Aethomys chrysophilus) and bushveld gerbils (Tatera leucogaster) for epifaunal arthropods in the southern Kruger National Park, South Africa. *The Onderstepoort journal of veterinary research,* 63**,** 149-158.

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***,** 575-583.

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.

COLBO, M. & MACLEOD, J. 1976. Ecological studies of ixodid ticks (Acari, Ixodidae) in Zambia. II. Ticks found on small mammals and birds. *Bulletin of Entomological Research,* 66**,** 489-500.

DUMBACHER, J. P., RATHBUN, G. B., OSBORNE, T. O., GRIFFIN, M. & EISEB, S. J. 2014. A new species of round-eared sengi (genus Macroscelides) from Namibia. *Journal of Mammalogy,* 95**,** 443-454.

DUMBACHER, J. P., RATHBUN, G. B., SMIT, H. A. & EISEB, S. J. 2012. Phylogeny and Taxonomy of the Round-Eared Sengis or Elephant-Shrews, Genus Macroscelides (Mammalia, Afrotheria, Macroscelidea). *Plos One,* 7.

EWING, H. 1944. The trombiculid mites (chigger mites) and their relation to disease. *The Journal of Parasitology,* 30**,** 339-365.

FLEMING, P. & NICOLSON, S. 2004. Sex differences in space use, body condition and survivorship during the breeding season in the Namaqua rock mouse, Aethomys namaquensis. *African Zoology,* 39**,** 123-132.

FOURIE, L. & HORAK, I. 1994. The life cycle of Ixodes rubicundus (Acari: Ixodidae) and its adaptation to a hot, dry environment. *Experimental & applied acarology,* 18**,** 23-35.

FOURIE, L., HORAK, I. & VAN DEN HEEVER, J. 1992. relative host status of rock elephant shrews Elephantulus myurus and Namaqua rock mice Aethomys namaquensis for economically important ticks. *South African journal of zoology= Suid-Afrikaanse tydskrif vir dierkunde*.

FOURIE, L., HORAK, I. & WOODALL, P. 2005. Elephant shrews as hosts of immature ixodid ticks. *Onderstepoort Journal of Veterinary Research,* 72**,** p. 293-301.

FOURIE, L., HORAK, I. G., KOK, D. & VAN ZYL, W. 2002. Hosts, seasonal occurrence and life cycle of Rhipicentor nuttalli (Acari: Ixodidae). *The Onderstepoort journal of veterinary research,* 69**,** 177.

FOURIE, L., TOIT, J. D., KOK, D. & HORAK, I. 1995. Arthropod parasites of elephant- shrews, with particular reference to ticks. *Mammal Review,* 25**,** 31-37.

HARRISON, A., BASTOS, A. D., MEDGER, K. & BENNETT, N. C. 2013. Eastern rock sengis as reservoir hosts of *Anaplasma bovis* in South Africa. *Ticks and tick-borne diseases* 4**,** 503-5.

HARRISON, A., BOWN, K. J. & HORAK, I. G. 2011. Detection of Anaplasma bovis in an undescribed tick species collected from the eastern rock sengi Elephantulus myurus. *Journal of Parasitology,* 97**,** 1012-6.

HARRISON, A., ROBB, G. N., BENNETT, N. C. & HORAK, I. G. 2012. Differential feeding success of two paralysis-inducing ticks, Rhipicephalus warburtoni and Ixodes rubicundus on sympatric small mammal species, Elephantulus myurus and Micaelamys namaquensis. *Vet Parasitol,* 188**,** 346-54.

HILLEGASS, M. A., WATERMAN, J. M. & ROTH, J. D. 2008. The influence of sex and sociality on parasite loads in an African ground squirrel. *Behavioral Ecology,* 19**,** 1006-1011.

HORAK, I., FOURIE, L. & BRAACK, L. 2005. Small mammals as hosts of immature ixodid ticks. *Onderstepoort Journal of Veterinary Research,* 72**,** p. 255-261.

HORAK, I. G. & BOOMKER, J. 1998. Parasites of domestic and wild animals in South Africa. XXXV. Ixodid ticks and bot fly larvae in the Bontebok National Park. *The Onderstepoort journal of veterinary research,* 65**,** 205.

HORAK, I. G. & FOURIE, L. 1986. Parasites of domestic and wild animals in South Africa. XIX. Ixodid ticks and fleas on rock dassies (Procavia capensis) in the Mountain-zebra National Park. *The Onderstepoort journal of veterinary research,* 53**,** 123-126.

HORAK, I. G., SPICKETT, A. M., BRAACK, L. E. O. & PENZHORN, B. L. 1993. PARASITES OF DOMESTIC AND WILD ANIMALS IN SOUTH-AFRICA .22. IXODID TICKS ON SCRUB HARES IN THE TRANSVAAL. *Onderstepoort Journal of Veterinary Research,* 60**,** 163-174.

HORAK, I. G., WELMAN, S., HALLAM, S. L., LUTERMANN, H. & MZILIKAZI, N. 2011. Ticks of four-toed elephant shrews and Southern African hedgehogs. *Onderstepoort J Vet Res,* 78**,** 243.

KARBOWIAK, G. 2004. Zoonotic reservoir of Babesia microti in Poland. *Pol J Microbiol*, 53**,** 61-65.

KIM, K. C. 2006. Blood-sucking lice (Anoplura) of small mammals: True parasites. *Micromammals and Macroparasites.* Springer.

KLEIN, S. 2004. Hormonal and immunological mechanisms mediating sex differences in parasite infection. *Parasite immunology,* 26**,** 247-264.

KRANTZ, G. & WALTER, D. 2009. A manual of acarology, 3rd. Lubbock, TX: Texas Tech University Press.

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. & MATTHEE, S. 2010. Spatial variation in gender-biased parasitism: host-related, parasite-related and environment-related effects. *Parasitology,* 137**,** 1527-36.

KRASNOV, B. R., MORAND, S., HAWLENA, H., KHOKHLOVA, I. S. & SHENBROT, G. I. 2005. Sex-biased parasitism, seasonality and sexual size dimorphism in desert rodents. *Oecologia,* 146**,** 209-17.

KRASNOV, B. R., SHENBROT, G. I., KHOKHLOVA, I. S. & POULIN, R. 2006. Is abundance a species attribute? An example with haematophagous ectoparasites. *Oecologia,* 150**,** 132-40.

LARESCHI, M. 2006. Interrelationship between the sex of the water rat Scapteromys aquaticus and its infestation with ectoparasites in La Plata river marshland, Argentina. *Rev Biol Trop,* 54**,** 673-679.

LARESCHI, M. 2010. Ectoparasite occurrence associated with males and females of wild rodents Oligoryzomys flavescens (Waterhouse) and Akodon azarae (Fischer)(Rodentia: Cricetidae: Sigmodontinae) in the Punta Lara wetlands, Argentina. *Neotropical entomology,* 39**,** 818-822.

LARESCHI, M. & KRASNOV, B. R. 2010. Determinants of ectoparasite assemblage structure on rodent hosts from South American marshlands: the effect of host species, locality and season. *Medical and Veterinary Entomology,* 24**,** 284-292.

LAUDISOIT, A., LEIRS, H., MAKUNDI, R. & KRASNOV, B. R. 2009. Seasonal and habitat dependence of fleas parasitic on small mammals in Tanzania. *Integr Zool,* 4**,** 196-212.

LEDGER, J. A. 1980. *The arthropod parasites of vertebrates in Africa south of the Sahara. Volume IV. Phthiraptera (Insecta)*, South African Institute for Medical Research.

LOUW, J., HORAK, I. G. & BRAACK, L. 1993. Fleas and lice on scrub hares (Lepus saxatilis) in South Africa. *The Onderstepoort journal of veterinary research,* 60**,** 95-101.

LOUW, J., HORAK, I. G., HORAK, M. L. & BRAACK, L. 1995. Fleas, lice and mites on scrub hares (Lepus saxatilis) in northern and eastern Transvaal and in KwaZulu-Natal, South Africa. *The Onderstepoort journal of veterinary research,* 62**,** 133-137.

LUTERMANN, H., MEDGER, K. & HORAK, I. G. 2012a. Abiotic and biotic determinants of tick burdens in the eastern rock sengi (Elephantulus myurus). *Med Vet Entomol,* 26**,** 255-62.

LUTERMANN, H., MEDGER, K. & HORAK, I. G. 2012b. Effects of life-history traits on parasitism in a monogamous mammal, the eastern rock sengi (Elephantulus myurus). *Naturwissenschaften,* 99**,** 103-110.

MACLEOD, J. 1970. Tick infestation patterns in the southern province of Zambia. *Bulletin of Entomological Research,* 60**,** 253-274.

MAKUNDI, R. & KILONZO, B. 1994. Seasonal dynamics of rodent fleas and its implication on control strategies in Lushoto district, north- eastern Tanzania. *Journal of Applied Entomology,* 118**,** 165-171.

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

MARTIN, L. B., WEIL, Z. M. & NELSON, R. J. 2008. Seasonal changes in vertebrate immune activity: mediation by physiological trade-offs. *Philos Trans R Soc Lond B Biol Sci,* 363**,** 321-39.

MATTHEE, S., MCGEOCH, M. A. & KRASNOV, B. R. 2010. Parasite-specific variation and the extent of male-biased parasitism; an example with a South African rodent and ectoparasitic arthropods. *Parasitology,* 137**,** 651-60.

MEDGER, K., CHIMIMBA, C. T., BENNETT, N. C. & KITCHENER, A. 2012. Seasonal reproduction in the eastern rock elephant-shrew: influenced by rainfall and ambient temperature? *Journal of Zoology,* 288**,** 283-293.

MIDGLEY, G., HANNAH, L., MILLAR, D., THUILLER, W. & BOOTH, A. 2003. Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biological Conservation,* 112**,** 87-97.

MOORE, S. L. & WILSON, K. 2002. Parasites as a viability cost of sexual selection in natural populations of Mammals. *Science,* 297**,** 2015-2018.

MORAND, S., DE BELLOCQ, J. G., STANKO, M. & MIKLISOVÁ, D. 2004. Is sex-biased ectoparasitism related to sexual size dimorphism in small mammals of Central Europe? *Parasitology,* 129**,** 505-510.

NEEDHAM, G. R. & TEEL, P. D. 1991. Off-host physiological ecology of ixodid ticks. *Annual review of entomology,* 36**,** 659-681.

NELSON, R. J. 2004. Seasonal immune function and sickness responses. *Trends in immunology,* 25**,** 187-192.

NELSON, R. J., DEMAS, G. E., KLEIN, S. L. & KRIEGSFELD, L. J. 2002. *Seasonal patterns of stress, immune function, and disease*, Cambridge University Press.

NORVAL, R. 1979. The limiting effect of host availability for the immature stages on population growth in economically important ixodid ticks. *The Journal of parasitology***,** 285-287.

OGUGE, N., DURDEN, L., KEIRANS, J., BALAMI, H. & SCHWAN, T. 2009. Ectoparasites (sucking lice, fleas and ticks) of small mammals in southeastern Kenya. *Medical and veterinary entomology,* 23**,** 387-392.

PETNEY, T., HORAK, I., HOWELL, D. & MEYER, S. 2004. Striped mice, Rhabdomys pumilio, and other murid rodents as hosts for immature ixodid ticks in the Eastern Cape Province. *Onderstepoort Journal of Veterinary Research,* 71**,** p. 313-318.

POULIN, R. 1996. Sexual inequalities in helminth infections: a cost of being a male? *American Naturalist***,** 287-295.

POULIN, R. 2007. *Evolutionary ecology of parasites*, Princeton university press.

PRESLEY, S. J. & WILLIG, M. R. 2008. Intraspecific patterns of ectoparasite abundances on Paraguayan bats: effects of host sex and body size. *Journal of Tropical Ecology,* 24**,** 75-83.

RANDOLPH, S., MIKLISOVA, D., LYSY, J., ROGERS, D. & LABUDA, M. 1999. Incidence from coincidence: patterns of tick infestations on rodents facilitate transmission of tick-borne encephalitis virus. *Parasitology,* 118**,** 177-186.

RANDOLPH, S. E. 2004. Tick ecology: processes and patterns behind the epidemiological risk posed by ixodid ticks as vectors. *Parasitology,* 129**,** S37-S65.

ROBERTS, L. & JANOVY JR, J. 2000. Foundations of Parasitology. 6th ed.: New York: McGraw-Hill Higher Education.

SCANTLEBURY, M., MAHER MCWILLIAMS, M., MARKS, N. J., DICK, J. T. A., EDGAR, H. & LUTERMANN, H. 2010. Effects of life-history traits on parasite load in grey squirrels. *Journal of Zoology,* 282**,** 246-255.

SEGERMAN, J. 1995. *Siphonaptera of southern Africa: handbook for the identification of fleas,* South African Institute for Medical Research.

SKINNER, J. D. & CHIMIMBA, C. T. 2005. *The mammals of the southern African subregion. 3rd revised edition*.

SONENSHINE, D. E. 1991. The biology of ticks, vol. I.

TRAUB, R. & WISSEMAN, C. 1974. THE ECOLOGY OF CHIGGER-BORNE RICKETTSIOSIS (SCRUB TYPHUS) 1, 2. *Journal of medical entomology,* 11**,** 237-303.

VAN DER MESCHT, L. 2011. *Ectoparasite assemblage of the four-striped mouse, Rhabdomys pumilio: the effect of anthropogenic habitat transformation and temporal variation.* University of Stellenbosch.

VILJOEN, H., BENNETT, N. C., UECKERMANN, E. A. & LUTERMANN, H. 2011. The role of host traits, season and group size on parasite burdens in a cooperative mammal. *PLoS One,* 6**,** e27003.

WALKER, J. B., KEIRANS, J. E. & HORAK, I. G. 2000. *The genus Rhipicephalus (Acari, Ixodidae): a guide to the brown ticks of the world,* Cambridge University Press.

WEIL, Z. M., MARTIN II, L. B. & NELSON, R. J. 2006. Interactions among immune, endocrine, and behavioural response to infection. *Micromammals and Macroparasites.* Springer.

WENGE, D., XIANGUO, G., XINGYUAN, M., TIJUN, Q. & DIAN, W. 2009. Ectoparasite communities on Tupaia belangeri (Scandentia: Tupaiidae) in surrounding areas of Erhai Lake in Yunnan, China. *Journal of Medical Colleges of PLA,* 24**,** 215-222.

WILSON, K., BJØRNSTAD, O., DOBSON, A., MERLER, S., POGLAYEN, G., RANDOLPH, S., READ, A. & SKORPING, A. 2002. Heterogeneities in macroparasite infections: patterns and processes. *The ecology of wildlife diseases***,** 6-44.

ZUMPT, F. 1966. The arthropod parasites of vertebrates in Africa south of the Sahara (Ethiopian region). Volume III (Insecta excl. Phthiraptera). *The arthropod parasites of vertebrates in Africa south of the Sahara (Ethiopian region). Volume III (Insecta excl. Phthiraptera).*

CHAPTER FOUR

THE LONG TERM DYNAMIC OF THE ECTOPARASITE COMMUNITY OF THE EASTERN ROCK SENGI (*Elephantulus myurus*) AND THE EFFECT OF PARASITISM ON HOST BODY CONDITION[3]

SUMMARY

Patterns of ectoparasite abundance among hosts can be linked to differences in abiotic and biotic factors. The latter also include interspecific interactions within the ectoparasite community. However, these are not well understood due to lack of studies investigating more than one parasite simultaneously. Furthermore, ectoparasites may have a negative effect on their host's body condition and such effects remain poorly studied in wild animals. In the present study, we investigated the entire ectoparasite community occurring on eastern rock sengis (*Elephantulus myurus*) over a period of three years. The main focus of the study was to manipulate the ectoparasite community of eastern rock sengis using Frontline® to reduce the abundance of fleas and ticks to document the effect of these ectoparasite taxa on the ectoparasite population dynamics as well as host body condition (BCI). Our treatment resulted in a decrease of *R. warburtoni/arnoldi* abundance, the dominant tick species while the prevalence and abundance of chiggers and *Ixodes* spp. increased suggesting a competitive interaction. Thus, the current study suggests that anti-parasite treatments can also have effects on non-target ectoparasite species (i.e. chiggers). In addition, treatment had an indirect effect on the host BCI that increased in the second year and third suggesting that the removal of ectoparasites could be beneficial to the host and highlighting the substantial cost of parasite burdens on host fitness.

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INTRODUCTION

Parasites depend on their hosts for resources and accordingly the parasite-host relationship may affect the host by reducing host fitness and altering host behaviour (Price *et al.* 1986; Schmidt and Robert 2009). Therefore, parasites are expected to play an important role in regulating their host populations (Price *et al.* 1986; Poulin 1999; Altizer *et al.* 2003). Host-parasite interactions depend on several factors such as parasite prevalence and abundance, the effect of parasites on fecundity and mortality of the host and the host immune system (Combes 2001). Each of these factors can potentially be affected by environmental (abiotic) conditions (Merino and Møller 2010) or parasite as well as host (biotic) life-history traits (Møller *et al.* 2006; Barbosa *et al.* 2007). Variation in abiotic factors such as temperature and rainfall can affect the developmental rates and survival of ectoparasites in the environment. In addition, seasonal variation in temperature and rainfall can affect the availability of resources for hosts and therefore lead to seasonal variation in parasite loads (Altizer *et al.* 2006). Seasonal patterns in parasitic infestation can be linked to the availability of immature stages (i.e. larvae and nymphs) in the environment, which also depends on microclimatic conditions affecting the adult stages behaviour and mortality (Randolph and Storey 1999; Randolph *et al.* 2002; Randolph 2004). In addition, the spatial distribution of immature stages and host density also affect contact rates as well as host exposure and hence infestation rates (Calabrese *et al.* 2011; Kiffner *et al.* 2011b). For example, ectoparasite species spend either part or their complete life cycle on the host (Kim 1985). The extent of the off host period (i.e. abiotic factors) effects on parasitic rates differ among ectoparasite taxa (Marshall 1981). During the periods off and on the host ectoparasites are exposed to different climatic conditions (Hopkins 1949). There is no general pattern of climatic conditions that determines success for any ectoparasite species or taxon (Bordes *et al.* 2010). For example, after taking the blood meal ticks drop off from the host to the surrounding vegetation to moult into the next stage and wait for a new potential host. In contrast, the majority of fleas and mites alternate between periods of time spent on the host or in the host's nest. Conversely, lice are permanent parasites that spend their entire life cycle on the host (Matthee *et al.* 2010). Therefore, the less time spent on the host, coupled with more time spent in the vegetation or host nest may lead to less time to get in direct contact with the host's immune system, also decreasing the risk of grooming as well as increasing contact rates with other host individuals (Matthee *et al.* 2010).

Similarly, host factors such as host sex can affect the distribution and abundance of parasites (Altizer *et al.* 2003). Differences in reproductive strategies between males and females cause many differences in their physiology, morphology and behaviour (Mooring *et al.* 2006; Rolff 2002). In mammals, males tend to have a larger body size and larger home ranges than females (Hoby *et al.* 2006; Perez-Orella and Schulte-Hostedde 2005). However, these characteristics may increase a male's exposure to parasites (Moore and Wilson 2002; Rolff 2002). In addition, differences in immune function may also lead to sex-biased parasitism (Folstad and Karter 1992; Sheldon and Verhulst 1996). The "immunocompetence handicap hypothesis" suggests that male reproductive investment may decrease the ability to resist parasites through steroid-dependent suppression of the immune system in males (Folstad and Karter 1992). However, various ectoparasite taxa have different life cycles and may respond differently to these host-related factors (Matthee *et al.* 2010).

Co-infection of hosts with multiple parasite species has been well documented (Petney and Andrews 1998; Pedersen and Fenton 2007). In a parasite community infesting an individual host, parasite species may interact directly through chemical and physical interference, or indirectly through competition for shared resources as well as immune-mediated competition (Bruce *et al.* 2000; Cox 2001; Pedersen and Fenton 2007; Randall *et al.* 2013). Direct interactions include competition for attachment sites (Lello *et al.* 2004; Mideo 2009). A number of studies investigating tick species have shown that preferences for particular attachment sites are common and it can differ between tick species (MacLeod *et al.* 1977). In contrast, indirect interactions are host-mediated and may involve variations in host immunity, i.e. cross immunity (competition-negative effect) as well as immune suppression (facilitation-positive effect) (Cattadori *et al.* 2007). Therefore, it is suggested that intra-host interactions between parasites affected by bottom-up controls (i.e. types of host resources used by parasites) and top-down controls (i.e. host immune defences, Graham 2008; Pedersen and Fenton 2007). Although these interactions are seldom studied, they are probably another biotic factor contributing to the observed parasite distribution across a host population. Unlike for endoparasites, interspecific interactions have so far not been investigated for ectoparasite communities (Knowles *et al.* 2013, Lello *et al.* 2004; Pedersen and Antonovics 2013). The majority of research on interspecific interactions between parasites relies on cross-sectional and observational data (Andrews and Petney 1981; Lello *et al*. 2004; Ezenwa *et al*. 2010; Baer-Lehman *et al.* 2012; Moreno *et al.* 2013). Interspecific interactions based on these data may result in incorrect conclusions regarding the prevalence and nature of such interactions due to confounding effects of similar temporal exposure or transmission routes (Fenton *et al*. 2010, 2014; Viney and

Graham 2013). In contrast, the selective experimental removal of certain parasite species from the community can reveal relationships not apparent in observational data (Hudson *et al.* 1998; Pedersen and Greives 2008). Combining experimental manipulation with longitudinal sampling can help to elucidate the processes leading to the outcome documented in cross-sectional studies (Viney and Graham 2013). Such approaches remain rare, but were employed by two recent longitudinal studies of small mammal parasite communities (Knowles *et al*. 2013; Pedersen and Antonovics 2013). By applying an anti-helminthic drug these studies provided evidence for competitive interactions within the endoparasite community of two small mammal species of the northern hemisphere.

One crucial factor shaping the nature of host-parasite interaction is the host's ability to fight and resist infections (Combes 2001). Hence, parasites will have to balance host resistance against food resources (e.g. blood meals) (Hanley *et al.* 1996). Host immunity and resources are known to improve with body condition (Combes 2001; Bize *et al.* 2008). Body condition is a measure of the energetic reserves a host has and are usually stored as fat (Schulte-Hostedde *et al.* 2001). Therefore, it is expected that if host resources affect parasite success, on the one hand parasites should exploit hosts in good body condition for optimal nourishment. On the other hand, such hosts should also exhibit the strongest immune defences that in turn negatively affect parasites success. Therefore, parasites may be expected to infest hosts in poor condition (i.e. weak immune response) (Giorgi *et al.* 2001). However, parasites may avoid hosts in poor condition because such hosts may not provide adequate food resources.

In turn ectoparasites can have dramatic effects on host body condition (Degen 2006). This can be caused either by directly competing for resources required by the hosts (for activity such as growth and reproduction) through absorption of nutrients or by forcing the hosts to increase their immune defences against parasitic infestations (Hall 1985). Parasitism may incur a cost on the fitness of the host by reducing energy intake or cause secondary symptoms at bite sites (Forbes *et al.* 2000; Chapman *et al.* 2007). Host responses employed to reduce parasitic burdens such as raising an immunological response can be energetically costly and reduce host body condition (Delahay *et al.* 1995; Goüy de Bellocq *et al.* 2006).

In the current study we employed experimental removal of target parasite taxa (i.e. ticks and fleas) to study interspecific relationships in the ectoparasite community of eastern rock sengis (*Elephantulus myurus*) in South Africa. Sengis are insectivorous, they have one or two precocial offspring per litter (Nicoll and Rathbun 1990; Skinner and Chimimba 2005). They are monogamous; exhibit no sexual dimorphism and have overlapping home ranges shared amongst pairs (Rathbun and and Rathbun 2006). The ectoparasite community infesting sengis is dominated by a large number of immature ticks (Fourie *et al.* 1995; Harrison *et al.* 2011; Horak *et al.* 2012). However, the dominant tick species is usually *Rhipicephalus warburtoni/arnoldi*, which far outnumbers other tick species (Harrison *et al*. 2011; Lutermann *et al.* 2012a; Fagir *et al*. 2015, previous chapter). In addition, several flea and mite species as well as *Neolinognathus elephantuli* (louse) have been reported for *E. myurus* (Fourie *et al.* 1995; Beaucournu *et al.* 2003; Fagir *et al.* 2015). After assessing the ectoparasite community of a sengi population for one year, we reduced the abundance of ticks and fleas experimentally over a period of two years and monitored the dynamics of the entire ectoparasite community. This constitutes the first study of this kind of small mammals in Africa. In addition, we evaluated the possible effects of ectoparasites on the body condition of sengis.

The present study aimed to:

- Document the long-term patterns for the ectoparasite community sustained by the study species.
- Evaluate possible effects of abiotic (climate) and host (sex) factors on parasite burdens.
- Determine the nature of interspecific relationships within the ectoparasite community of eastern rock sengis and to obtain first insights into the potential mechanism mediating these interactions.
- Evaluate the effect of ectoparasite burdens on the body condition of sengis.

MATERIALS AND METHODS

Study area and collection of animals

The collection of sengis was carried out in Telperion/Ezemvelo Nature Reserve, South Africa (25° 41’ S, 28° 56’ E). Animals were captured from eight rocky outcrops using Sherman traps (H.B. Sherman Traps, Inc., Tallahassee, Florida, USA) baited with a mixture of peanut butter and oats. Plots were about 0.5-0.7 ha in size with distance between plots ranging from 3 to 5 km. A total of 12 trips were conducted during the period from April 2010 until February 2013 to cover all seasons (2010: April, July, October; 2011: January, April, July, October; 2012: February, April, July, October; 2013: February). In each site, traps were set in four parallel lines approximately 10 m apart and each line consisted of 18 traps (in total 72 traps per site). Traps were set for four consecutive nights and checked daily during the early morning.

Laboratory procedures

Captured animals were transferred to a research facility on the reserve and immediately processed. Sengis were removed from the traps using Ziplock® bags and then restrained by hand, sexed, weighed using a digital scale (Ohaus Scout Pro, model sp-202, accurate to 0.01g) and body length of all animals was measured from the back of the neck to the base of the tail using callipers. Ectoparasites were removed from the ear margins, back, legs, thighs and base of the tail using fine tweezers. All ectoparasites recovered were stored in 70% alcohol for later counting and identification. Each animal was marked with unique ear notches and released in the late afternoon at their site of capture. All individuals from four randomly selected rocky outcrops were treated against ectoparasites using Frontline® (Merial Pty, Ltd, South Africa). The treatment was applied only during the second and third study year. Frontline® was applied by spraying it onto the gloved hands of the handler and then rubbing it on the animals (as instructed by the manufacturer). This treatment was applied only one time during each trip i.e. the Frontline® treatment was only repeated for the first capture in each subsequent trip.

Ticks were identified to species or specific group following descriptions provided by Walker *et al.* (2000). Mites were counted and identified to family level following Krantz and Walter (2009). Lice and fleas were cleared (using 15% KOH solution), counted and identified following morphological keys of Ledger (1980) and Segerman (1995), respectively (for further details see previous chapters). The total number of specimens of each ectoparasite species was counted.

Statistical analysis

Different stages of ectoparasite species (i.e. larvae, nymphs, males and females) were pooled for analyses. The prevalence and abundance as defined by Bush *et al*. (1997) were calculated for each of the four higher taxa (i.e. fleas, lice, mites and ticks) as well as the individual parasite species collected. For the analyses only the first capture per trip of each individual was included. None of the data collected were normally distributed (Kolmogorov-Smirnov test: $P < 0.004$), therefore generalized linear mixed models (GLMMs) were carried out for the most common parasite species (>20% prevalence, see results section) with year (i.e. first, second and third), season (i.e. April/May: autumn, June/July: winter, October: spring, January/February: summer), treatment (i.e. treated, untreated) and sex as well as the 2-way interactions between these factors as independent variables. Animal ID nested in study plot was included as random factor. For prevalence models with a binary logistic data distribution with a logit-link function were selected, while a negative-binomial distribution with a log-link function was chosen for abundance data. Post-hoc analyses were done with pairwise comparisons using the least significant difference (LSD). Due to the low prevalence and/or abundance of some of the parasite species found, data were analysed on a taxonomic level only for some ectoparasites (see results section). With the exception of a single individual all animals were infested with *Rhipicephalus warburtoni/arnoldi* (see results section). In this one animal *Rhipicephalus warburtoni/arnoldi* was replaced by 653 *Rhipicephalus appendiculatus*. Therefore, for the analyses it was included as if being infested with *Rhipicephalus warburtoni/arnoldi*.

The body condition index (BCI) was calculated by dividing the body mass of the animal by its body length. The data for BCI did not satisfy the criteria for a parametric distribution (Kolmogorov-Smirnov test: $P < 0.001$). The GLMMs were then modelled with a Gamma regression distribution; the main effects were year, season, sex, treatment and abundance of the five most common ectoparasite species (*Rhipicephalus warburtoni/arnoldi*, *Ixodes* spp., *Rhipicephalus* spp., *Rhipicentor* spp. and chiggers). Interaction factors were calculated for year, season, sex and treatment. All statistical analyses were carried out in IBM SPSS version 21 (IBM SPSS statistics 21 Ink 2013).

RESULTS

Ectoparasite community

A total of 182 animals (89 males, 93 females) were captured and examined for the presence of ectoparasites during the course of this study (Table 1).

Table 1 Summary of number of sengis captured during the study.

Trip	Males	Females	Total
April 2010	10	9	19
July 2010	6	1	7
October 2010	5	9	14
January 2011	8	8	16
April 2011	7	7	14
July 2011	3	5	8
October 2011	7	11	18
February 2012	8	9	17
April 2012	9	10	19
July 2012	7	3	10
October 2012	12	11	23
February 2013	7	10	17
Total	**89**	**93**	**182**

Ectoparasites from four taxa (i.e. fleas, lice, mites and ticks) were recorded. These comprised five species of tick from four genera (*Rhipicephalus*, *Rhipicentor*, *Haemaphysalis* and *Ixodes*), one species of mite and one mite family, two species of louse and five species of flea from three genera (*Xenopsylla*, *Chiastopsylla* and *Dinopsyllus*, Table 2). Larvae and nymphs of *Rhipicephalus warburtoni* and *Rhipicephalus arnoldi* closely resemble each other and it is difficult to distinguish between these two species (see chapter 3). Therefore individuals of these ticks were pooled as *Rhipicephalus warburtoni/arnoldi*. Similarly, *Haemaphysalis* sp. and *Haemaphysalis spinulosa* were also pooled as *Haemaphysalis* spp. for the same reason (see chapter 3). Due to their low prevalence and abundance (Table 2) *Rhipicephalus distinctus, R. decoloratus, R. evertsi evertsi, R. lunulatus, R. exophthalmos* and *Rhipicephalus* sp. were all pooled together as *Rhipicephalus* spp. for the analyses. In addition, *Rhipicentor* spp. could not be identified to the species level. Only the immature stages of ticks were collected from the animals. The most common species of parasite were four ticks (*Rhipicephalus warburtoni/arnoldi, Ixodes* spp., *Rhipicephalus* spp. and *Rhipicentor* spp., see results section, Chapter 3) and one mite (i.e. chiggers) and analyses of long-term patterns was restricted to these five taxa (Table 2). Only one animal was infected with the mite *Androlaelaps rhabdomysi*. Chiggers were the dominant mite (Table 2) and could only be identified to the family level. Few species of louse were recovered (Table 2). Only two animals were infected with *Polyplax praomydis,* while the remainder of the animals were infected with *Neolinognathus elephantuli* (Table 2). Five species of flea were recovered from the animals, namely, *Xenopsylla brasiliensis, Chiastopsylla godfreyi, Dinopsyllus ellobius, Demeillonia granti* and *Ctenocephalides felis damarensis* (Table 2).

Table 2 Summary of the ectoparasite species found on sengis and their infection parameters.

Parasites		**Total**	**Prevalence (%)**	**Mean abundance (±SE)**
Ticks	***Rhipicephalus warburtoni/arnoldi***	**51,103**	**99.5%**	**280.79 (±15.79)**
	***Ixodes* spp.**	**886**	**44.5%**	**4.87 (±1.11)**
	***Rhipicephalus* spp.**	**139**	**28.0%**	**0.76 (±0.21)**
	***Rhipicentor* spp.**	**143**	**24.2%**	**0.79 (±0.15)**
	Haemaphysalis spp.	27	8.2%	0.15 (±0.04)
Mites	**Chigger**	**32,137**	**87%**	**176.58 (±26.04)**
	Androlaelaps rhabdomysi	1	0.5%	0.01 (±0.005)
Fleas	*Xenopsylla brasiliensis*	6	0.5%	0.03 (±0.01)
	Chiastopsylla godfreyi	1	0.5%	0.01 (±0.005)
	Dinopsyllus ellobius	5	1.1%	0.03 (±0.02)
	Demeillonia granti	47	3.4%	0.26 (±0.10)
	Ctenocephalides felis damarensis	7	2.1%	0.04 (±0.01)
Lice	*Neolinognathus elephantuli*	122	6.6%	0.67 (±0.38)
	Polyplax praomydis	3	0.8%	0.02 (±0.01)

* More detailed analyses have been carried out for species highlighted in bold.

Effect of abiotic factors (year and season), host sex and treatment on the distribution of the five most common ectoparasites

Rhipicephalus warburtoni/arnoldi had a prevalence close to 100% (Table 2) and hence no GLMM could be carried out for this taxon. The abundance of *R. warburtoni/arnoldi* varied significantly between years (Table 4). Post-hoc analyses showed that the abundance of *R. warburtoni/arnoldi* was significantly lower in the third year (44.3±26.1) compared to the first year (102.1±31.4, LSD: P = 0.001). In contrast, no significant differences in abundance between first and second year (57.6±36.3, LSD: P = 0.113) as well as the second and third year (LSD: P = 0.092) were observed. Furthermore, the abundance of *R. warburtoni/arnoldi* differed significantly between seasons (Table 4). It was significantly higher in spring (407.0±36.5) compared to autumn (315.9±27.8, LSD: $P \leq 0.045$) and summer (139.2±11.3, LSD: $P < 0.0001$). In contrast, there was no significant difference between summer and winter (36.5±26.2, LSD: P = 0.167). None of the remaining factors had a significant effect on the abundance of *R. warburtoni/arnoldi* (Table 4).

The prevalence of *Ixodes* spp. varied significantly between seasons (Table 3). Post-hoc analyses showed that the prevalence of *Ixodes* spp. was significantly lower in spring (4.3%) than in autumn (81.1%) and summer (43.5%, LSD: $P < 0.0001$, for both), but significantly higher in summer than winter (66%, LSD: P = 0.006). None of the remaining factors had any significant effect on the prevalence of *Ixodes* spp. (Table 3). The abundance of *Ixodes* spp. varied significantly between seasons (Table 4). Post-hoc analyses showed that it was significantly higher in autumn (4.4±1.4) than in spring (0.05±0.04, LSD: P = 0.003) but significantly lower in spring than in summer (0.9±0.3, LSD: P = 0.006). In addition, treated animals (0.9±0.2) had a significantly

Table 3 Results of the GLMMs evaluating the effect of study year, season, treatment and host sex on the prevalence of the five most common ectoparasite species of sengis in the study area. Note that the prevalence for *R. warburtoni/arnoldi* was 100%.

Factors	**df**	***R. warburtoni/arnoldi***		***Ixodes* spp.**		***Rhipicephalus* spp.**		***Rhipicentor* spp.**		**Chigger**	
		F	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**
Year	2, 157	-	-	1.737	0.179	0.000	1.000	0.525	0.593	7.559	0.001*
Season	3, 157	-	-	7.217	<0.0001*	1.404	0.244	1.367	0.255	0.489	0.691
Treatment	1, 157	-	-	2.030	0.156	0.000	0.993	0.041	0.840	0.028	0.868
Sex	1, 157	-	-	0.175	0.676	0.005	0.944	0.000	0.991	0.108	0.743
Year x season	6, 157	-	-	1.674	0.131	1.931	0.079	0.977	0.443	0.935	0.471
Year x treatment	2, 157	-	-	1.254	0.288	2.408	0.093	0.563	0.570	0.029	0.972
Year x sex	2, 157	-	-	0.871	0.421	1.055	0.351	2.870	0.060	0.568	0.568
Season x treatment	3, 157	-	-	1.579	0.197	0.685	0.563	0.706	0.550	0.485	0.693
Season x sex	3, 157	-	-	0.171	0.916	0.463	0.709	0.749	0.525	0.255	0.858
Treatment x sex	1, 157	-	-	2.399	0.123	0.318	0.574	3.476	0.064	0.019	0.891

* Indicates significant results.

Table 4 Results of the GLMMs evaluating the effect of study year, season, treatment and host sex on the abundance of the five most common ectoparasite species of sengis in the study area.

Factors	**df**	***R. warburtoni/arnoldi***		***Ixodes* spp.**		***Rhipicephalus* spp.**		***Rhipicentor* spp.**		**Chigger**	
		F	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**
Year	2, 157	6.519	0.002*	2.420	0.092	0.002	0.998	0.106	0.900	26.202	<0.0001
Season	3, 157	32.509	<0.0001*	13.333	<0.0001*	2.246	0.085	2.824	0.041*	60.810	<0.0001*
Treatment	1, 157	0.007	0.933	4.694	0.032*	0.002	0.966	0.000	0.993	0.501	0.480
Sex	1, 157	1.899	0.170	0.113	0.737	0.017	0.896	0.825	0.365	3.373	0.068
Year x season	6, 157	0.689	0.658	3.500	0.003*	1.623	0.144	5.226	<0.0001*	7.839	<0.0001*
Year x treatment	2, 157	0.440	0.645	0.726	0.485	2.207	0.113	1.649	0.196	0.217	0.805
Year x sex	2, 157	1.470	0.233	0.501	0.607	3.211	0.043*	5.306	0.006*	0.320	0.727
Season x treatment	3, 157	2.213	0.089	0.995	0.397	2.663	0.050*	0.285	0.836	1.183	0.318
Season x sex	3, 157	0.406	0.749	0.348	0.791	0.285	0.836	2.120	0.100	1.210	0.308
Treatment x sex	1, 157	0.036	0.849	6.583	0.011*	3.950	0.049*	5.111	0.025*	1.131	0.289

* Indicates significant results.

higher abundance of *Ixodes* spp. than untreated animals (0.2±0.1, LSD: P = 0.024, Table 4). Furthermore, the interaction between year and season was significant (Table 4, Figure 1). Post-hoc analyses showed no significant difference between seasons in the first and second year (LSD: P = 0.108). However, in the third year abundance was significantly higher in autumn than in spring and summer (Figure 1). The interaction between treatment and sex was significant (Table 4). Post-hoc analyses showed that treated males (1.6±0.6) had a higher abundance of *Ixodes* spp. than untreated males (0.1±0.1, LSD: P = 0.015). None of the other pairwise comparisons were significant (P ≥ 0.88). In addition, none of the remaining factors considered did affect the abundance of *Ixodes* spp. (Table 4).

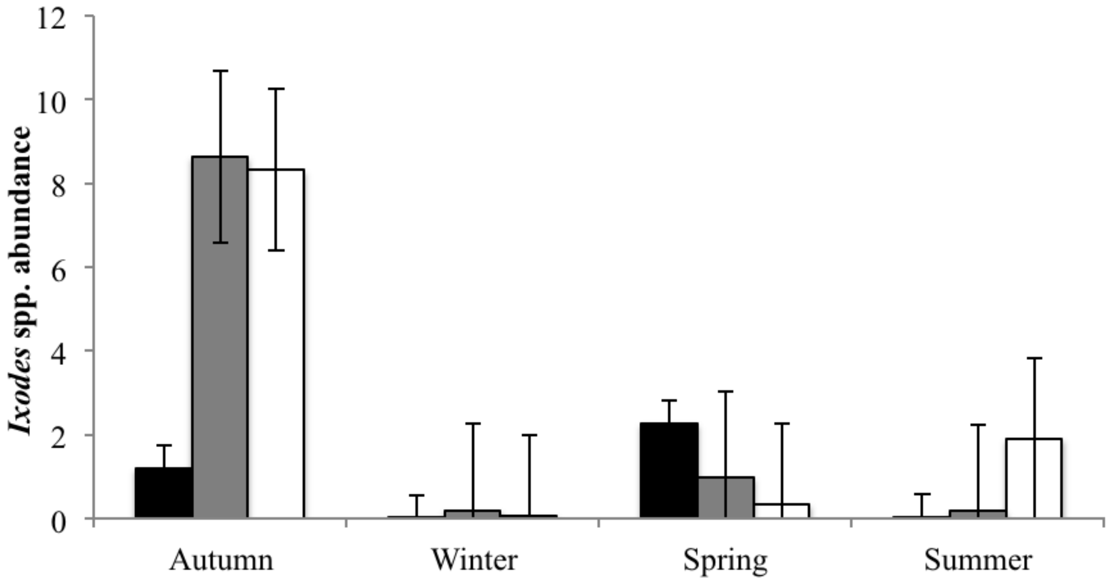

Figure 1 Effects of study year and season on the abundance of *Ixodes* spp. Displayed are means ± standard errors (SE). Black bars represent the first year of capture, grey bars represent the second year and white bars represent the third year.

None of the factors considered had a significant effect on the prevalence of *Rhipicephalus* spp. (Table 3). In contrast, the interaction between year and sex and between treatment and sex was significant for the abundance of *Rhipicephalus* spp. (Table 4). However, post-hoc analyses did not confirm these effects (LSD: $P \geq 0.97$). The interaction between season and treatment was significant (Table 4, Figure 2). Post-hoc analyses showed that in spring treated animals had a lower abundance of *Rhipicephalus* spp. than untreated ones (LSD: $P = 0.038$, Figure 2). In addition, treated animals had higher abundance in autumn than in spring (LSD: $P = 0.041$), but untreated animals had a significantly lower abundance in winter than in spring (LSD: $P = 0.012$, Figure 2). None of the remaining factors had a significant effect on the abundance of *Rhipicephalus* spp. (Table 4).

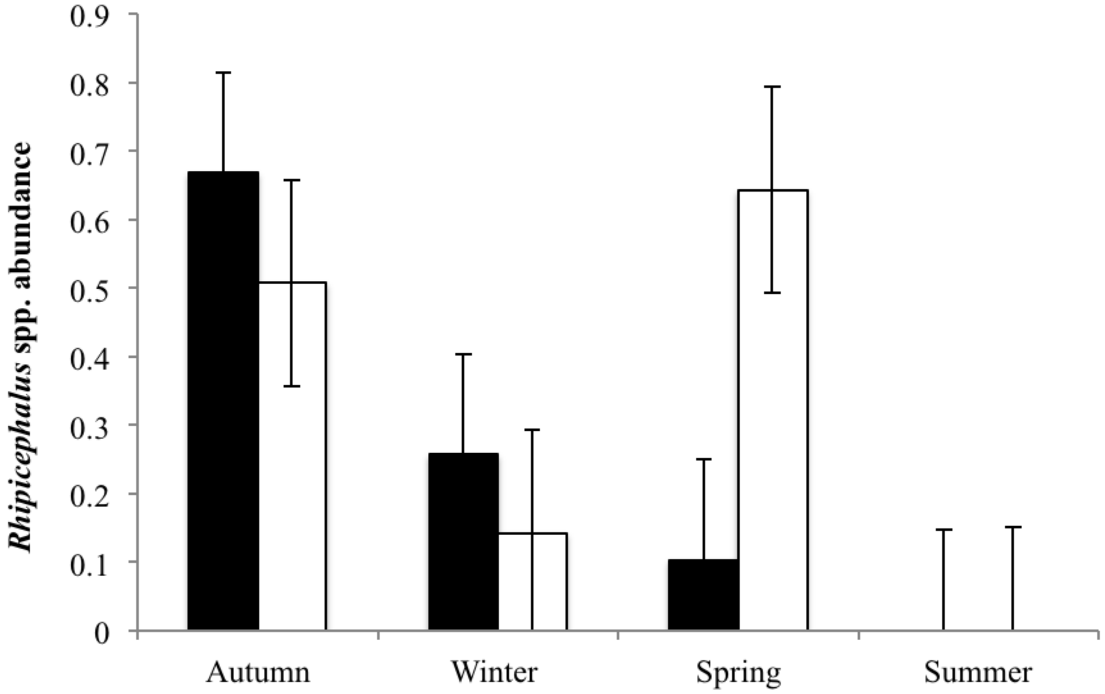

Figure 2 The effect of season and treatment on the abundance of *Rhipicephalus* spp. Displayed are means ± standard errors (SE). Black bars represent treated animals and white bars represent untreated animals.

The prevalence of *Rhipicentor* spp. did not vary significantly with any of the factors considered (Table 3). In contrast, the abundance of *Rhipicentor* spp. varied significantly with season (Table 4). Post-hoc analyses showed that the abundance of *Rhipicentor* spp. was significantly higher in autumn (0.40±0.16) than in summer (0.04±0.03, LSD: P = 0.03). None of the other pairwise comparisons were significant (P ≥ 0.18). The interaction between year and season was significant (Table 4, Figure 3). In autumn the abundance of *Rhipicentor* spp. was significantly lower in the second than in the third year (LSD: P = 0.009, Figure 3). In addition, it was significantly greater in summer of the first year compared to the third year (LSD: P = 0.014). Furthermore, in the third year, the abundance of *Rhipicentor* spp was significantly higher in autumn compared to spring (LSD: P = 0.006), and in summer compared to spring (LSD: P = 0.017, Figure 3). The interactions between year and sex and between treatment and sex were significant (Table 4). However, post-hoc tests did not confirm this (LSD: P ≥ 0.17). None of the remaining factors did significantly affect the abundance of *Rhipicentor* spp. (Table 4).

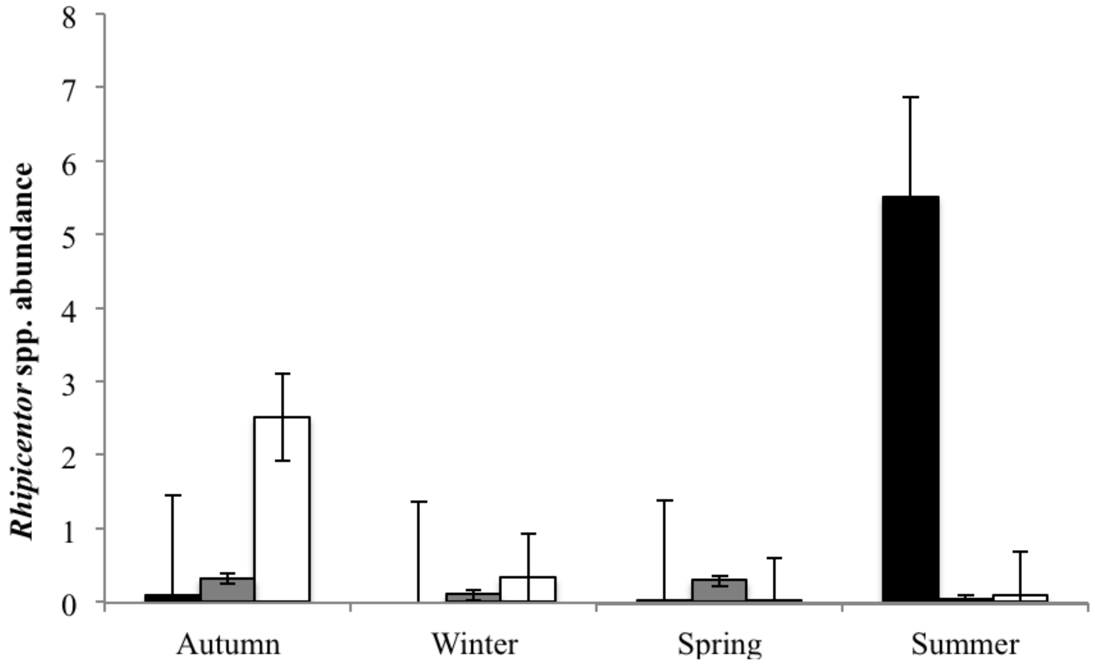

Figure 3 The effect of year and season on the abundance of *Rhipicentor* spp. Displayed are means ± standard errors (SE). Black bars represent the first year of capture, grey bars represent the second year and white bars represent the third year.

The prevalence of chiggers varied significantly between years (Table 3). Post-hoc analyses showed that the chigger prevalence was significantly lower in the first year (62.6%) compared to the second (96.7%, LSD: $P = 0.006$) and third year (97.3%, LSD: $P = 0.004$). None of the other factors considered did significantly affect the chigger prevalence. Similarly, the abundance of chiggers varied significantly between years (Table 4). Post-hoc analyses indicated that abundance of chiggers was significantly higher in second year (138.3±28.6) than in first year (17.6±4.1, LSD: $P < 0.0001$). None of the other pairwise comparisons were significant ($P \geq 0.15$). Furthermore, the abundance of chiggers differed significantly between seasons (Table 4). The abundance of chiggers was higher in spring (399.9±70.3) compared to summer (17.3±3.6) and autumn (99.1±19.1, LSD: $P < 0.0001$) and significantly lower in winter (20.3±6.1) than in autumn (99.11±19.05, $P < 0.0001$). None of the remaining comparison was significant ($P \geq 0.66$). The interaction between year and season was significant (Table 4, Figure 4). Post-hoc analyses showed that in first year the abundance of chiggers was significantly higher in autumn than in winter (LSD: $P = 0.008$) and lower in summer compared to spring (LSD: $P = 0.001$, Figure 4). Similarly, in the second year, abundance was significantly higher in spring compared to summer (LSD: $P = 0.003$, Figure 4) while none of the other comparisons were significant ($P \geq 0.25$). In the third year, the abundance of chiggers was significantly higher in autumn than winter (LSD: $P = 0.01$) and higher in spring compared to summer (LSD: $P = 0.003$, Figure 4). In addition, post-hoc analyses revealed that the abundance of chiggers was significantly lower in first year than in second year in autumn (LSD: $P = 0.019$, Figure 4). Similarly, it was significantly higher in second year than the first year in summer (LSD: $P = 0.004$) and winter ($P = 0.046$, Figure 4). None of the other pairwise comparisons were significant ($P \geq 0.28$). In addition, none of the remaining factors considered did significantly affect the abundance of chiggers (Table 4).

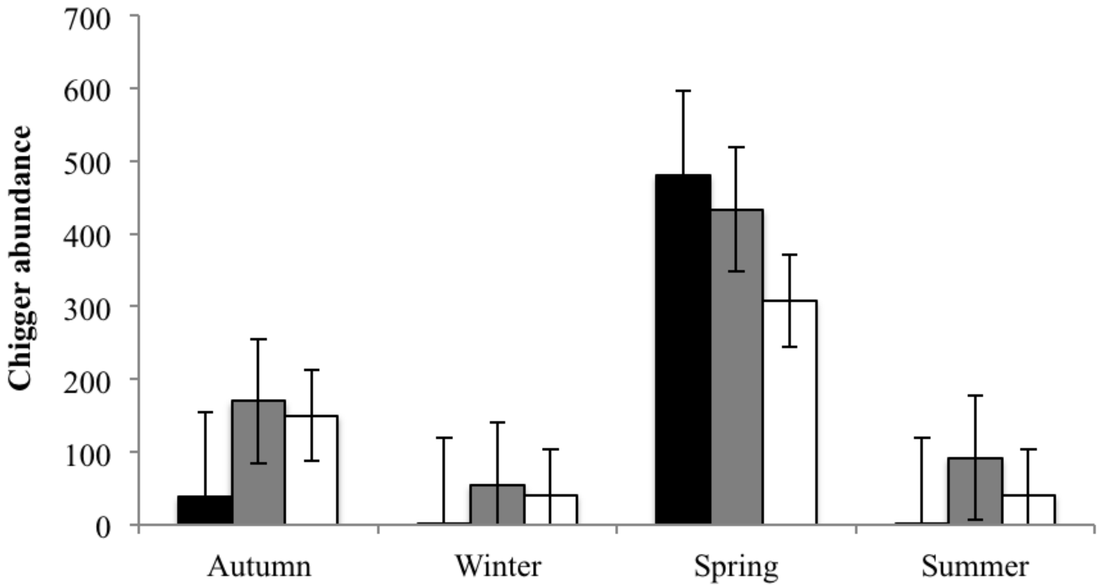

Figure 4 The effect of year and season on the abundance of chiggers. Displayed are means ± standard errors (SE). Black bars represent the first year of capture, grey bars represent the second year and white bars represent the third year.

Effect of abiotic factors (year and season), host sex, treatment and ectoparasite burden on host BCI

The BCI differed significantly between years (Table 5). Post-hoc analyses showed that animals in the second (0.86±0.02 LSD: P = 0.002) and third year (0.87±0.01 LSD: P = 0.0001) had a significantly higher BCI than in first year (0.77±0.02). No significant difference in BCI was found between the second and third study year (LSD: P = 0.638). In addition, the BCI varied significantly with season (Table 5). In winter (0.76±0.03) and summer (0.82±0.02) the BCI was significantly lower in comparison to spring (0.92±0.02, LSD: P = 0.0001 and P = 0.002, respectively). The BCI did not differ significantly between autumn and winter (LSD: P = 0.19). The interaction between year and season was significant (Table 5). Post-hoc analyses showed that in the first year, BCI was significantly higher in spring compared to winter (LSD: P = 0.001) and summer (LSD: P = 0.0001, Figure 5). There was no significant difference in BCI between autumn and winter (LSD: P = 0.192) in the first study year. In contrast, in the second year, BCI was significantly lower in winter than in spring (P = 0.003, Figure 5). None of the remaining comparisons were significant (P ≥ 0.237). None of the comparisons between seasons in the third year was significant (P ≥ 0.278). In addition, neither sex nor any of the five common ectoparasite species had a significant effect on BCI (P ≥ 0.368, Table 5).

Table 5 Summary table for the GLMM looking at effect of abiotic factors, host sex, treatment and abundance of the most common ectoparasite species on the BCI of sengis.

Factors	**Df**	**F**	**P**
Year	2, 144	7.603	0.001*
Season	3, 144	7.583	0.0001*
Treatment	1, 144	2.156	0.144
Sex	1, 144	0.050	0.824
Year x season	6, 144	2.567	0.022*
Year x treatment	2, 144	1.315	0.272
Year x sex	2, 144	0.686	0.505
Season x treatment	3, 144	0.958	0.414
Season x sex	3, 144	2.413	0.069
Treatment x sex	1, 144	0.084	0.773
***R. warburtoni/arnoldi* abundance**	1, 144	0.0816	0.368
***Ixodes* spp. abundance**	1, 144	0.075	0.784
***Rhipicephalus* spp. abundance**	1, 144	0.019	0.890
***Rhipicentor* spp. abundance**	1, 144	0.038	0.845
Chigger abundance	1, 144	0.665	0.416

* Indicates significant results.

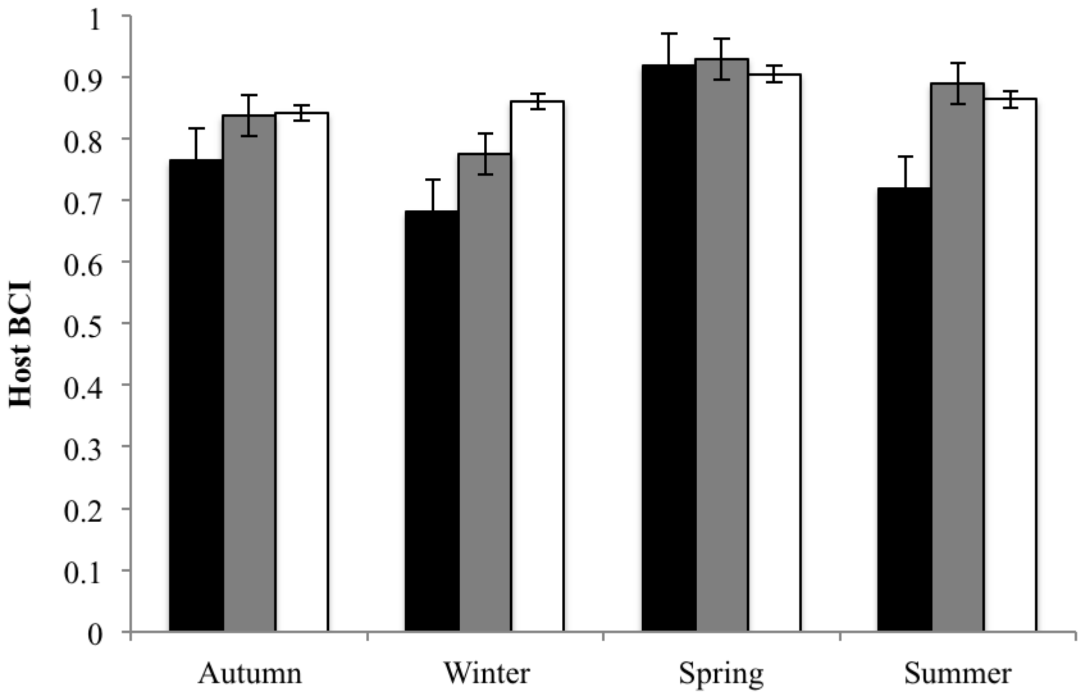

Figure 5 The effect of year and season on the host BCI. Displayed are means ± standard errors (SE). Black bars represent the first year of capture, grey bars represent the second year and white bars represent the third year.

DISCUSSION

A total of 14 ectoparasite species were collected in the present study, of these ectoparasites, five species were most prevalent. These were four ticks (*R. warburtoni/arnoldi*, *Ixodes* spp., *Rhipicephalus* spp. and *Rhipicentor* spp.) and one mite family (chiggers). Long-term changes in abundance and/or prevalence were apparent for two of the most prevalent and abundant ectoparasites, *R. warburtoni/arnoldi* and chigger. The abundance of *R. warburtoni/arnoldi* was significantly decreased throughout the third year, while the prevalence and abundance of chiggers was increased in the second and third year. The removal of the immature stages of *R. warburtoni/arnoldi* could substantially reduce the adult stages of the tick population and in turn the next generation of immature stages that sengis are exposed to. In addition, our treatment would have reduced the number of larvae and nymphs feeding on sengis and this in turn would reduce the number of resulting adults in the environment. In the present study the abundance of *R. warburtoni/arnoldi* was significantly greater in the first year of collection compared to the following two years when the Frontline® treatment was applied. This suggests that the manual removal of *R. warburtoni/arnoldi* nymphs and larvae once per season (first year) does affect the population of this tick to a much lesser degree than the action of the experimental treatment which extends over several weeks. Differences in long-term patterns for abundances of *R. warburtoni/arnoldi* and chiggers suggest that there may be a competitive relationship between these two species. The presence of *R. warburtoni/arnoldi* throughout the year might have masked additional competitive interactions between this species and any of the others due to the low number of other tick species.

Seasonal patterns were observed for all the species, but not for *Rhipicephalus* spp. The peak in abundance of *R. warburtoni/arnoldi* was observed in spring, while lowest numbers were observed in summer. In addition, the peak abundances of *Ixodes* spp. and *Rhipicentor* spp. was in autumn and lowest in spring, while peak abundance of chiggers was in summer and also lowest in spring. These seasonal patterns in tick species and chigger abundances can be attributed to changes in climatic changes, i.e. rainfall and changes in temperature (Marshall 1981). Previous studies on ticks and mites indicated that climatic changes can affect immature stages (i.e. eggs, larvae and nymphs) activity, growth and reproductive cycles (Randolph 2004). In addition, seasonal patterns in ectoparasite species can be attributed to the on-host and off-host life cycle, i.e. ectoparasites patterns differ with respect to their host association. Hence, they are expected to react differently to changes in environmental conditions (Midgley *et al.* 2003; Oguge *et al.* 2009).

Only weak effects of host sex on the abundance of some of the parasites collected were observed in the present study. Since sengis are monogamous, do not exhibit sexual dimorphism and ectoparasite burden has previously been shown to be independent of both body mass and length (Fagir *et al.* 2015; Lutermann *et al.* 2012b) this was not unexpected. This is furthermore supported by a study that showed that testosterone levels in male sengis are generally low (Medger *et al.* 2012).

With the exception of *Ixodes* spp., the Fronline® treatment did have no direct effects on any of the main parasites. The time elapsed between consecutive trips exceeded the period indicated by the manufacturer for the effectiveness of Frontline® of four to six weeks for ticks that has been confirmed in several laboratory studies (Wiedemann 2000; Dryden *et al.* 2008; Kužner *et al.* 2013). This may partially account for the lack of treatment effects. In addition, a study in another locality on the same host species has provided evidence for the effectiveness of the treatment employed in the current study (Hoffmann *et al.* 2016). The effects of treatment on the abundance of *Ixodes* spp. might be attributed to the large numbers of *R. warburtoni/arnoldi*, which may result in spatial constraints with regards to attachment sites as well as competition for food resources (i.e. blood meals) for both tick species. Although treatment did not have any direct effect on the abundance of any of the other main parasites, the significant decrease in numbers of *R. warburtoni/arnoldi* in the second and third years of the study when sengis were treated suggests that treatment was actually effective. The observed patterns in *R. warburtoni/arnoldi* as well as prevalence and abundance of *Ixodes* spp. and chiggers suggest a competitive interaction between these parasite species. Such relationships could also explain the observed drop in the abundance of *R. warburtoni/arnoldi* in summer that coincides with the peak in chigger abundance. This hypothesis is supported by the observation that the abundance of *R. warburtoni/arnoldi* was substantially greater prior to and after the peak in abundance of chiggers. In addition, an antagonistic interaction between *R. warburtoni/arnoldi* and chiggers would account for the observed increase in the prevalence of *Ixodes* spp. in autumn as well as the abundance of chiggers in autumn, winter and summer during the second and third year of study when the Frontline® treatment would have reduced the number of *R. warburtoni/arnoldi.*

No evidence for interspecific interactions was observed for the remaining tick species, which may be attributed to their low abundances compared to the other three species. Parasite species that spend the majority of their life cycle off-host (i.e. fleas, mites and ticks) are expected to be characterized by high turn-over rates. Therefore, our treatment should facilitate higher invasion rates for species that are prevented from invading a particular host by the presence of another parasite species (e.g. *R. warburtoni/arnoldi*) (Ferrari *et al.* 2009; Lutermann *et al.* 2015). Hence, although all ectoparasites were removed in the first year of the present study and our treatment targeted specifically ticks and fleas, but not lice and mites, the increased infestation rates of other parasite species provide evidence for competitive relationships between parasites. The observed long-term changes resulting from treatment effects in the present study contrasts with observations reported by Knowles *et al.* (2013) for endoparasite community interactions. These differences can be linked to the targeted species, i.e. ectoparasites in the present study and endoparasites in the study by Knowles *et al.* (2013). The nematode species targeted by Knowles *et al.* (2013) have a direct life cycle, in contrasts tick species in the present study spend the major part of their life cycle off-host and moult to the next stage after each completed blood meal (Sonenshine 1991). The interspecific interaction between chiggers and *R. warburtoni/arnoldi* is likely to be mediated by direct competition for attachment sites. Unlike ticks, chiggers are not haematophagous i.e. chiggers attach to the host, pierce the skin, inject enzymes into the bite wound that digest cellular contents, and then suck up the digested tissue (Arnold 1986). Therefore, it is unlikely that the competitive relationship between chiggers and the two tick species is mediated by direct competition for host resources, but rather it is a competitive relationship for sites of attachment (Combes 2001; Pedersen and Fenton 2007). In addition, immature stages of ticks (i.e. larvae and nymphs) are substantially larger in size compared to chiggers (D. Fagir, personal observation). Hence this size difference between ticks and chiggers may give the ticks a competitive advantage over chiggers. This hypothesis is supported by the fact that the majority of *R.*

warburtoni/arnoldi attach to the ridges of the ear pinnae as well as on the lower back,while chiggers attach on the rear and around the base of the tail (Fagir *et al.* 2015; Lutermann *et al.* 2015). A study by Fagir *et al* (2014) on a sympatric rodent (*Micaelamys namaquensis*) reported that *R. warburtoni/arnoldi* is largely absent and chiggers are mostly found on the ear ridges. Furthermore, because of the differences between ticks and chiggers with regards to their feeding methods and duration as well as differences in behaviour, ticks and chiggers may trigger distinct immune responses (Pollock *et al.* 2012). Several studies have supported the hypothesis of interspecific competition for feeding sites, e.g. between seabirds mites (Choe and Kim 1989), rodent fleas (Krasnov *et al.* 2005) and rodent fleas and Ixodid ticks (Krasnov *et al.* 2010). Similarly, an antagonistic interaction relationship between *R. warburtoni/arnoldi* and *Ixodes* spp. could be mediated by direct competition for attachment sites. In addition, competition for host resources (i.e. blood) for these haematophagous species may play a role.

Although there was no significant direct effect of our treatment on the BCI it increased significantly through the three years of study. However, the increased BCI coincided with the decrease in the abundance of *R. warburtoni/arnoldi* suggesting that the removal of parasites neutralised the negative costs usually associated with high parasitic infections (Ebert *et al.* 2000; Medley 2002) suggesting an indirect effect of our treatment. Several studies have suggested that parasitic infestation bears a cost, such as reducing host condition as a result of the combination (i.e. the reduction of host resources and increased expenditure due to the triggered immune responses) of opportunistic parasites infesting already immune compromised individuals (Ebert *et al.* 2000; Ebert and Herre 1996; Lafferty and Kuris 1999). The low BCI in winter is expected as in winter food availability is low and thermoregulatory demands are high but the low BCI in the summer was unexpected and can be linked to the increasing number of juveniles that have been recruited into the host population (Hillegass *et al.* 2010). Although the capture state was not included in the present study, it has been suggested that on their first capture animals had lower body condition than recaptures suggesting that the removal of ectoparasites for any period of time could be of great benefit to the animal (Hillegass *et al.* 2010; Scantlebury *et al.* 2007). The observed lack of direct effects of ectoparasites in the present study provides no support for host condition dependent host choice by parasites or for costs of parasitism. However, the year effect would suggest there is an indirect negative effect of parasites on host BCI and that the actual BCI might be a result of more long-term patterns. Previous studies have suggested that there is limited effect apparent of parasitic infestation, most likely due to the co-evolution of host-parasite interactions when considering untreated animals (Kiffner *et al.* 2011a; Medley 2002; Rigby *et al.* 2002). However, once treated there might be some cost involved to harbouring high abundances of parasites (e.g. ticks found on sengis) and this cost may not be apparent due to the strong co-evolution of host-parasite interactions (Morand and Krasnov 2006). Furthermore, the removal of ectoparasites may have freed more energy and time for host to invest in other activities (e.g. reproductive activities and territory defense and food acquisition) (Patterson *et al.* 2015). In addition, body mass measures may hide some of the hidden parasite-driven variation in the mass of certain organs such as spleen and fat storage (Scantlebury *et al.* 2010).

The present study investigates the long-term patterns of the five most common ectoparasites exploiting eastern rock sengis as well as the effects of experimental perturbation on the resilience of the ectoparasite community and host BCI. While the abundance of the most prevalent and abundant tick species decreased over the course of the study the opposite pattern was observed for the second most common parasite, chiggers. In addition, the prevalence and abundance of ticks and chiggers differed significantly with season, but few sex effects on prevalence and abundance of ectoparasite were found. Our data suggests a competitive relationship between the two dominant ectoparasite species that is likely to be linked to competition over attachment sites. The experimental perturbation employed in the current study resulted in substantial changes in ectoparasite community composition suggesting long-term effects of our treatment. Our results highlight the complexity of interspecific interactions within an ectoparasite community and stress the need for longitudinal studies on small mammal ectoparasites.

REFERENCES

ALTIZER, S., DOBSON, A., HOSSEINI, P., HUDSON, P., PASCUAL, M. & ROHANI, P. 2006. Seasonality and the dynamics of infectious diseases. *Ecology letters,* 9**,** 467-484.

ALTIZER, S., NUNN, C. L., THRALL, P. H., GITTLEMAN, J. L., ANTONOVICS, J., CUNNINGHAM, A. A., DOBSON, A. P., EZENWA, V., JONES, K. E., PEDERSEN, A. B., POSS, M. & PULLIAM, J. R. C. 2003. Social Organization and Parasite Risk in Mammals: Integrating Theory and Empirical Studies. *Annual Review of Ecology, Evolution, and Systematics,* 34**,** 517-547.

ANDREWS, R. & PETNEY, T. 1981. Competition for sites of attachment to hosts in three parapatric species of reptile tick. *Oecologia,* 51**,** 227-232.

ARNOLD, E. N. 1986. MITE POCKETS OF LIZARDS, A POSSIBLE MEANS OF REDUCING DAMAGE BY ECTOPARASITES. *Biological Journal of the Linnean Society,* 29**,** 1-21.

BAER-LEHMAN, M. L., LIGHT, T., FULLER, N. W., BARRY-LANDIS, K. D., KINDLIN, C. M. & STEWART JR, R. L. 2012. Evidence for competition between Ixodes scapularis and Dermacentor albipictus feeding concurrently on white-tailed deer. *Experimental and applied acarology,* 58**,** 301-314.

BARBOSA, P., CALDAS, A. & GODFRAY, H. C. J. 2007. Comparative food web structure of larval macrolepidoptera and their parasitoids on two riparian tree species. *Ecological Research,* 22**,** 756-766.

BEAUCOURNU, J., HORAK, I. & FOURIE, L. 2003. Fleas of elephant shrews (Mammalia, Macroscelididae), and a new host and locality record for *Macroscelidopsylla albertyni* De Meillon & Marcus, 1958 (Siphonaptera, Chimaeropsyllidae). *The Onderstepoort journal of veterinary research,* 70**,** 251.

BIZE, P., JEANNERET, C., KLOPFENSTEIN, A. & ROULIN, A. 2008. What makes a host profitable? Parasites balance host nutritive resources against immunity. *American Naturalist,* 171**,** 107-118.

BORDES, F., MORAND, S., KRASNOV, B. R. & POULIN, R. 2010. Parasite diversity and latitudinal gradients in terrestrial mammals. *The Biogeography of Host-Parasite Interactions***,** 89-98.

BRUCE, M. C., DONNELLY, C. A., ALPERS, M. P., GALINSKI, M. R., BARNWELL, J. W., WALLIKER, D. & DAY, K. P. 2000. Cross-species interactions between malaria parasites in humans. *Science,* 287**,** 845-848.

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***,** 575-583.

CALABRESE, J. M., BRUNNER, J. L. & OSTFELD, R. S. 2011. Partitioning the aggregation of parasites on hosts into intrinsic and extrinsic components via an extended Poisson-gamma mixture model. *PLoS One,* 6**,** e29215.

CATTADORI, I. M., ALBERT, R. & BOAG, B. 2007. Variation in host susceptibility and infectiousness generated by co-infection: the myxoma–Trichostrongylus retortaeformis case in wild rabbits. *Journal of the Royal Society Interface,* 4**,** 831-840.

CHAPMAN, C. A., SAJ, T. L. & SNAITH, T. V. 2007. Temporal dynamics of nutrition, parasitism, and stress in colobus monkeys: implications for population regulation and conservation. *American Journal of Physical Anthropology,* 134**,** 240-250.

CHOE, J. C. & KIM, K. C. 1989. Microhabitat selection and coexistence in feather mites (Acari: Analgoidea) on Alaskan seabirds. *Oecologia,* 79**,** 10-14.

COMBES, C. 2001. *Parasitism: the ecology and evolution of intimate interactions,* Chicago & London, University of Chicago Press.

COX, F. 2001. Concomitant infections, parasites and immune responses. *Parasitology,* 122**,** S23-S38.

DEGEN, A. A. 2006. Effect of macroparasites on the energy budget of small mammals. *Morand et al. 2009. Micromammals and Macroparasites, from Evolutionary Ecology ro Management* Japan Springer.

DELAHAY, R., SPEAKMAN, J. & MOSS, R. 1995. The energetic consequences of parasitism: effects of a developing infection of *Trichostrongylus tenuis* (Nematoda) on red grouse (*Lagopus lagopus scoticus*) energy balance, body weight and condition. *Parasitology,* 110**,** 473-482.

DRYDEN, M. W., PAYNE, P. A., MCBRIDE, A., MAILEN, S., SMITH, V. & CARITHERS, D. 2008. Efficacy of Fipronil (9.8% w/w)+(S)-Methoprene (8.8% w/w) and Imidacloprid (8.8% w/w)+ Permethrin (44% w/w) against *Dermacentor variabilis* (American Dog Tick) on Dogs. *Veterinary therapeutics,* 9**,** 15.

EBERT, D. & HERRE, E. A. 1996. The evolution of parasitic diseases. *Parasitology today,* 12**,** 96-101.

EBERT, D., LIPSITCH, M. & MANGIN, K. L. 2000. The effect of parasites on host population density and extinction: experimental epidemiology with Daphnia and six microparasites. *The American Naturalist,* 156**,** 459-477.

EZENWA, V. O., ETIENNE, R. S., LUIKART, G., BEJA- PEREIRA, A. & JOLLES, A. E. 2010. Hidden consequences of living in a wormy world: nematodeinduced immune suppression facilitates tuberculosis invasion in African buffalo. *The American Naturalist,* 176**,** 613-624.

FAGIR, D. M., HORAK, I. G., UECKERMANN, E. A., BENNETT, N. C. & LUTERMANN, H. 2015. Ectoparasite diversity in the eastern rock sengis (*Elephantulus myurus*): the effect of seasonality and host sex. *African Zoology,* 50**,** 109-117.

FAGIR, D. M., UECKERMANN, E. A., HORAK, I. G., BENNETT, N. C. & LUTERMANN, H. 2014. The Namaqua rock mouse (*Micaelamys namaquensis*) as a potential reservoir and host of arthropod vectors of diseases of medical and veterinary importance in South Africa. *Parasites & Vectors,* 7.

FENTON, A., KNOWLES, S. C., PETCHEY, O. L. & PEDERSEN, A. B. 2014. The reliability of observational approaches for detecting interspecific parasite interactions: comparison with experimental results. *International journal for parasitology,* 44**,** 437-445.

FENTON, A., VINEY, M. E. & LELLO, J. 2010. Detecting interspecific macroparasite interactions from ecological data: patterns and process. *Ecology letters,* 13**,** 606-615.

FERRARI, N., CATTADORI, I., RIZZOLI, A. & HUDSON, P. 2009. Heligmosomoides polygyrus reduces infestation of Ixodes ricinus in free-living yellow-necked mice, *Apodemus flavicollis*. *Parasitology,* 136**,** 305-316.

FOLSTAD, I. & KARTER, A. J. 1992. Parasites, bright males, and the immunocompetence handicap. *American Naturalist***,** 603-622.

FORBES, A., HUCKLE, C., GIBB, M., ROOK, A. & NUTHALL, R. 2000. Evaluation of the effects of nematode parasitism on grazing behaviour, herbage intake and growth in young grazing cattle. *Veterinary parasitology,* 90**,** 111-118.

FOURIE, L., TOIT, J. D., KOK, D. & HORAK, I. 1995. Arthropod parasites of elephantshrews, with particular reference to ticks. *Mammal Review,* 25**,** 31-37.

GIORGI, M. S., ARLETTAZ, R., CHRISTE, P. & VOGEL, P. 2001. The energetic grooming costs imposed by a parasitic mite (*Spinturnix myoti*) upon its bat host (*Myotis myotis*). *Proceedings of the Royal Society of London B: Biological Sciences,* 268**,** 2071-2075.

GOÜY DE BELLOCQ, J., KRASNOV, B., KHOKHLOVA, I., GHAZARYAN, L. & PINSHOW, B. 2006. Immunocompetence and flea parasitism of a desert rodent. *Functional Ecology,* 20**,** 637-646.

GRAHAM, A. L. 2008. Ecological rules governing helminth–microparasite coinfection. *Proceedings of the National Academy of Sciences,* 105**,** 566-570.

HALL, H. T. B. 1985. *Diseases and parasites of livestock in the Tropics*, Longman, London & New York.

HANLEY, K., BIARDI, J., GREENE, C., MARKOWITZ, T., O'CONNELL, C. & HORNBERGER, J. 1996. The behavioral ecology of host-parasite interactions: an interdisciplinary challenge. *Parasitology Today,* 12**,** 371-372.

HARRISON, A., BOWN, K. J. & HORAK, I. G. 2011. Detection of *Anaplasma bovis* in an undescribed tick species collected from the eastern rock sengi *Elephantulus myurus*. *Journal of Parasitology,* 97**,** 1012-6.

HILLEGASS, M. A., WATERMAN, J. M. & ROTH, J. D. 2010. Parasite removal increases reproductive success in a social African ground squirrel. *Behavioral Ecology,* 21**,** 696-700.

HOBY, S., SCHWARZENBERGER, F., DOHERR, M. G., ROBERT, N. & WALZER, C. 2006. Steroid hormone related male biased parasitism in chamois, *Rupicapra rupicapra rupicapra*. *Veterinary parasitology,* 138**,** 337-348.

HOFFMANN, S., HORAK, I.G., BENNETT, N.C. AND LUTERMANN, H., 2016. Evidence for interspecific interactions in the ectoparasite infracommunity of a wild mammal. *Parasites & vectors*, *9* (1), p.1.

HOPKINS, G. H. E. 1949. The Hostassociations of the lice of mammals. Proceedings of the Zoological Society of London. Wiley Online Library, 387-604.

HORAK, I. G., LUTERMANN, H., MEDGER, K., APANASKEVICH, D. A. & MATTHEE, C. A. 2012. Natural hosts of the larvae of *Nuttalliella* sp. (*N. namaqua*) (Acari: Nuttalliellidae). *Onderstepoort Journal of Veterinary Research,* 79**,** E1-2.

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

KIFFNER, C., LÖDIGE, C., ALINGS, M., VOR, T. & RÜHE, F. 2011a. Bodymass or sexbiased tick parasitism in roe deer (*Capreolus capreolus*). A GAMLSS approach. *Medical and veterinary entomology,* 25**,** 39-45.

KIFFNER, C., VOR, T., HAGEDORN, P., NIEDRIG, M. & RUEHE, F. 2011b. Factors affecting patterns of tick parasitism on forest rodents in tick-borne encephalitis risk areas, Germany. *Parasitology Research,* 108**,** 323-335.

KIM, K. C. 1985. *Coevolution of parasitic arthropods and mammals,* New York, USA, John Wiley & Sons.

KNOWLES, S. C. L., FENTON, A., PETCHEY, O. L., JONES, T. R., BARBER, R. & PEDERSEN, A. B. 2013. Stability of within-host - parasite communities in a wild mammal system. *Proceedings of the Royal Society Biological Sciences Series B,* 280**,** 1-9.

KRANTZ, G. & WALTER, D. 2009. A manual of acarology, 3rd. Lubbock, TX: Texas Tech University Press.

KRASNOV, B. R., BURDELOVA, N. V., KHOKHLOVA, I. S., SHENBROT, G. I. & DEGEN, A. 2005. Larval interspecific competition in two flea species parasitic on the same rodent host. *Ecological Entomology,* 30**,** 146-155.

KRASNOV, B. R., STANKO, M. & MORAND, S. 2010. Competition, facilitation or mediation via host? Patterns of infestation of small European mammals by two taxa of haematophagous arthropods. *Ecological Entomology*, 35**,** 37-44.

KUŽNER, J., TURK, S., GRACE, S., SONI-GUPTA, J., FOURIE, J. J., MARCHIONDO, A. A. & RUGG, D. 2013. Confirmation of the efficacy of a novel fipronil spot-on for the treatment and control of fleas, ticks and chewing lice on dogs. *Veterinary parasitology,* 193**,** 245-251.

LAFFERTY, K. D. & KURIS, A. M. 1999. How environmental stress affects the impacts of parasites. *Limnology and Oceanography,* 44**,** 925-931.

LEDGER, J. A. 1980. *The arthropod parasites of vertebrates in Africa south of the Sahara. Volume IV. Phthiraptera (Insecta),* South African Institute for Medical Research.

LELLO, J., BOAG, B., FENTON, A., STEVENSON, I. R. & HUDSON, P. J. 2004. Competition and mutualism among the gut helminths of a mammalian host. *Nature,* 428**,** 840-844.

LUTERMANN, H., FAGIR, D. M. & BENNETT, N. C. 2015. Complex interactions within the ectoparasite community of the eastern rock sengi (*Elephantulus myurus*). *International Journal of Parasitology: Parasites and Wildlife,* 4**,** 148-58.

LUTERMANN, H., MEDGER, K. & HORAK, I. G. 2012a. Abiotic and biotic determinants of tick burdens in the eastern rock sengi (*Elephantulus myurus*). *Medical and Veterinary Entomology,* 26**,** 255-62.

LUTERMANN, H., MEDGER, K. & HORAK, I. G. 2012b. Effects of life-history traits on parasitism in a monogamous mammal, the eastern rock sengi (*Elephantulus myurus*). *Naturwissenschaften,* 99**,** 103-110.

MACLEOD, J., COLBO, M., MADBOULY, M. & MWANAUMO, B. 1977. Ecological studies of ixodid ticks (Acari: Ixodidae) in Zambia. III. Seasonal activity and attachment sites on cattle, with notes on other hosts. *Bulletin of Entomological Research,* 67**,** 161-173.

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

MATTHEE, S., MCGEOCH, M. A. & KRASNOV, B. R. 2010. Parasite-specific variation and the extent of male-biased parasitism; an example with a South African rodent and ectoparasitic arthropods. *Parasitology,* 137**,** 651-60.

MEDGER, K., CHIMIMBA, C. T., BENNETT, N. C. & KITCHENER, A. 2012. Seasonal reproduction in the eastern rock elephant-shrew: influenced by rainfall and ambient temperature? *Journal of Zoology,* 288**,** 283-293.

MEDLEY, G. 2002. The epidemiological consequences of optimisation of the individual host immune response. *Parasitology,* 125**,** S61-S70.

MERINO, S. & MØLLER, A. P. 2010. Host-parasite interactions and climate change. *Effects of climate change on birds. Oxford University Press, New York***,** 213-226.

MIDEO, N. 2009. Parasite adaptations to within-host competition. *Trends in parasitology,* 25**,** 261-268.

MIDGLEY, G., HANNAH, L., MILLAR, D., THUILLER, W. & BOOTH, A. 2003. Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biological Conservation,* 112**,** 87-97.

MØLLER, A., NIELSEN, J. & GARAMSZEGI, L. Z. 2006. Song post exposure, song features, and predation risk. *Behavioral Ecology,* 17**,** 155-163.

MOORE, S. L. & WILSON, K. 2002. Parasites as a viability cost of sexual selection in natural populations of Mammals. *Science,* 297**,** 2015-2018.

MOORING, M. S., PATTON, M. L., REISIG, D. D., OSBORNE, E. R., KANALLAKAN, A. L. & AUBERY, S. M. 2006. Sexually dimorphic grooming in bison: the influence of body size, activity budget and androgens. *Animal Behaviour,* 72**,** 737-745.

MORAND, S. & KRASNOV, B. R. E. 2006. *Micromammals and Macroparasites: From Evolutionary Ecology to Management,* Tokyo: Springer-Verlag, Japan.

MORENO, P., EBERHARDT, M., LAMATTINA, D., PREVITALI, M. & BELDOMENICO, P. 2013. Intra-phylum and inter-phyla associations among gastrointestinal parasites in two wild mammal species. *Parasitology research,* 112**,** 3295-3304.

NICOLL, M. E. & RATHBUN, G. B. 1990. *African Insectivora and elephant-shrews: an action plan for their conservation,* IUCN.

OGUGE, N., DURDEN, L., KEIRANS, J., BALAMI, H. & SCHWAN, T. 2009. Ectoparasites (sucking lice, fleas and ticks) of small mammals in southeastern Kenya. *Medical and veterinary entomology,* 23**,** 387-392.

PATTERSON, J. E. H., NEUHAUS, P., KUTZ, S. J. & RUCKSTUHL, K. E. 2015. Patterns of ectoparasitism in North American red squirrels (*Tamiasciurus hudsonicus*): Sex-biases, seasonality, age, and effects on male body condition. *International journal for parasitology. Parasites and wildlife,* 4**,** 301-6.

PEDERSEN, A. B. & ANTONOVICS, J. 2013. Anthelmintic treatment alters the parasite community in a wild mouse host. *Biology Letters,* 9**,** 1-4.

PEDERSEN, A. B. & FENTON, A. 2007. Emphasizing the ecology in parasite community ecology. *Trends in Ecology & Evolution,* 22**,** 133-139.

PEDERSEN, A. B. & GREIVES, T. J. 2008. The interaction of parasites and resources cause crashes in a wild mouse population. *Journal of Animal Ecology,* 77**,** 370-377.

PEREZ-ORELLA, C. & SCHULTE-HOSTEDDE, A. I. 2005. Effects of sex and body size on ectoparasite loads in the northern flying squirrel (*Glaucomys sabrinus*). *Canadian Journal of Zoology,* 83**,** 1381-1385.

PETNEY, T. N. & ANDREWS, R. H. 1998. Multiparasite communities in animals and humans: frequency, structure and pathogenic significance. *International journal for parasitology,* 28**,** 377-393.

POLLOCK, N. B., VREDEVOE, L. K. & TAYLOR, E. N. 2012. The effect of exogenous testosterone on ectoparasite loads in freeranging western fence lizards. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology,* 317**,** 447-454.

POULIN, R. 1999. The functional importance of parasites in animal communities: many roles at many levels? *International journal for parasitology,* 29**,** 903-914.

PRICE, P. W., WESTOBY, M., RICE, B., ATSATT, P. R., FRITZ, R. S., THOMPSON, J. N. & MOBLEY, K. 1986. Parasite mediation in ecological interactions. *Annual Review of Ecology and Systematics,* 17**,** 487-505.

RANDALL, J., CABLE, J., GUSCHINA, I., HARWOOD, J. L. & LELLO, J. 2013. Endemic infection reduces transmission potential of an epidemic parasite during co-infection. *Proceedings of the Royal Society of London B: Biological Sciences,* 280**,** 20131500.

RANDOLPH, S., GREEN, R., HOODLESS, A. & PEACEY, M. 2002. An empirical quantitative framework for the seasonal population dynamics of the tick Ixodesricinus. *International journal for parasitology,* 32**,** 979-989.

RANDOLPH, S. E. 2004. Tick ecology: processes and patterns behind the epidemiological risk posed by ixodid ticks as vectors. *Parasitology,* 129**,** S37-S65.

RANDOLPH, S. E. & STOREY, K. 1999. Impact of microclimate on immature tick-rodent host interactions (Acari: Ixodidae): implications for parasite transmission. *Journal of Medical Entomology,* 36**,** 741-748.

RATHBUN, G. & RATHBUN, C. 2006. Social structure of the bushveld sengi (*Elephantulus intufi*) in Namibia and the evolution of monogamy in the Macroscelidea. *Journal of Zoology,* 269**,** 391-399.

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

ROLFF, J. 2002. Bateman's principle and immunity. *Proceedings of the Royal Society of London B: Biological Sciences,* 269**,** 867-872.

SCANTLEBURY, M., MAHER MCWILLIAMS, M., MARKS, N. J., DICK, J. T. A., EDGAR, H. & LUTERMANN, H. 2010. Effects of life-history traits on parasite load in grey squirrels. *Journal of Zoology,* 282**,** 246-255.

SCANTLEBURY, M., WATERMAN, J., HILLEGASS, M., SPEAKMAN, J. & BENNETT, N. 2007. Energetic costs of parasitism in the Cape ground squirrel *Xerus inauris*. *Proceedings of the Royal Society of London B: Biological Sciences,* 274**,** 2169-2177.

SCHMIDT, G. & ROBERT, L. 2009. Phylum apicomplexa: malaria organisms and piroplasms. *Foundation of Parasitology, 8th ed.(Roberts, L. and Janovy, J. Jr eds.), McGraw-Hill, New York***,** 147-174.

SCHULTE-HOSTEDDE, A., MILLAR, J. & HICKLING, G. 2001. Evaluating body condition in small mammals. *Canadian Journal of Zoology,* 79**,** 1021-1029.

SEGERMAN, J. 1995. *Siphonaptera of southern Africa: handbook for the identification of fleas,* South African Institute for Medical Research.

SHELDON, B. C. & VERHULST, S. 1996. Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. *Trends in ecology & evolution,* 11**,** 317-321.

SKINNER, J. D. & CHIMIMBA, C. T. 2005. *The mammals of the southern African subregion. 3rd revised edition.*

SONENSHINE, D. E. 1991. The biology of ticks, vol. I.

VINEY, M. E. & GRAHAM, A. L. 2013. Patterns and processes in parasite co-infection. *Advances in Parasitology,* 82**,** 321-369.

WALKER, J. B., KEIRANS, J. E. & HORAK, I. G. 2000. *The genus Rhipicephalus (Acari, Ixodidae): a guide to the brown ticks of the world*, Cambridge University Press.

WIEDEMANN, C. 2000. Studies on the efficacy of Fipronil against ectoparasites-II. Tick control. *Tierarztliche Umschau*, 55**,** 211-+.

CHAPTER FIVE

GENERAL DISCUSSION

Despite the large number of incidental reports and studies on the ectoparsite fauna of African small mammals, most of these studies are descriptive, only focus on a single-host-single-parasite or are limited to investigating the role of a particular parasite taxon (e.g. ticks) as a reservoir of zoonotic diseases (De Graaff 1981; Fagir and El-Rayah 2009; Harrison *et al.* 2011, 2012; Horak *et al.* 2005; Yonas *et al.* 2011). In contrast, the present study looked at the entire ectoparasite community of two host species, the Namaqua rock mouse (*Micaelamys namaquensis*) and the eastern rock sengi (*Elephantulus myurus*) over a number of years. Both host species were infested by a wide diversity of ectoparasite species. A total of 6,725 ectoparasites were collected from the mice, whereas sengis were infested by a total of 37,175 ectoparasites (including fleas, lice, mites and ticks for both hosts). In addition to harbouring vastly different numbers of parasites the two species also sustained very different ectoparasite species assemblages. For the Namaqua rock mouse, the most prevalent parasites were three species of flea (*Xenopsylla brasiliensis*, *Epirimia aganippes* and *Chiastopsylla godfreyi*), two species of tick (*Rhipicephalus distinctus* and *Haemaphysalis* spp.) and one family of mites (chiggers). In addition, chiggers were the most abundant parasite recovered from the mice. As for sengis, the most prevalent ectoparasites were four species of ticks (*Rhipicephalus warburtoni*/*arnoldi, Ixodes* spp., *R. distinctus* and *Rhipicentor* spp.) and chiggers, while fleas only occurred at very low prevalence and abundance. Only *Rhipicephalus warburtoni*/*arnoldi* and chiggers occurred in large numbers and were most abundant on sengis. Chiggers favoured both hosts and this can be attributed to the fact that chiggers are generalist ectoparasites with a worldwide distribution (Bordes *et al.* 2010; Fain *et al.* 1980; Hoffmann *et al.* 2016). In contrast, sengis were heavily infested and favoured by ticks compared to the mice. Infestation of sengis by a large numbers of immature stages of *R. warburtoni*/*arnoldi, Ixodes* spp., *R. distinctus* and *Rhipicentor* spp. has been reported in previous studies (Fourie *et al.* 1995, 2005; Harrison *et al.* 2012; Lutermann *et al.* 2012a, b). In an experimental study by Harrison *et al* (2012) investigating feeding success in two species of tick (*R. warburtoni* and *Ixodes rubicundus*) on Namaqua rock mouse and sengi, ticks attached and fed successfully on sengis, but not on the mice, suggesting that these ticks exhibit true host specificity. Furthermore, there are several factors that could explain the differences in number of parasite species infecting these two hosts. Although the two hosts inhabit the same habitat (i.e. rocky outcrops), they have different life-history traits. For instance, sengis are a monogamous species (Ribble and Perrin 2005) while the Namaqua rock mouse is communal (Skinner and Chimimba 2005). In a social system (or group living species), individuals proximity as well as number and contact rates are directly affected by the size, composition of the social group and differences in mating success between sexes (Altizer *et al.* 2003; Thrall *et al.* 2000). Hence, sociality could facilitate parasite transmission rates in particular for directly transmitted parasites (e.g. fleas) (Arneberg 2002; Cote and Poulin 1995; Roberts *et al.* 2002). On the other hand, communal animals may benefit from allogrooming (Bordes *et al.* 2007; Hillegass *et al.* 2008). Activity differences between the two hosts may play a role in infestation rates; *M. namaquensis* is nocturnal (Fleming and Nicolson 2004) while *E. myurus* is active throughout the day and night (Ribble and Perrin 2005). Parasites such as ticks may also exhibit daily detachment and questing patterns (Du Toit *et al.* 1994; Madden and

Madden 2005). Therefore, differences in host daily activity patterns may determine the frequency with which hosts come in contact with ticks. Furthermore, mice keep nests in which fleas as well as non-chigger mites spend some time of their life cycle while these environments (i.e. the nests) are not very conducive to ticks. In contrast sengis just shelter between rocks where they also leave their altricial young, thus sengis might be easier targets for ticks seeking humid microclimates between the rocks (Skinner and Chimimba 2005).

The present study showed that as with many studies from the northern hemisphere (Kiffner *et al.* 2011a, b; Laudisoit *et al.* 2009; Maher and Timm 2014; Morand and Krasnov 2006), seasonal patterns are prevalent in subtropical systems as well. All ectoparasites recovered from both hosts exhibited strong seasonal patterns. With the exception of lice, the prevalence of all parasite taxa infesting *M. namaquensis* showed seasonal variation in prevalence and abundance. We recorded seasonal peaks for fleas and lice exploiting rock mice in spring, while for mites and ticks peaks occurred in summer. As for *E. myurus*, ticks and chiggers were present throughout the year and tick abundance was higher in autumn and spring, while chigger abundance was higher in autumn and summer. When investigating seasonal patterns at the species level, *R. warburtoni*/*arnoldi*, abundance was higher in spring, *Ixodes* spp. abundance was higher in autumn and summer and the remaining two species of tick (*R. distinctus* and *Rhipicentor* spp.) did not show any seasonal variation, which might be attributed to their low abundance. Parasite burdens often vary with season and abiotic factors (e.g. temperature, rainfall and humidity), which can affect parasite burdens (Poulin 2007). Ectoparasite taxa may respond differently to seasonal changes due to the fact that they differ in their host associations (Krasnov and Matthee 2010). Seasonal variation might be linked to the different life-history traits of the parasite species. For example, lice are closely associated with their hosts, they live, feed, reproduce and die on the host from generation to generation until the host dies (Kim 2006; Marshall 1981). Therefore seasonal patterns in louse burden can be expected to be weak. In contrast, seasonal variations in the number of ticks are expected to be stronger, as they spend only a limited time of their life on the host for blood meals and the remainder of the time in the vegetation (Lareschi 2010; Lareschi and Krasnov 2010; Matthee *et al.* 2010).

In the present study, all parasites (except for fleas) collected from *M. namaquensis* showed sex-biased patterns, while in *E. myurus* three of the most common parasites showed sex-biases. Sex-biases and in particular male-biased patterns have been recorded from many mammal species (Poulin 1996; Moore and Wilson 2002; Morand *et al.* 2004; Krasnov *et al.* 2005; Hillegass *et al.* 2008). However, very few studies have been carried out to investigate and compare sex-biased patterns of parasite species (belonging to the same or different higher taxa) infesting the same host species (Lareschi 2006; Presley and Willig 2008). The sex-biased patterns of ticks might be attributed to differences between host sexes as well as differences in parasite life cycles. For instance, the movement of males and their interactions with the surrounding environment and multiple potential mates may expose males to greater numbers of ticks (Lane *et al*. 2009; Moore and Wilson 2002; Morand *et al.* 2004).

Potential reasons or evidence for interactions in parasite infra-communities might be linked to the different life-history traits of the parasite species. For example, lice are permanent parasites spending their whole life cycle on their hosts, (i.e. they live, feed, reproduce and die on the host) from generation to generation until the host dies (Kim 2006). Therefore seasonal patterns in louse burden can be expected to be weak. While, seasonal variations in ticks are expected to be stronger, as they spend only limited time of their life on the host for blood meals and the remainder of the time in the vegetation (Lareschi 2010; Lareschi and Krasnov 2010; Matthee *et al.* 2010). Therefore, such changes in species dynamics make it harder to demonstrate the host-parasite relationship and differences in the intraspecific interactions between parasite taxon/species are frequently neglected. Furthermore, seasonal heterogeneities in parasite distributions across their hosts can also be linked to differences between individual hosts in exposure and susceptibility to parasites due to host physiology and/or behaviour (Weil *et al.* 2006; Lutermann *et al.* 2012a). In general, multiple parasites tend to infest an individual host forming a community of co-infecting parasites that may shape the host population as well as the dynamic of other parasite species (Graham 2008; Lello *et al.* 2004). The apparent interspecific competition between *R. warburtoni*/*arnoldi* and chiggers as has been observed in sengis in the present study is likely to be linked to competition over attachment sites. A study by Pedersen and Antonovics (2013) has demonstrated the importance of parasite community interactions by treating deer mice and white-footed mice against endoparasites. This resulted in a reduction of the prevalence of intestinal nematodes, while significant increases in cestode and coccidian prevalence were observed. This demonstrates the importance of considering the whole parasite community when trying to understand patterns of parasite distribution, which often is neglected (Pedersen and Fenton 2007; Knowles *et al.* 2013). In addition, competition for sites of attachment as well as competition for host resources has been suggested for *R. warburtoni*/*arnoldi,* and *Ixodes* spp. Similarly competition for attachment sites has previously been reported between co-infecting tick species (Andrews and Petney 1981; Hoffmann *et al.* 2016).

Although treatment with Frontline® had no direct effect on sengi BCI, the significant increase in sengi BCI after the first year of study suggests that there might be an indirect effect of treatment on sengi BCI. Likely given the huge numbers of ticks recorded in the first year of study. The increase in BCI coincided with the decrease in *R. warburtoni*/*arnoldi* abundance, which suggest that removal of parasites have neutralised the negative costs of high parasite burdens (Medley 2002). This evidence proves that there is an indirect effect of treatment on sengis BCI. Furthermore, the low BCI in winter is expected due to low food availability and thermoregulatory demands in winter are high, but the low BCI in the summer was unexpected and can be explained by the increasing number of juveniles that have been recruited into the host population (Hillegass *et al.* 2010). Previous studies suggested that parasites may affect many aspects of host behavior and some of these effects may be mediated via their impact on host energy budgets (Scantlebury *et al.* 2007; Zuk and Stoehr 2002). However, these studies, unlike the present study, applied short-term treatments and observations. In addition, the present study did not find any direct effects of ectoparasites on BCI.

Unlike the present study, most of the studies addressing the topic of interactions in parasite infra-communities focused on endoparasites and rely on observational rather than experimental data. Hence these studies may miss or mis-identify interspecific interactions in parasite communities. Our present study highlighted the complexity of interspecific interactions within a parasite community and the need for more longitudinal studies on small mammal-ectoparasite systems. In addition, our results stressed that interspecific interactions between parasites may play an important role in generating seasonal patterns for the different parasite species and this needs further attention in future studies. Furthermore, the relationships between host condition and parasite burdens are complicated and the work presented here is a step towards further understanding of the body condition implications of parasites. It is hoped that future work will develop a better understanding of the parasite infracommunity and the biology and physiology of the host.

REFERENCES

ALTIZER, S., NUNN, C. L., THRALL, P. H., GITTLEMAN, J. L., ANTONOVICS, J., CUNNINGHAM, A. A., CUNNNINGHAM, A. A., DOBSON, A. P., EZENWA, V. & JONES, K. E. 2003. Social organization and parasite risk in mammals: integrating theory and empirical studies. *Annual Review of Ecology, Evolution, and Systematics*, 517-547.

ANDREWS, R. & PETNEY, T. 1981. Competition for sites of attachment to hosts in three parapatric species of reptile tick. *Oecologia,* 51, 227-232.

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.

BORDES, F., BLUMSTEIN, D. T. & MORAND, S. 2007. Rodent sociality and parasite diversity. *Biology Letters,* 3, 692-4.

BORDES, F., MORAND, S., KRASNOV, B. R. & POULIN, R. 2010. Parasite diversity and latitudinal gradients in terrestrial mammals. *The Biogeography of Host-Parasite Interactions*, 89-98.

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

DE GRAAFF, G. 1981. *The rodents of Southern Africa: notes on their identification, distribution, ecology, and taxonomy*, Butterworth-Heinemann, Durban, South Africa, 267p.

DU TOIT, J., FOURIE, L. & HORAK, I. G. 1994. Detachment rhythms of immature Ixodes rubicundus from their natural host, the rock elephant shrew (*Elephantulus myurus*). *The Onderstepoort journal of veterinary research,* 61, 149-153.

FAGIR, D. M. & EL-RAYAH, E.-A. 2009. Parasites of the Nile rat in rural and urban regions of Sudan. *Integrative Zoology,* 4, 179-187.

FAIN, A., LUKOSCHUS, F. & NADCHATRAM, M. 1980. Malaysian parasitic mites II. Myobiidae (prostigmata) from rodents. *International Journal of Acarology,* 6, 109-120.

FLEMING, P. & NICOLSON, S. 2004. Sex differences in space use, body condition and survivorship during the breeding season in the Namaqua rock mouse, *Aethomys namaquensis*. *African Zoology,* 39, 123-132.

FOURIE, L., HORAK, I. & WOODALL, P. 2005. Elephant shrews as hosts of immature ixodid ticks. *Onderstepoort Journal of Veterinary Research,* 72, p. 293-301.

FOURIE, L., TOIT, J. D., KOK, D. & HORAK, I. 1995. Arthropod parasites of elephantshrews, with particular reference to ticks. *Mammal Review,* 25, 31-37.

GRAHAM, A. L. 2008. Ecological rules governing helminth–microparasite coinfection. *Proceedings of the National Academy of Sciences,* 105, 566-570.

HARRISON, A., BOWN, K. J. & HORAK, I. G. 2011. Detection of *Anaplasma bovis* in an undescribed tick species collected from the eastern rock sengi *Elephantulus myurus*. *Journal of Parasitology,* 97, 1012-6.

HARRISON, A., ROBB, G. N., BENNETT, N. C. & HORAK, I. G. 2012. Differential feeding success of two paralysis-inducing ticks, *Rhipicephalus warburtoni* and *Ixodes rubicundus* on sympatric small mammal species, *Elephantulus myurus* and *Micaelamys namaquensis*. *Veterinary Parasitology,* 188, 346-54.

HILLEGASS, M. A., WATERMAN, J. M. & ROTH, J. D. 2008. The influence of sex and sociality on parasite loads in an African ground squirrel. *Behavioral Ecology,* 19**,** 1006-1011.

HILLEGASS, M. A., WATERMAN, J. M. & ROTH, J. D. 2010. Parasite removal increases reproductive success in a social African ground squirrel. *Behavioral Ecology,* 21**,** 696-700.

HOFFMANN, S., HORAK, I. G., BENNETT, N. C. & LUTERMANN, H. 2016. Evidence for interspecific interactions in the ectoparasite infracommunity of a wild mammal. *Parasites & vectors,* 9**,** 1.

HORAK, I., FOURIE, L. & BRAACK, L. 2005. Small mammals as hosts of immature ixodid ticks. *Onderstepoort Journal of Veterinary Research,* 72**,** p. 255-261.

KIFFNER, C., LÖDIGE, C., ALINGS, M., VOR, T. & RÜHE, F. 2011a. Bodymass or sexbiased tick parasitism in roe deer (*Capreolus capreolus*). A GAMLSS approach. *Medical and veterinary entomology,* 25**,** 39-45.

KIFFNER, C., VOR, T., HAGEDORN, P., NIEDRIG, M. & RUEHE, F. 2011b. Factors affecting patterns of tick parasitism on forest rodents in tick-borne encephalitis risk areas, Germany. *Parasitology Research,* 108**,** 323-335.

KIM, K. C. 2006. Blood-sucking lice (Anoplura) of small mammals: True parasites. *Micromammals and Macroparasites.* Springer.

KNOWLES, S. C. L., FENTON, A., PETCHEY, O. L., JONES, T. R., BARBER, R. & PEDERSEN, A. B. 2013. Stability of within-host-parasite communities in a wild mammal system. *Proceedings of the Royal Society Biological Sciences Series B,* 280**,** 1-9.

KRASNOV, B. R. & MATTHEE, S. 2010. Spatial variation in gender-biased parasitism: host-related, parasite-related and environment-related effects. *Parasitology,* 137**,** 1527-36.

KRASNOV, B. R., MORAND, S., HAWLENA, H., KHOKHLOVA, I. S. & SHENBROT, G. I. 2005. Sex-biased parasitism, seasonality and sexual size dimorphism in desert rodents. *Oecologia,* 146**,** 209-17.

LANE, J. E., BOUTIN, S., GUNN, M. R. & COLTMAN, D. W. 2009. Sexually selected behaviour: red squirrel males search for reproductive success. *Journal of Animal Ecology,* 78**,** 296-304.

LARESCHI, M. 2006. Interrelationship between the sex of the water rat *Scapteromys aquaticus* and its infestation with ectoparasites in La Plata river marshland, Argentina. *International Journal of Tropical Biology and Conservation,* 54**,** 673-679.

LARESCHI, M. 2010. Ectoparasite occurrence associated with males and females of wild rodents *Oligoryzomys flavescens* (Waterhouse) and *Akodon azarae* (Fischer) (Rodentia: Cricetidae: Sigmodontinae) in the Punta Lara wetlands, Argentina. *Neotropical entomology,* 39**,** 818-822.

LARESCHI, M. & KRASNOV, B. R. 2010. Determinants of ectoparasite assemblage structure on rodent hosts from South American marshlands: the effect of host species, locality and season. *Medical and Veterinary Entomology,* 24**,** 284-292.

LAUDISOIT, A., LEIRS, H., MAKUNDI, R. & KRASNOV, B. R. 2009. Seasonal and habitat dependence of fleas parasitic on small mammals in Tanzania. *Integrative Zoology,* 4**,** 196-212.

LELLO, J., BOAG, B., FENTON, A., STEVENSON, I. R. & HUDSON, P. J. 2004. Competition and mutualism among the gut helminths of a mammalian host. *Nature,* 428**,** 840-844.

LUTERMANN, H., MEDGER, K. & HORAK, I. G. 2012a. Abiotic and biotic determinants of tick burdens in the eastern rock sengi (*Elephantulus myurus*). *Medical and Veterinary Entomology,* 26**,** 255-62.

LUTERMANN, H., MEDGER, K. & HORAK, I. G. 2012b. Effects of life-history traits on parasitism in a monogamous mammal, the eastern rock sengi (*Elephantulus myurus*). *Naturwissenschaften,* 99**,** 103-110.

MADDEN, S. C. & MADDEN, R. C. 2005. Seasonality in diurnal locomotory patterns of adult blacklegged ticks (Acari: Ixodidae). *Journal of medical entomology,* 42**,** 582-588.

MAHER, S. P. & TIMM, R. M. 2014. Patterns of host and flea communities along an elevational gradient in Colorado. *Canadian Journal of Zoology,* 92**,** 433-442.

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

MATTHEE, S., MCGEOCH, M. A. & KRASNOV, B. R. 2010. Parasite-specific variation and the extent of male-biased parasitism; an example with a South African rodent and ectoparasitic arthropods. *Parasitology,* 137**,** 651-60.

MEDLEY, G. 2002. The epidemiological consequences of optimisation of the individual host immune response. *Parasitology,* 125**,** S61-S70.

MOORE, S. L. & WILSON, K. 2002. Parasites as a viability cost of sexual selection in natural populations of Mammals. *Science,* 297**,** 2015-2018.

MORAND, S., DE BELLOCQ, J. G., STANKO, M. & MIKLISOVÁ, D. 2004. Is sex-biased ectoparasitism related to sexual size dimorphism in small mammals of Central Europe? *Parasitology,* 129**,** 505-510.

MORAND, S. & KRASNOV, B. R. E. 2006. *Micromammals and Macroparasites: From Evolutionary Ecology to Management*, Tokyo: Springer-Verlag, Japan.

PEDERSEN, A. B. & ANTONOVICS, J. 2013. Anthelmintic treatment alters the parasite community in a wild mouse host. *Biology Letters,* 9**,** 1-4.

PEDERSEN, A. B. & FENTON, A. 2007. Emphasizing the ecology in parasite community ecology. *Trends in Ecology & Evolution,* 22**,** 133-139.

POULIN, R. 1996. Sexual inequalities in helminth infections: a cost of being a male? *American Naturalist***,** 287-295.

POULIN, R. 2007. Are there general laws in parasite ecology? *Parasitology,* 134**,** 763-76.

PRESLEY, S. J. & WILLIG, M. R. 2008. Intraspecific patterns of ectoparasite abundances on Paraguayan bats: effects of host sex and body size. *Journal of Tropical Ecology,* 24**,** 75-83.

RIBBLE, D. O. & PERRIN, M. R. 2005. Social organization of the eastern rock elephant-shrew (*Elephantulus myurus*): the evidence for mate guarding. *Belgian Journal of Zoology,* 135**,** 167.

ROBERTS, M., DOBSON, A., ARNEBERG, P., DE LEO, G., KRECEK, R., MANFREDI, M., LANFRANCHI, P. & ZAFFARONI, E. 2002. Parasite community ecology and biodiversity. *The ecology of wildlife diseases***,** 63-82.

SCANTLEBURY, M., WATERMAN, J., HILLEGASS, M., SPEAKMAN, J. & BENNETT, N. 2007. Energetic costs of parasitism in the Cape ground squirrel *Xerus inauris. Proceedings of the Royal Society of London B: Biological Sciences,* 274**,** 2169-2177.

SKINNER, J. D. & CHIMIMBA, C. T. 2005. *The mammals of the southern African subregion. 3rd revised edition*.

THRALL, P. H., ANTONOVICS, J. & DOBSON, A. P. 2000. Sexually transmitted diseases in polygynous mating systems: prevalence and impact on reproductive success. *Proceedings of the Royal Society of London B: Biological Sciences,* 267**,** 1555-1563.

WEIL, Z. M., MARTIN II, L. B. & NELSON, R. J. 2006. Interactions among immune, endocrine, and behavioural response to infection. *Micromammals and Macroparasites.* Springer.

YONAS, M., WELEGERIMA, K., LAUDISOIT, A., BAUER, H., GEBREHIWOT, K., DECKERS, S., KATAKWEBA, A., MAKUNDI, R. & LEIRS, H. 2011. Preliminary investigation on rodent–ectoparasite associations in the highlands of Tigray, Northern Ethiopia: implications for potential zoonoses. *Integrative zoology,* 6**,** 366-374.

ZUK, M. & STOEHR, A. M. 2002. Immune defense and host life history. *The american naturalist,* 160**,** S9-S22.