# Personality, hormonal correlates and parasite load in the eastern rock elephant shrew

by

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# Declaration

I, **Sasha Hoffmann**, declare that the thesis, which I hereby submit for the degree of MSc. 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: ...24/02/14...................................

# Summary

Inter-individual variation in behaviour, or as it has now come to be known, personality, has been shown to affect many different components of fitness in animals. A concept that used to be thought of as background ‘noise’ has come to explain much of the variation we observe within populations and between individuals. The personality of an animal can affect how an animal utilises its environment. In a heterogeneous environment this may increase the potential to find limiting resources, such as mates. However, it may also result in different risks experienced by the animal, such as the number of parasites in may be exposed to. To date, links between personality and parasites have rarely been studied although it is a commonly held concept that more exploratory, bolder individuals should have greater parasite loads. As with individual differences in behaviour, individuals may differ in their circulating hormone profiles. Hence it has been proposed that personality can potentially be shaped by these circulating hormone concentrations with shyer individuals having higher corticosteroid (i.e. cortisol and corticosterone) concentrations while bolder ones may have higher testosterone levels. However, corticosteroids may also be elevated by stressors such as parasites. Similarly, animals that produce more testosterone may have reduced immune-abilities as suggested by the immunocompetence handicap hypothesis. These animals would also protect larger territories and fight rather than flee from potential conspecifics. Consequently, correlations between personality with both parasitic infestation and hormone concentrations have been suggested. In the current study we examined this relationship in the eastern rock sengi (*Elephantulus myurus*) or elephant shrew that is endemic to southern Africa. They are monogamous, sexually monomorphic and both sexes maintain and defend home ranges year-round. In the wild these animals also have large diversity of ectoparasites with two tick, one mite and one louse species being the most important. Burdens of these varied seasonally but not with sex. Personality was highly correlated across time and contexts suggesting a behavioural syndrome with reactive (more exploratory, bold and aggressive) and reactive (less exploratory, shy and submissive) types for E. *myurus*. In addition, personality was repeatable within individuals captured over a long term period. Personality scores suggested increasing reactivity with increasing body condition. At the same time only one of the four main ectoparasite species was affected by personality with burdens increasing with increasing reactivity. This suggests that correlations between personality and parasites may depend on the parasite species and that more studies should be done with multiple parasites when evaluating this relationship. We found consistently high levels of urinary C and low T throughout the study with no correlations of either hormone with our personality measures. The former may in part be due to the large abundances of ectoparasites while the monogamous mating system and year-round territorial defense by both sexes could account for low T. Consequently, the current study does not support some of the frequently assumed links between personality and other traits but highlights the need to explicitly consider mating system and multiple parasite species when addressing similar questions.

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# Chapter 1

## General Introduction

*Personality*

The ability of an animal to change its behavioural responses across different circumstances makes sense from an adaptive perspective but the consistent persistent individual differences that remain are harder to explain (Sih *et al.* 2004; Dall *et al.* 2004; Dingemanse & Réale 2005). In other words it makes sense for an animal to adjust behaviours according to current conditions, such as roaming farther during periods of low food availability, but those consistent tendencies, or personality, of certain individuals to be more exploratory regardless of internal state is more problematic. Despite this personality is being studied more frequently in a greater diversity of taxa, although much of the initial work has been done on rodents (Archer 1973; Boyer *et al.* 2010), canids (Svartberg & Forkman 2002) and a number of fish (Wilson *et al.* 1994; Toms *et al.* 2010). This has given support to the hypothesis that many animals vary consistently in their behavioural responses and has led to the identification of animal personality (Wilson *et al.* 1994; Dingemanse & Réale 2005). However there is still some discord with many studies in terms of what to label these consistent individual differences in behaviour (Bergmüller & Taborsky 2007). Besides the later personality has also been, and often still is, referred to as temperament (Archer 1973), coping styles (Koolhaas *et al.* 1999) and individual difference in behaviour (Sih *et al.* 2004). Personality however, has come to be an accepted term for the study of behaviour in non-human animals, referring to the individual differences in behaviour animals' exhibit consistently. Behavioural syndromes, which is often equated to animal personality (Schurch & Heg 2010), refers to the suites of correlated behaviours across different contexts and takes into account less than optimal behaviours in certain context (Sih *et al.* 2004). We define personality as the consistent individual differences in behaviour an animal exhibits compared to other individuals within certain contexts. Many studies have shown that personality may significantly affect the way individuals interact with their environment (Dall *et al.* 2004; Boon *et al.* 2008; Smith & Blumstein 2008; Fucikova *et al.* 2009). Something that used to be considered as merely a bias around the mean, or background noise, has come to explain much of the variation we see in populations (Svartberg & Forkman 2002).

Personality in animals has also been shown to affect many factors of individual variation, including diet, predation rate and dispersal of an individual (Yeo *et al.* 1997; Blumstein *et al.* 2006; Cote *et al.* 2010). For example in cichlid fish (*Neolamprologus multifasciatus*) it was found that females that had initiated more aggressive encounters in a dyad, had larger subterritories, while less aggressive females had smaller subterritories and emigrated (Schradin & Lamprecht 2002). In another study by Kurvers *et al.* (2009) on barnacle geese (*Branta leucopsis*) they found that bold individuals led more while shy individuals followed more often.

These factors may have implications for fitness of an individual or even a population and as such personality has become an important factor to consider. For example in pumpkin seed fish *(Lepomis gibbosus*) bold fish forage at a greater rate but in a riskier way, so a greater reward may be hampered by a greater risk of predation and a fitness trade off exists (Wilson *et al.* 1993). Similarly territorial behaviour or mate guarding, which is more common in males has been found to result in increased parasite loads (Mooring *et al.* 1996; Negro *et al.* 2010). Boyer *et al.* (2010) found that there was an indirect effect of personality on Siberian chipmunks (*Tamias sibiricus*) on space use behaviour and in turn on tick load through behavioural activity. They showed that males with increased activity patterns had higher tick loads than female conspecifics. In a study by Mooring *et al.* (1996) on impala; an increase in tick load in the more territorial males was attributed to a significant drop in grooming behaviour as a result of the increased aggressive behaviour of males. Often the increase in aggressive behaviour is linked to an increase in testosterone in some mammals, most often seen during the breeding season where males are required to defend mates or fight other males for breeding rights (Folstad & Karter 1992; Cavigelli & Pereira 2000; While *et al.*

2010). However even with the interest in testosterone as a male specific hormone, specifically with regards to seasonal variation in seasonal breeders, few have investigated the possible link to personality of an individual and their concurrent hormone levels.

### *Host physiology*

Individuals of the same species may differ remarkably in their circulating hormone concentrations and the associated phenotypic traits associated with varying hormone profiles (While *et al.* 2010). Animals under stress produce hormones, such as glucocorticoids, which are beneficial in helping the animal cope for short periods of times. However long term chronic stress, such as is bought on by parasitic infections may have long lasting negative effects on the fitness of an animal. As such, animals stressed from larger parasite loads should have an increase in these glucocorticoids (Martin *et al.* 2011) and a trade-off exists between differing physiological needs. An example of such a trade-off can be seen between reproduction and the immune defence and is often found in female hosts where immune function throughout reproduction can be reduced during gestation and lactation due to the large energy requirements associated with these reproductive processes (Altizer *et al.* 2006). This has been demonstrated clearly in studies on bats, where the individuals with the highest ectoparasite loads were females that were pregnant or lactating (Pearce & O’Shea 2007; Sundari *et al.* 2012).

In males however the variation is often attributed to varying levels of testosterone. Testosterone concentration plays a role in the development and maturation of secondary sexual characteristics such as brighter plumages in birds and increased social aggression behaviours (Saino & Møller 1994; Salvador *et al.* 1997). It has often been proposed that males that produce more testosterone may have slightly reduced immune-abilities due to the long term negative effects of testosterone production, similar to the action of corticosteroids (Hughes & Randolph 2001). Testosterone has been found to act as an immunosuppressant (Klein 2000) and a few studies in male small mammals and lizards with manipulated testosterone concentrations have shown that elevated testosterone levels may result in increased parasite loads (Salvador *et al.* 1995; Hughes & Randolph 2001).This is often referred to as the immunocompetence handicap and was proposed by Folstad & Karter (1992) based on studies with birds.

Besides the immune function which can affect susceptibility of a host to parasites, hormones may also be linked to animal behaviour. Personality has been found to affect the learning abilities of animals (Hoffmann 2011), food choice and quality (Wilson *et al.* 1994), as well as habituation to stressful situations (Seltmann *et al.* 2012). Needless to say personality has also been proposed to be related to varying hormone concentrations of an individual (Guinn Sellers *et al.* 2007; While *et al.* 2010). Also some animals, for example more timid animals, when compared to bolder individuals, may be more prone to stress initially and therefore have high levels of corticosteroids, decreasing immune abilities and therefore increasing parasite infection (Wilson *et al.* 1993).

Personality can potentially be shaped by circulating hormone concentrations; animals that are considered to display more stressed behaviours may have higher levels of cortisol, whereas those that are more aggressive may exhibit higher levels of testosterone (Cote *et al.* 2010; Montiglio *et al.* 2012). It has been shown that animals with increased levels of testosterone roam more to protect their larger territories, come across more females and fight rather than flee from potential opponents (Ribble & Perrin 2005). All of these behaviours would be associated with a bolder, more aggressive individual and these personality aspects are linked to the testosterone concentration of the individual which could then possibly explain varying parasite levels in the animal as well (Wilson *et al.* 1993).

Despite some references, few studies have specifically looked at the link between hormone levels and personality. Although much work has been done with regards to stress and reduced immune function looking at glucocorticoids (Sapolsky *et al.* 2000; Romero 2002; Thomason *et al.* 2013) and androgens, such as testosterone (Folstad & Karter 1992; Cox 2001; Hews & Abell Baniki 2013), few have investigated individual host personality and the link to varying hormones. Hormones in the body may also determine individual host susceptibility to parasites or exposure due to differences in behaviours. Few studies have found direct links between increased glucocorticoids and androgens with increased parasite burdens and there is little support for what is accepted as a given trend (Folstad & Karter 1992; Cavigelli & Pereira 2000; Cox 2001; Hillegass *et al.* 2008; Nunn *et al.* 2009). Much work on hormones tend to also focus on species, such as birds, fish and rodents, specifically bred or chosen for their well-documented expected physiological responses (Langley & Fairley 1982; Folstad & Karter 1992; Heinrichs & Koob 2006; Hillegass *et al.* 2008; Gerlach & Ketterson 2013).

### *Parasites*

Parasites are organisms that live either internally or externally on their host. They derive their nutritional requirements from the host and can experience either parts of or their complete life cycle on the host (Kim 1985). Due to their abundant distribution, parasites can infest all free-living animals and this in turn results in animals having to adapt and deal with these infestations (Combes 2001; Roberts & Janovy Jr. 2005). This results in the interactions between hosts and parasites being rather complex as hosts attempt to decrease parasite burdens, while parasites are dependent on hosts for their own survival (Marcogliese 2005; Morand *et al.* 2006). Consequently, parasites can potentially have dramatic impacts on their hosts. Despite this, their relative importance in wildlife populations remains underestimated when compared to other factors such as predation and competition (Irvine 2006; Dunn *et al.* 2013). Parasites can affect the fitness of a host in that they can be detrimental to both host survival and reproductive output (Combes 2001; Hillegass *et al.* 2008; Patterson & Schulte-Hostedde 2011).

Parasite populations tend to fluctuate both spatially and temporally (Wilson *et al.* 2001). Many studies have investigated these differences in parasitic infestations on different hosts and their possible causes. A common hypothesis is that it is due to differences in host exposure (Poulin 2007; Bordes *et al.* 2010). Host exposure refers to the number of parasites that a host can come into contact with in its habitat. This can be determined by the biotic factors of the host such as the individual differences in susceptibility of to the hosts to particular parasites due to immune system (Wilson *et al.* 2001). Not only are there trade-offs between host fitness and parasite infestation, but there are trade-offs between competing physiological demands such as those operational on the hosts immune system (Morand *et al.* 2006). Another example of biotic or host-related factors is personality. Boyer *et al.* (2010) suggested that bolder individuals had higher parasite abundances, likely due to an increase in exploratory behaviour. Host personality can explain differences in parasite burdens of a population since some behaviours such as roaming or aggressiveness can increase the risk of infestation either by a greater chance of coming into contact either with other infested hosts or a greater number of parasites (Boyer *et al.* 2010; Dunn *et al.* 2011). However there are also many studies that investigate behavioural changes in response to parasite infestation rather than parasite infestation due to host behaviour (Barber & Dingemanse 2010 and references reviewed within; Poulin 2013). The link between behavioural changes in an animal and parasite infestation has been well studied in parasites with complex life-cycles (such as cestodes or trematodes) that cause the host to endanger itself via suicidal behavioural tendencies to continue the parasites life cycle (Biron *et al.* 2005; Lefèvre *et al.* 2009; van Houte *et al.* 2013). These are cases such as seen in *Toxoplasma gondii* infestations where the host behaviour is manipulated by the parasite (Webster 2001).

In addition to biotic effects, abiotic factors have been found to affect parasite burdens amongst host individuals and is often more studied (Poulin 2007). The abundances (how many are on the host) and prevalence (how many individuals in a population are infected with a specific parasite) of ectoparasites have been shown to be affected by abiotic factors such as climate. Ectoparasites refer to parasites specifically found externally on the host and as such tend to be more susceptible to climatic factors. Many studies report that higher levels of humidity in a habitat may provide a guard against desiccation for ectoparasites, which are found externally on the host, specifically when in the sensitive immature phases (Moyer *et al.* 2002; Abd El-Halim *et al.* 2009; Bordes *et al.* 2010). As such ectoparasite abundances are higher during periods of greater humidity since ectoparasites such as ticks and mites may quest with a lower risk of desiccation to find potential hosts (Basu & Bandyopadhyay 2004). However, the opposite has also been found, suggesting that what works for one taxon or even species, does not necessarily improve fitness for another (Carmichael *et al.* 2007; Lareschi & Krasnov 2010).

Variations in ectoparasite burdens between populations of the same host have also been found to be linked to differences in temperature and rainfall (Fabiyi 1996; Vinarski *et al.* 2007; Korallo-Vinarskaya *et al.* 2009). What this suggests is that the effect of the environment may differ between ectoparasites species and this is mostly due to differing life history strategies (Bordes *et al.* 2010). For example potential hosts would be less likely to be infested by ticks when rainfall is low as questing ticks are more prone to desiccation (Horak *et al.* 1995). Immature ticks spend a portion of their life cycle off-host, before reaching maturity, for processes such as moulting and therefore are susceptible and reliant on the temperature and rainfall of their environment (Needham & Teel 1991). In contrast desiccation may not be an important constraint for the transmission of lice as the entire lice life cycle is completed on the host and the risk for desiccation due to questing is lower (Hopkins 1948). Within a host population, different ectoparasite taxa (i.e. ticks, lice or mites) may reach peak abundances at different times of the year depending on their preference to various weather conditions (Merino & Potti 1996). In our study site specifically some work has been done to determine tick burdens as the area is considered relatively dry with warm summer temperatures which are considered less optimal climatic variables for ticks (see Lutermann *et al.* 2012 for climate data).

The few studies investigating personality with varying individual hormone concentrations suggests that there is much to be learnt from investigating this relatively novel concept. Although many studies suggest that there ought to be a link; few have directly examined the interplay between personality and hormone concentrations and those that have are relatively new (Guinn Sellers *et al.* 2007; While *et al.* 2010; Cockrem 2013). Similarly few studies have investigated personality on parasite burdens in wild populations (Barber & Dingemanse 2010 and references within; Boyer *et al.* 2010). Studies that have tend to focus on lab-based experiments as it is more readily possible to obtain repeatable measures and manipulate parasite burdens (Butler *et al.* 2012; Hammond-Tooke *et al.* 2012; Koprivnikar *et al.* 2012) although the need for wild studies is being addressed (Archard & Braithwaite 2010). Hormone concentrations and the effect on parasite burdens, or vice versa, seem simple and well-studied, although the general trends commonly accepted have little support in wild populations and animals outside of fish (Kubokawa *et al.* 1999), rodents(Langley & Fairley 1982; Hillegass *et al.* 2008) and birds (Folstad & Karter 1992; Owen *et al.* 2004; Roberts *et al.* 2004). This suggests a need to investigate personality in a non-domestic, wild population and determine if the generally accepted trend of hormones and parasites hold true for another species outside of the usual suspects.

### *Study Animal*

The eastern rock sengi (*Elephantulus myurus*) or elephant shrew as they have been more commonly known until recently, is a small mammal (40-55g) belonging to the order Macroscelidea. There has been much discord in terms of their taxonomy and they were grouped at one point with true shrews and even hedgehogs due to superficial similarities with the order Insectivora  (Rathbun 2009). However with the development of improved molecular techniques to assess relationships it was found that they are a monophyletic family (Macroscelididae). This has resulted in many scientists preferring the term sengi rather than elephant shrew as they are not related to shrews, moving away from the incorrect taxonomic labelling from the 19th century (Rathbun 2009). The order comprises of 17 species, all of which are endemic to Africa (Skinner & Chimimba 2005). This is an ancient order belonging in the supergroup Afrotheria, which includes a diverse collection of animals such as elephants, aardvark and hyraxes (Asher *et al.* 2003; Redi *et al.* 2007). Most studies to date that have investigated personality have focused on rodents, fish and domesticated animals (Archer 1973; Wilson *et al.* 1994; Svartberg & Forkman 2002), often in lab based studies (Edelaar *et al.* 2012; Pruitt *et al.* 2012). The lack of knowledge in wild populations and especially in different taxa is an area that requires much more exploration to assist in the methodology and understanding of the importance of personality.

The males are known to exhibit seasonal variation in testosterone levels with a peak in July (Medger *et al.* 2012) although very few studies have investigated hormone concentrations in sengis. One such study looked at urinary corticosteroid concentrations in round-eared sengis and aggressive behaviours but found no significant effect (Schubert *et al.* 2009).

Eastern rock sengis have a long breeding season, from August – March (Medger *et al.* 2012), and it is likely the offspring stay within parental territories for a few months before being excluded and forced to establish their own as has been found in other sengi species (Fitzgibbon 1997). Both males and females defend individual territories from conspecifics, with a male-female pair usually having overlapping home-ranges (Ribble & Perrin 2005) and monogamy has been identified in most sengi species (Rathbun & Rathbun 2006; Rathbun 2009). The breeding season is also longer than what is normally found for other small mammals which occur in the same region, such as the spiny mouse (*Acomys spinosissimus*) which has a breeding season from August - December (Medger *et al.* 2011). This comparatively longer breeding season could have massive impacts on the basal hormone concentrations of the animal and highlight interesting dynamics with regards to seasonal parasite variation which is often thought to be somewhat dependant on hormonal changes brought on by seasonal breeding.

Eastern rock sengis have mostly been studied in terms of reproduction and thermoregulation (Roxburgh & Perrin 1994; Lovegrove *et al.* 1999). They inhabit rocky outcrops, which they use to thermoregulate passively, and they usually produce two precocial young which are capable of following their mother within a few hours of birth (Rathbun 1979) which is an unusual strategy for small mammals. Sengis are insectivorous and are well equipped for hunting small soft-bodied insects using their fast, cursorial locomotion (Rathbun 1979; Nicoll & Rathbun 1990).

Some studies have investigated their ectoparasite abundances as eastern rock sengis have large ectoparasites burdens, specifically with regards to ticks (Fourie *et al.* 1995; Horak *et al.* 2011). Despite the large tick burden these animals carry in the wild (Lutermann *et al.* 2012), especially when compared to sympatric species such as the Namaqua rock mouse (*Micaelamys namaquensis*) which plays host to an average of 4 ticks (Fourie *et al.* 1995), none have investigated the potential reasons for the great variance in tick abundances seen between individuals. Coupled with the lack of research in wild populations in general, they pose an interesting challenge to measure personality, hormone correlates and the subsequent effects on or of ectoparasitic burden.

### *Aims and Justification*

We aimed to establish whether eastern rock sengis displayed behavioural syndromes and whether this was repeatable across time. We aimed to determine which abiotic and biotic factors may contribute to the personalities of sengis and potentially what effect varying personalities may have on the fitness of the individuals. We predicted that due to the physiology and social ecology of our species that sex ought not to play a role in personality although this has been found for other small mammals exhibiting sexual dimorphism. Personality of individuals of wild populations of sengis remains understudied due to the difficulties in logistics. Also with personality being a relatively novel field there is still much to be investigated, especially in relation to wild animal studies as our knowledge on personality outside of lab-based studies is lacking. There is also still much conflict in terms of how to measure personality and what behaviours should be considered with many studies lacking in cohesion, making direct comparisons difficult. We proposed to incorporate a battery of tests using more than a single behaviour per test, rather than the norm of a single measure for personality as undertaken by many studies. We felt that this gave us a more solid basis for any conclusions drawn and provided a clearer view of personality. The aim here was to enhance a framework within which to better measure personality for sengis that may be repeatable by others. We also aimed to measure steroid hormones in eastern rock sengis as hormone measures have not been validated for urinary hormone concentrations. We aimed to determine individual hormone profiles of the sengis and investigate relation thereof to personality and parasite burden. Very few studies have measured urinary hormone determinants in any sengi species. Those that have measured this looked at corticosteroid in round-eared sengis (*Macroscelides proboscideus*) whereas we found cortisol to be the predominant corticoid hormone in eastern rock sengis. Similarly many studies that focus on testosterone have examined concentrations in terms of seasonal variation linked to reproduction in males. Most work to date has investigated mainly on thermoregulation and tick load determinants in *E. myurus*. Little is known about the ecology and parasite community of these animals and this study investigated to some degree how these animals interact with their environment, in terms of parasite infestation and the interaction between specific personalities within the field.

We predicted that parasite burdens would vary with individual personality and hormone profiles, as has been suggested by others. We aimed to determine the ectoparasite community of sengis in our study site in the Limpopo province. This was done first as the knowledge on ectoparasites of sengis are poor and much of the work done is dated or focuses predominantly on ticks. For the ectoparasite work we also initiated a Frontline® treatment plan throughout the study. This was done to control to some extent the ectoparasite burdens on sengis and evaluate whether changes of burdens affected individual variation in both personality and hormones. Also little work has been done to investigate the effects that parasites have on the behaviour and hormone concentrations of eastern rock sengis. The relative novelty of investigating personality in relation to parasite loads and hormone concentrations suggest there is much work to be done in these fields

*Thesis chapters*

Each chapter presented in this thesis focussed on analysing a different aspect of the host-parasite relationship and effects thereof on varying biotic factors with the main focus being on personality in the second chapter.

Chapter 1 investigated the ectoparasite community associated with *E. myurus*. Much of the literature investigating parasites on the eastern rock sengi deals with only one or two species at a time; and indeed mostly ticks. We provided an extensive review of the ectoparasites found on *E. myurus* in the Limpopo province. We investigated host factors as well as seasonal variation in parasite burden in our study area.

Chapter 2 concentrated on investigating the individual behavioural differences of the host and whether *E. myurus* exhibited behavioural syndromes under natural conditions and whether the personality measured was consistent over time. We then examined factors that might affect these personality measures and lastly we evaluated how the personality of the sengi affected abundances and prevalence of their ectoparasites. Since the study of personality is also a relatively new field of interest when considering ectoparasite burdens in wild sengis, the aim of this chapter was to determine the variation in personality in our study population. In this chapter we focused on which biotic factors affect the personality, i.e. sex and body condition, as well as the repeatability and robustness of our measures used.

Chapter 3 investigated the steroid hormone profiles and how these might be affected by personality and/or parasite burdens. The impact of ectoparasite abundance and prevalence on host testosterone and cortisol concentrations was analysed. In addition the personality measures from Chapter 2 were included in the analyses. This potentially could help explain the mechanisms bringing about individual variation, something which has been difficult to explain despite its inherent variability found in populations. Overall, this thesis provides a description of the parasites of *E. myurus* as well as which factors may potentially affect host infestation rates. Additionally the thesis investigates individual variation of infestation rates to personality as well as what may potentially be a physiological driver for personality differences.

## References

**Abd El-Halim, A. S., Allam, K. A. M., Metwally, A. M. & El Boraey, A. M.** 2009. Seasonal variation of infestation rate with lice, tick and mite among rodents in certain Egyptian regions. *Journal of the Egyptian Society of Parasitology*, **39**, 617–624.

**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.

**Archard, G. A. & Braithwaite, V. A.** 2010. The importance of wild populations in studies of animal temperament. *Journal of Zoology*, **281**,

**Archer, J.** 1973. Tests for emotionality in rats and mice: a review. *Animal Behaviour*, **21**, 205–235.

**Asher, R. J., Novacek, M. J. & Geisler, J. H.** 2003. Relationships of endemic African mammals and their fossil relatives based on morphological and molecular evidence. *Journal of Mammalian Evolution*, **10**, 131–194.

**Barber, I. & Dingemanse, N. J.** 2010. Parasitism and the evolutionary ecology of animal personality. *Philisophical Transactions of the Royal Society of London*, **365**, 4077–4088.

**Basu, A. K. & Bandyopadhyay, P. K.** 2004. The effect of season on the incidence of ticks. *Bulletin of Animal Health and Production in Africa*, **52**, 39–42.

**Bergmüller, R. & Taborsky, M.** 2007. Adaptive behavioural syndromes due to strategic niche specialization. *BMC Ecology*, **7**, 12.

**Biron, D. G., Marché, L., Ponton, F., Loxdale, H. D., Galéotti, N., Renault, L., Joly, C. & Thomas, F.** 2005. Behavioural manipulation in a grasshopper harbouring hairworm: a proteomics approach. *Proceedings of the Royal Society of Britain*, **272**, 2117–2126.

**Blumstein, D. T., Holland, B.-D. & Daniel, J. C.** 2006. Predator discrimination and "personality" in captive Vancouver Island marmots (*Marmota vancouverensis*). *Animal Conservation*, **9**, 274–282.

**Boon, A. K., Réale, D. & Boutin, S.** 2008. Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*. *Oikos*, **117**, 1321–1328.

**Bordes, F., Morand, S., Krasnov, B. R. & Poulin**. 2010. Parasite diversity and latitudinal gradients in terrestrial mammals. In: *The Biogeography of Host-Parasite Interactions*, (Ed. by S. Morand & B. R. Krasnov), pp. 89–98. UK: Oxford University Press.

**Boyer, N., Réale, D., Marmet, J., Pisanu, B. & Chapuis, J.-L.** 2010. Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus*. *The Journal of Animal Ecology*, **79**, 538–47.

**Butler, M. W., Toomey, M. B., Rowe, M. & McGraw, K. J.** 2012. Ontogenetic immune challenges shape adult personality in mallard ducks. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 326–333.

**Carmichael, J. A., Strauss, R. E. & McIntyre, N. E.** 2007. Seasonal variation of North American form of *Gigantolaelaps mattogrossensis* (Acari: Laelapidae) on marsh rice rat in southern coastal Texas. *Journal of Medical Entomology*, **44**, 80–84.

**Cavigelli, S. A. & Pereira, M. E.** 2000. Mating season aggression and fecal testosterone levels in male ring-tailed lemurs (*Lemur catta*). *Hormones and Behavior*, **37**, 246–255.

**Cockrem, J. F.** 2013. Corticosterone responses and personality in birds : Individual variation and the ability to cope with environmental changes due to climate change. *General and Comparative Endocrinology*, **190**, 156–163.

**Combes, C.** 2001. *Parasitism: The ecology and evolution of intimate interactions.* USA: University of Chicago Press.

**Cote, J., Clobert, J., Brodin, T., Fogarty, S. & Sih, A.** 2010. Personality-dependent dispersal : characterization, ontogeny and consequences for spatially structured populations. *Philisophical Transactions of the Royal Society of London*, **365**, 4065–4076.

**Cox, F. E.** 2001. Concomitant infections, parasites and immune responses. *Parasitology*, **122**, 23–38.

**Dall, S. R. X., Houston, A. I. & McNamara, J. M.** 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, **7**, 734–739.

**Dingemanse, N. J. & Réale, D.** 2005. Natural selection and animal personality. *Behaviour*, **142**, 1159–1184.

**Dunn, J. C., Cole, E. F. & Quinn, J. L.** 2011. Personality and parasites: sex-dependent associations between avian malaria infection and multiple behavioural traits. *Behavioral Ecology and Sociobiology*, **65**, 1459–1471.

**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**, 30–50.

**Edelaar, P., Serrano, D., Carrete, M., Blas, J., Potti, J. & Tella, J. L.** 2012. Tonic immobility is a measure of boldness toward predators : an application of Bayesian structural equation modeling. *Behavioral Ecology*, **23**, 619–626.

**Fabiyi, J. P.** 1996. Association between duration of humid season and geographical distribution patterns of different species of chewing lice (Mallophaga:Insecta) infesting domestic chickens in Nigeria. *The Journal of Parasitology*, **82**, 1034–1036.

**Fitzgibbon, D.** 1997. The adaptive significance of monogamy in the golden-rumped elephant-shrew. *The Zoological Society of London*, **242**, 167–177.

**Folstad, I. & Karter, A. J.** 1992. Parasites, bright males, and the immunocompetence handicap. *The American Naturalist*, **139**, 603–622.

**Fourie, L. J., Du Toit, J. S., Kok, D. J. & Horak, I. G.** 1995. Arthropod parasites of elephant-shrews, with particular reference to ticks. *Mammal Review*, **25**, 31–37.

**Fucikova, E., Drent, P. J., Smits, N. & van Oers, K.** 2009. Handling stress as a measurement of personality in great tit nestlings (*Parus major*). *Ethology*, **115**, 366–374.

**Gerlach, N. M. & Ketterson, E. D.** 2013. Experimental elevation of testosterone lowers fitness in female dark-eyed juncos. *Hormones and Behavior*, **63**, 782–790.

**Guinn Sellers, J., Mehl, M. R. & Josephs, R. A.** 2007. Hormones and personality : Testosterone as a marker of individual differences. *Journal of Research in Personality*, **41**, 126–138.

**Hammond-Tooke, C. A., Nakagawa, S. & Poulin, R.** 2012. Parasitism and behavioural syndromes in the fish *Gobiomorphus cotidianus*. *Behaviour*, **149**, 601–622.

**Heinrichs, S. C. & Koob, G. F.** 2006. Application of experimental stressors in laboratory rodents. *Current Protocols in Neuroscience*,**8**,8-4.

**Hews, D. K. & Abell Baniki, A. J.** 2013. The breeding season duration hypothesis : acute handling stress and total plasma concentrations of corticosterone and androgens in male and female striped plateau lizards (*Sceloporus virgatus*). *Journal of Comparative Physiology B*, **183**, 933–946.

**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.

**Hoffmann, S.** 2011. The effects of captivity, environmental enrichment and personality on memory and spatial learning in the eastern rock elephant shrew (*Elephantulus myurus*). Honours Project, University of Pretoria.

**Hopkins, M.** 1948. The host-asociations of the lice of mammals. *Proceedings of the Zoological Society of London*, **119**, 387 – 604.

**Horak, I. G., Fourie, L. J. & van Zyl, J. M.** 1995. Arthropod parasites of impalas in the Kruger National Park with particular reference to ticks. *South African Journal of Wildlife Research*, **25**, 123–126.

**Horak, I. G., Welman, S., Hallam, S. L., Lutermann, H. & Mzilikazi, N.** 2011. Ticks of four-toed elephant shrews and Southern African hedgehogs. *Onderstepoort Journal of Veterinary Research*, **78**, 1–3.

**Hughes, V. L. & Randolph, S. E.** 2001. Testosterone depresses innate and acquired resistance to ticks in natural rodent hosts: a force for aggregated distributions of parasites. *The Journal of Parasitology*, **87**, 49–54.

**Irvine, R. J.** 2006. Parasites and the dynamics of wild mammal populations. *Animal Science,* **82**, 775–781.

**Kim, K.** 1985. *Coevolution of parasitic arthropods and mammals.* 1st edn. New York: Wiley and Sons.

**Klein, S. L.** 2000. The effects of hormones on sex differences in infection :from genes to behavior. *Neuroscience and Biobehavioral reviews*, **24**, 627–638.

**Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. & Blokhuis, H. J.** 1999. Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience and Biobehavioral Reviews,* **23**, 925–935.

**Koprivnikar, J., Gibson, C. H. & Redfern, J. C.** 2012. Infectious personalities: behavioural syndromes and disease risk in larval amphibians. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 1544–1550.

**Korallo-Vinarskaya, N. P., Krasnov, B. R., Vinarski, M. V., Shenbrot, G. I., Mouillot, D. & Poulin, R.** 2009. Stability in abundance and niche breadth of gamasid mites across environmental conditions, parasite identity and host pools. *Evolutionary Ecology,* **23**, 329–345.

**Kubokawa, K., Watanabe, T., Yoshioka, M. & Iwata, M.** 1999. Effects of acute stress on plasma cortisol, sex steroid hormone and glucose levels in male and female sockeye salmon during the breeding season. *Aquaculture,* **172**, 335–349.

**Kurvers, R. H. J. M., Eijkelenkamp, B., Oers, K. Van, van Lith, B., van Wieren, S. E., Ydenberg, R. C. & Prins, H. H. T.** 2009. Personality differences explain leadership in barnacle geese. *Animal Behaviour,* **78**, 447–453.

**Langley, R. & Fairley, N. D. J. S.** 1982. Seasonal variations in infestations of parasites in a Wood mouse Apodemus sylvuticus population in the West of Ireland. *Journal of Zoology London,* **198**, 249–261.

**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.

**Lefèvre, T., Adamo, S. A., Biron, D. G., Missé, D., Hughes, D. & Thomas, F.** 2009. Invasion of the body snatchers: the diversity and evolution of manipulative strategies in host-parasite interactions. *Advances in Parasitology*, **68**, 45–83.

**Lovegrove, B. G., Lawes, M. J. & Roxburgh, L.** 1999. Confirmation of pleisiomorphic daily torpor in mammals: the round-eared elephant shrew *Macroscelides proboscideus* (Macroscelidea). *Journal of comparative physiology: B, Biochemical, systemic, and environmental physiology*, **169**, 453–60.

**Lutermann, H., Medger, K. & Horak, I. G.** 2012. Abiotic and biotic determinants of tick burdens in the eastern rock sengi (*Elephantulus myurus*). *Medical and Veterinary Entomology*, **26**, 1–9.

**Marcogliese, D. J.** 2005. Parasites of the superorganism : Are they indicators of ecosystem health ? *International Journal for Parasitology*, **35**, 705–716.

**Martin, L. B., Hawley, D. M. & Ardia, D. R.** 2011. An introduction to ecological immunology. *Functional Ecology*, **25**, 1–4.

**Medger, K., Chimimba, C. T. & Bennett, N. C.** 2011. Reproductive photoresponsiveness in male spiny mice from South Africa. *Journal of Zoology*, **1**, 1–7.

**Medger, K., Chimimba, C. T. & Bennett, N. C.** 2012. Seasonal reproduction in the eastern rock elephant-shrew: influenced by rainfall and ambient temperature? *Journal of Zoology*, **288**, 283–293.

**Merino, S. & Potti, J.** 1996. Weather dependent effects of nest ectoparasites on their bird hosts. *Ecography*, **19**, 107–113.

**Montiglio, P., Garant, D., Pelletier, F. & Réale, D.** 2012. Personality differences are related to long term stress reactivity in a population of wild eastern chipmunks, *Tamias striatus*. *Animal Behaviour*, **84**, 1071–1079.

**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., Krasnov, B. R. & Poulin, R.** 2006. *Micromammals and Macroparasites From Evolutionary Ecology to Management.* Japan: Springer.

**Moyer, B. R., Drown, D. M. & Clayton, D. H.** 2002. Low humidity reduces ectoparasite pressure: implications for host life history evolution. *Oikos*, **97**, 223–228.

**Needham, G. R. & Teel, P. D.** 1991. Off-host physiological ecology of ixodid ticks. *Annual Review of Entomology*, **36**, 659–681.

**Negro, S. S., Caudron, A. K., Dubois, M., Delahaut, P. & Gemmell, N. J.** 2010. Correlation between male social status, testosterone levels, and parasitism in a dimorphic polygynous mammal. *PloS ONE*, **5**, e12507.

**Nicoll, M. & Rathbun, G. B.** 1990. *African Insectivora and elephant-shrews: an action plan for their conservation.* 1st edn. Gland, Switzerland: IUCN.

**Nunn, C. L., Altizer, S., Jones, K. E. & Sechrest, W.** 2003. Comparative tests of parasite species richness in primates. *The American Naturalist*, **162**, 597–614.

**Owen, N. T., Hasselquist, D., Wingfield, J. C. & Owen-ashley, N. T.** 2004. Androgens and the immunocompetence handicap hypothesis : unraveling direct and indirect pathways of immunosuppression in song sparrows. *The American naturalist*, **164**, 490–505.

**Patterson, L. D. & Schulte-Hostedde, A. I.** 2011. Behavioural correlates of parasitism and reproductive success in male eastern chipmunks, *Tamias striatus*. *Animal Behaviour*, **81**, 1129–1137.

**Pearce, R. D. & O'Shea, T. J.** 2007. Ectoparasites in an urban population of big brown bats (*Eptesicus fuscus*) in Colorado. *The Journal of Parasitology*, **93**, 518–530.

**Poulin, R.** 2007. Are there general laws in parasite ecology? *Parasitology*, **134**, 763–776.

**Poulin, R.** 2013. Parasite manipulation of host personality and behavioural syndromes. *The Journal of Experimental Biology*, **216**, 18–26.

**Rathbun, G. B.** 1979. The social structure and ecology of elephant-shrews. *Advances in Ethology*, **20**, 1–75.

**Rathbun, G. B.** 2009. Why is there discordant diversity in sengi (Mammalia: Afrotheria : Macroscelidea) taxonomy and ecology? *African Journal of Ecology*, **47**, 1–13.

**Rathbun, G. B. & Rathbun, C. D.** 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.

**Redi, C. A., Garagna, S., Zuccotti, M. & Capanna, E.** 2007. Genome size: a novel genomic signature in support of Afrotheria. *Journal of Molecular Evolution*, **64**, 484–487.

**Ribble, D. O. & Perrin, M. R.** 2005. Social organization of the eastern rock elephant-shrew (*Elephantulus myurus*): the evidence for mate guarding. *Nature*, **135**, 167–173.

**Roberts, L. S. & Janovy Jr., J.** 2005. *Foundations of Parasitology.* 7th edn. New York, USA: McGraw Hill.

**Roberts, M. L., Buchanan, K. L. & Evans, M. R.** 2004. Testing the immunocompetence handicap hypothesis: a review of the evidence. *Animal Behaviour*, **68**, 227–239.

**Romero, L. M.** 2002. Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. *General and Comparative Endocrinology*, **128**, 1–24.

**Roxburgh, L. & Perrin, M. R.** 1994. Temperature regulation and activity pattern of the round-eared elephant shrew *Macroscelides proboscideus*. *Journal of Thermal Biology*, **19**, 13–20.

**Saino, N. & Møller, A. P.** 1994. Secondary sexual characters, parasites and testosterone in the barn swallow, *Hirundo rustica*. *Animal Behaviour*, **48**, 1325–1333.

**Salvador, A., Veiga, J. P., Martín, J. & López, P.** 1997. Testosterone supplementation in subordinate, small male lizards: consequences for aggressiveness, color development, and parasite load. *Behavioral Ecology*, **8**, 135–139.

**Sapolsky, R. M., Romero, L. M. & Munck, A. U.** 2000. How do glucocorticoids influence stress responses? Preparative actions. *Endocrine Reviews*, **21**, 55–89.

**Schradin, C. & Lamprecht, J.** 2002. Causes of female emigration in the group-living cichlid fish *Neolamprologus multifasciatus*. *Ethology*, **108**, 237–248.

**Schubert, M., Pillay, N., Ribble, D. O. & Schradin, C.** 2009. The round-eared sengi and the evolution of social monogamy: Factors that constrain males to live with a single female. *Ethology*, **115**, 972–985.

**Schurch, R. & Heg, D.** 2010. Life history and behavioral type in the highly social cichlid *Neolamprologus pulcher*. *Behavioral Ecology*, **21**, 588–598.

**Seltmann, M. W., Öst, M., Jaatinen, K., Atkinson, S., Mashburn, K. & Hollmén, T.** 2012. Stress responsiveness, age and body condition interactively affect flight initiation distance in breeding female eiders. *Animal Behaviour*, **84**, 889–896.

**Sih, A., Bell, A. & Johnson, J. C.** 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, **19**, 372–378.

**Smith, B. R. & Blumstein, D. T.** 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, **19**, 448–455.

**Sundari, A. A., Bogdanowicz, W., Varman, D. R., Marimuthu, G. & Rajan, K. E.** 2012. Ectoparasite *Raymondia iobulata* infestation in relation to the reproductive cycle of its host—the greater false vampire bat *Megaderma lyra*. *Journal of Parasitology*, **98**, 60–62.

**Svartberg, K. & Forkman, B.** 2002. Personality traits in the domestic dog (*Canis familiaris*). *Applied Animal Behaviour Science*, **79**, 133–155.

**Thomason, C. A., Hedrick-Hopper, T. L. & Derting, T. L.** 2013. Social and nutritional stressors: agents for altered immune function in. *Canadian Journal of Zoology*, **320**, 313–320.

**Toms, C. N., Echevarria, D. J. & Jouandot, D. J.** 2010. A methodological review of personality-related studies in fish: focus on the shy-bold axis of behavior. *International Journal of Comparative Psychology*, **23**, 1–25.

**Van Houte, S., Ros, V. I. D. & van Oers, M. M.** 2013. Walking with insects: molecular mechanisms behind parasitic manipulation of host behaviour. *Molecular Ecology*, **22**, 3458–3475.

**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.

**Webster, J. P.** 2001. Rats, cats, people and parasites: the impact of latent toxoplasmosis on behaviour. *Microbes and Infection*, **3**, 1037–1045.

**While, G. M., Isaksson, C., McEvoy, J., Sinn, D. L., Komdeur, J., Wapstra, E. & Groothuis, T. G. G.** 2010. Repeatable intra-individual variation in plasma testosterone concentration and its sex-specific link to aggression in a social lizard. *Hormones and Behavior*, **58**, 208–213.

**Wilson, D. S., Coleman, K., Clark, A. B. & Biederman, L.** 1993. Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology*, **107**, 250–260.

**Wilson, D. S., Clark, A., Coleman, K. & Dearstyne, T.** 1994. Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, **9**, 442–446.

**Wilson, K., Bjørnstad, O. N., Dobson, A. P., Merler, S., Poglayen, G., Ran, Read, A. F. & Skorping, A.** 2001. Heterogeneities in macroparasite infections: patterns and processes. In: *The Ecology of Wildlife Diseases*, 1st edn. (Ed. by P. J. Hudson, A. Rizzoli, B. T. Grenfell, H. Heesterbeek, & A. P. Dobson), pp. 6–44. New York, USA: Oxford University Press.

**Yeo, M., Treloar, S., Marks, G., Heath, A. & Martin, N. G.** 1997. What are the causes of individual differences in food consumption and are they modified by personality? *Journal of Personality and Individual Difference*, **23**, 535–542.

# Chapter 2

## Arthropod ectoparasite burdens of eastern rock sengis (*Elephantulus myurus*) and their effect on host body condition

### Abstract

Ectoparasites can be important in the ecology of host populations due to the detrimental effects they may have on host fitness. However, such fitness effects remain poorly studied in wild mammal populations. It is not always clear however, whether abundances of parasites are due to direct influence of abiotic factors as seasonal fluctuations of rainfall, or biotic factors of the host such as fluctuating hormones, potentially leading to changes in host behaviour. Similarly, the effects parasites have on one another are not well considered due to a lack of studies investigating more than one parasite. Eastern rock sengis (*E. myurus*) are insectivores that occur in arid, rocky regions of southern Africa. They are known as hosts to large tick burdens while their other ectoparasites are poorly studied. In this study we investigated the entire ectoparasite community of sengis over the period of 14 months. By manipulating ectoparasite burdens, using Frontline® treatment, we studied their effect on host body condition and ectoparasite population dynamics. We found four main ectoparasites on eastern rock sengis, two tick species, *Rhipicephalus warburtoni* and *Rhipicentor nuttalli,* one louse species, *Neolignathus elephantuli* and a mite family Trombiculidea or chiggers. We found that treatment resulted in increased body condition of sengis. We also found a negative effect of treatment on *R. warburtoni* abundances while the opposite was found for chiggers. Chiggers were also the only ectoparasite to be correlated with sengi body condition and larger abundances positively correlated with body condition.

## Introduction

An ectoparasite is defined as an organism that lives externally on a host, from which it derives either food or other biological necessities. These organisms can experience either a part of, or its complete life cycle on the host (Kim 1985). The ecology of many ectoparasites makes them susceptible to climatic variation when spending time off-host, as they are occasionally required to undergo activities such as moulting (Hopkins 1948; Keetch 1971; Arnaudov & Antov 1977; Milutinovic *et al.* 1996). There is no exact pattern of temperature, rainfall or humidity that determines success for any one ectoparasite taxon (Bordes *et al.* 2010). Many studies have shown a trend that higher levels of humidity can provide some protection from desiccation for ectoparasites, specifically when in the sensitive larval or nymphal phases (Moyer *et al.* 2002; Abd El-Halim *et al.* 2009; Bordes *et al.* 2010). As such abundances are higher during periods of greater humidity as ectoparasites such as ticks and lice may quest with greater safety and find potential hosts (Basu & Bandyopadhyay 2004). However the opposite has also been found suggesting that what works for one taxon, does not necessarily improve fitness for another (Carmichael *et al.* 2007; Lareschi & Krasnov 2010).

It is not always clear however, whether seasonal changes in the abundance of parasites are due to direct influence of abiotic factors as seasonal fluctuations of rainfall and hormones in hosts could also potentially lead to changes in host behaviour. This makes the interactions between hosts and parasites particularly complex as hosts attempt to decrease ectoparasite burdens while ectoparasites are dependent on hosts for their own survival (Marcogliese 2005; Morand *et al.* 2006). Despite the importance of ectoparasites they remain relatively under studied when taking into account that over 50% of the organism diversity in a given ecosystem consists of parasites and potentially they can have dramatic biological impacts (Morand *et al.* 2006). Their relative importance in wildlife populations is generally underestimated in relation to other factors such as predation and competition (Irvine 2006; Dunn *et al.* 2013). One such impact is the effect that ectoparasites can have on body condition of an animal. As such ectoparasites can potentially have dramatic impacts on their hosts. This can be caused by directly competing for resources required by the animal through absorption of nutrients or by forcing the animals to increase defences against parasitism (Hall 1985; Bize *et al.* 2008). The resources an animal has available for factors such as growth, maintenance and reproduction are finite and parasites can force animals to relocate resources which is an expensive endeavour and can have huge implications for the host fitness (Sheldon & Verhulst 1996; Rigby *et al.* 2002, Clayton & Tompkins 1995; De Lope *et al.* 1998; Pryce *et al.* 2001). This can often translate into an animal with a large parasite burden having decreased body condition compared to less parasitized hosts in the population (Turner *et al.* 2012). Studies have demonstrated that it is not always easy to determine direct negative effects of parasite burdens (Lehmann 1992; Tella *et al.* 1995; Ebert *et al.* 2000; Poulin & George-Nascimento 2007). These have added to the growing body of knowledge on the concept that hosts have abilities to contest parasites and balance the level of positive to negative reactions (Irvine 2006; Miller *et al.* 2006; Dunne *et al.* 2013). Much research has been done on parasite-host interactions although many small mammal papers tend to have mainly focused on the impact of diseases on organisms and the role that ectoparasites, or host, play in the transmission of pathogens throughout a population (Fernandes *et al.* 1992; Patz *et al.* 2000; Ueti *et al.* 2008; Li *et al.* 2009). Some of the more common ectoparasites studied in small mammal populations are ticks, mites, and lice due to the disease transmitting abilities of these ectoparasites (Durden & DeBruyn 1984; Clayton & Tompkins 1995; Randolph & Storey 1999; Weiss 2009). Many studies also tend to focus on a single species or taxon, with few looking at the link between different parasites (Pedersen & Fenton 2007; Graham 2008). What recent studies suggest though is that the parasite community could have dramatic effects on the host due to changes bought about my manipulation of the population structure on a host (Druilhe *et al.* 2005; Ferrari *et al.* 2009; Pedersen & Antonovics 2013). In the study by Pedersen and Antonovics (2013), Ivermectin treatment in mice, *Peromyscus* species, reduced prevalence of intestinal nematodes, target parasite, but increased prevalence of the non-target parasites coccidian and cestodes. They proposed that competition could be a mechanism driving these interactions and also found that reducing the nematode infection did not increase fitness. This is often the case in many studies and they proposed that it may be due to the complex interactions in parasite populations which are often not seen as most studies focus on a single parasite species.

The implication of ectoparasitism for life history and population dynamics on the host is an important factor and as such studies have investigated sex-biased differences of ectoparasite infestation, which is especially important when considering survival of a population (Kokko *et al.* 2006; Kahn *et al.* 2013). In general the trend appears to be a male-bias in parasite burdens (Moyer *et al.* 2002; Boyer *et al.* 2010). This seems to be based on sexual dimorphism in populations with larger males and/or the effect of the testosterone. As posited in the immunocompetence handicap hypothesis, animals with higher testosterone levels should have higher levels of parasite burden due to a testosterone linked reduction in immunocompetence (Folstad & Karter 1992). Males in many species tend to have larger territories that they defend more aggressively and roam more actively within their environment possibly due to increased testosterone (Silverin 1998; Apfelbeck *et al.* 2013). As such males in many small mammal populations could be the drivers of ectoparasite distribution throughout a host population or area. Most studies to date have investigated this but have used sexually dimorphic rodent species (Krasnov *et al.* 2005; Hillegass *et al.* 2008; Scantlebury *et al.* 2010).There is however a distinct lack of studies investigating these phenomenon in African small mammals, with most having investigated only African rodents (Hillegass *et al.* 2008; Viljoen *et al.* 2011; Archer 2013).

Sengis or elephant shrews are small mammals belonging to the order Macroscelidea. The order comprises some 17 species all of which are endemic to Africa (Skinner & Chimimba 2005). This is an ancient order that recently, after years of discordant taxonomy, was included in the supergroup

Afrotheria, which includes a diverse assemblage of animals such as elephants, aardvark and hyraxes, dugongs, and golden moles (Asher *et al.* 2003; Redi *et al.* 2007).

Sengis are insectivorous and are well equipped for hunting small soft-bodied insects using their fast, cursorial locomotion (Rathbun 1979; Nicoll & Rathbun 1990). A unique characteristic of sengis in relation to other small mammals, such as rodents, is that they have one or two precocial offspring per litter that are capable of following the mother around a few hours after birth (Skinner & Chimimba 2005) and sengis do not use nests or burrows. Sengis are also considered monogamous and exhibit no sexual dimorphism with overlapping home ranges shared amongst pairs (Rathbun 1979; Rathbun & Rathbun 2006).

Twenty-seven ixodid tick species belonging to six genera have been previously recorded from sengis and these have been solely immature stages (Fourie *et al.* 1995). More remarkable is the fact that some species of sengi have been noted to harbour large tick abundances (Harrison *et al.* 2011; Horak *et al.* 2011; Lutermann *et al.* 2012a). Abundances of ticks are substantially higher than those of the sympatrically occurring Namaqua rock mice (*Micaelamys namaquensis*) which plays host to an average of 4 ticks (Fourie *et al.* 1995; Harrison *et al.* 2011).

In this study we focused on the eastern rock sengi (*Elephantulus. myurus*). To date 12 tick species have been recorded on this animal with large abundances (Fourie *et al.* 1995, 2005). This despite the fact that *E. myurus* inhabits an arid region (Skinner & Chimimba 2005) and it is generally perceived that ticks are faced with major constraints in terms of survival off host due the risk of desiccation and high temperatures (Needham & Teel 1991; Buczek 1999; Estrada-Pena 2009). Other ectoparasite taxa have also been recorded to infest this species (Fourie *et al.* 2005) but the general population structure of ectoparasites occurring on *E. myurus* has not been recorded.

Most studies to date have focused mainly on tick burdens on eastern rock sengis due to the potential economic threat these ectoparasites pose to livestock as a result of these large tick infestations (McCartan *et al.* 1987; Dreyer *et al.* 1997; Ghosh *et al.* 2006). In southern Africa the economic importance of tick-borne diseases may be even more considerable due to their reliance on livestock for sustenance and cultural property in rural communities (Perry *et al.* 1991; Bardosh *et al.* 2011; Spickett *et al.* 2011). The relationship of rural communities with livestock, i.e. sleeping in close proximity to livestock to protect them from predators, also adds to the medical concern for tick-borne diseases manifesting and causing serious illness in humans (Coertze 1986; De Garine-Wichatitsky *et al.* 2012). Some have made mention of the other parasites found on sengis, namely lice, fleas and mites, but these have been mainly of a general descriptive nature (Fourie 1995, Beaucournu *et al.* 2003).

The aim of this study was firstly, to determine the population composition of ectoparasites infesting wild *E. myurus*. Furthermore, we intended to document seasonal fluctuation of ectoparasite burdens. Finally, we aimed to evaluate possible effects of ectoparasites on the body condition of the host.

## M**aterials and methods**

### *Collection of Animals*

Animals used in the study were captured from Goro Game Reserve in the Limpopo Province, South Africa (22°58’S; 29°25’E). Animals were caught using Sherman traps (H. B. Sherman Traps, Inc. Tallahassee, Florida, U.S.A.) baited with a mixture of sardines, oats and peanut butter. Animals were caught during March 2012 - April 2013 under the permit number 001-CPM401-0002 from the Department of Environmental Affairs, Limpopo Province. The period of capture was broken down into six different trips of four weeks each over the one year period (March-April 2012, June 2012, August 2012, October – November 2012, January – February 2013 and March-April 2013). This was broken down into six different seasons for the analysis.

A total of 150 traps were laid out in parallel lines with ten paces between traps and between lines in the late afternoon and left out overnight to be picked up the following morning. Traps were laid out for three nights every second night at eight different sites. The sites consisted of areas with a mixture of rocky outcrops and arid vegetation that eastern rock sengis inhabit (Mzilikazi & Lovegrove 2005). There were eight sites approximately 300 metres apart. The furthest two sites were approximately 3 km apart and the sites varied roughly 75 metres in altitude

*Procedure for ectoparasite processing*

Captured animals were immediately weighed upon returning to the camp to the nearest 0.01g using a digital scale (Scout Pro SPU123; Ohaus Corporation, USA) and sexed. Sengis were restrained by hand and treated by removing all ectoparasites. Ectoparasites were removed by manually searching through fur and extremities and picking them off using forceps (Lasec Laboratory & Scientific Equipment Company, South Africa, number 4). This has proven to be a successful method for removing ectoparasites on *E. myurus* (Lutermann *et al.* 2012a). The parasites were stored in Eppendorf tubes containing 70% ethanol. Each taxon of parasites, i.e. lice, mites and ticks, were put into separate Eppendorfs as they were removed from the animal. Sengis were then given unique ear clips for recapture identification and body length was taken using an electronic calliper (INSIZE Co., Ltd). The length of the body from the back of the neck to the base of the tail was defined as body length. Half of the animals caught were also additionally treated against ectoparasites. This treatment consisted of applying Frontline® (Merial Pty, Ltd, South Africa), a topical tick and flea dip, on the animals before releasing them. Frontline® was applied by spraying onto the gloved hand of a handler and rubbing it on the animal, as recommend on by the manufacturer for puppies and kittens. Individuals were randomly assigned to this particular secondary treatment group (labelled either as treated or untreated) to achieve an even distribution between the sexes and sites. The second treatment was repeated for animals, when caught on each successive trip. Some studies that investigate ectoparasites can count ectoparasites directly on the host and as such do not remove them to obtain accurate species numbers (Salvador *et al.* 1997; Boyer *et al.* 2010). Due to the large number of ectoparasites found on *E. myurus* it was necessary to remove them in order to obtain accurate population and species breakdowns. This resulted in all animals being treated, technically, by removing the parasites and half being treated additionally with Frontline®. It should be noted that treatment, used throughout the thesis, refers to the secondary treatment of applying Frontline® to half of the animals and untreated animals refers to those that did not have Frontline® applied. The treatment was repeated for animals, when caught on each successive trip. All animals were released at the point of capture in the afternoon.

Since there were three nights per site per trip recaptures occurred within a trip. For those individuals recaptures within a trip, body mass was measured and ectoparasites were collected again but Frontline® treatment was not repeated until the first capture in a subsequent trip.

Ticks were identified to species level and the total and mean abundances of each species in nymph and larval stage were counted under a standard dissecting microscope (Walker *et al.* 2000)

Mites were mounted using a drop of polyvinyl acetate (PVA) on a glass slide. A specimen was then placed into the PVA with a needle and a cover slip was lightly pressed on top. After drying for 3-4 days the slides were ringed with clear nail polish and dried in an oven at 30-35˚C for 24 hours. After identification of family (Krantz & Walter 2009), mites were counted and abundances noted.

Lice were cleared by treating them with 15% KOH solution for between 10 – 15 hours and returned to 70% ethanol. Lice were then identified to species level (Ledger & Konigsmann 1980) and sexed under a compound microscope by pipetting the lice onto a glass slide with a cover slip placed over them to make a temporary mounted slide.

### *Statistical Analysis*

Total abundances, mean abundances and prevalence of all parasites, were calculated using Quantitative Parasitology 3.0 (Reiczigel J, Rózsa L 2005. *Quantitative Parasitology 3.0.* Budapest). Terms were used as defined by Bush *et al.* (Bush *et al.* 1997). Prevalence refers to the number of hosts infected with one or more individuals of the particular parasite divided by the number of hosts examined. Total abundances refer to the total number of parasites for each species found during the sampling period. Mean abundance is the total number of a specific parasite species divided by the total number of hosts in the sample. Ectoparasite species that had a prevalence of more than 4% were analysed in detail while only descriptive statistics are provided for the remaining species to reduce models and increase robustness of the analyses.

There was a strong significant correlation between the different immature stages for abundant parasites (Appendix, Table 1). Consequently, to improve robustness of comparing different parasites by reducing models data of different stages/sexes of each species of parasites, these were combined for the statistical analysis.

None of the ectoparasite data collected satisfied the criteria for a normal distribution (Shapiro-Wilk Test: $p<0.001$). Therefore, analysis of all ectoparasite data consisted of a generalised linear mixed model (GLMM) in SPSS v.21 (SPSS Inc., Chicago, Illinois, U.S.A) with random effects for all models run consisting of individual ID of sengis nested within sites. For prevalence of ectoparasites a binary logistic data distribution in the GLMM using a logit link was used with sex, treatment, capture status (see below) and season (for long term data) as independent variables as well as possible interactions thereof. The interactions terms consisted of sex*treatment, sex*capture status, treatment*capture status and treatment*season. The interactions of sex*season and capture status*season were not possible due to inadequate sample sizes as one season (October) only females were captured and for the first season there were no recaptures yet.

The analyses of short term effects were restricted to individuals that were recaptured within the same trip. For the analyses the animals were classified as being captured for the first time (1st capture), second (RCT/1) or third time within a trip (RCT/2) When analysing long term effects only the first capture of an individual during a particular trip was considered and individuals were classified as either new animals when first captured or as being recaptures in a subsequent trip. For parasite abundances a negative binomial data distribution with a log-link function in a GLMM was used and independent variables remained the same. Post-hoc tests consisted of least significant pairwise comparisons (LSD) for the different analysis.

Body condition was calculated by dividing the mass of the animal by its body length to give a more robust indicator of the animal's overall resource assimilation. Body condition was found to be not normally distributed for the population when taking into account short term data (Shapiro-Wilk Test: $p > 0.001$). Consequently a GLMM with a gamma distribution was used to evaluate the effects of sex, treatment, capture status, and trip with prevalence of common ectoparasite species (see results) on body condition. A second model was run with parasites abundances added as covariates. As before these were carried out separately for short- and long term effects but for long term data it was found that body condition was normally distributed when log-transformed (Shapiro-Wilk Test: $p = 0.424$). This resulted in GLMM for body condition for long term data being run with a linear distribution with an identity link function. Due to the similarity between effects on prevalence and effects on abundances we have decided to include only effects on abundances in this chapter. Results for GLMMs on short term effects on prevalence of the different ectoparasites are included in the appendix (Appendix Table 2).

## Results

### *Ectoparasite burdens*

A total of 125 animals were caught (68 ♂, 57 ♀) between one and ten times during March 2012 - April 2013. Of these 53 individuals were recaptured at least once between trips while 64 animals were captured more than once within trips (Table 1). Ectoparasites from three taxa (ticks, mites and lice) were encountered

***Table 1*** **–** Number of *E. myurus* captured throughout the trapping period.

| | **Males** | | **Females** | |
|---|---|---|---|---|
| **Season** | **New** | **Recapture** | **New** | **Recapture** |
| **March 12** | 34 | 0 | 26 | 0 |
| **June** | 11 | 14 | 8 | 8 |
| **August** | 3 | 15 | 4 | 12 |
| **October** | 0 | 0 | 1 | 4 |
| **January** | 4 | 5 | 8 | 4 |
| **March 13** | 15 | 7 | 10 | 12 |

***Table 2*** - Arthropod ectoparasites species found on *E. myurus* in Goro Game Reserve, in the Limpopo Province, South Africa.

| | **Order** | **Suborder/Superfamily** | **Family** | **Species** |
|---|---|---|---|---|
| Ticks | Ixodida | Ixodoidea | Ixodidae | *Amblyoma brumpti* |
| | | | | *Amblyoma hebraeum* |
| | | | | *Amblyoma marmoreum* |
| | | | | *Haemaphysalis elliptica* |
| | | | | *Haemaphysalis leche* |
| | | | | *Rhipicentor nuttalli* |
| | | | | *Rhipicephalus arnoldi* |
| | | | | *Rhipicephalus simus* |
| | | | | *Rhipicephalus warburtoni* |
| | | | Nuttalliellidae | *Nuttalliella namaqua* |
| Mites | Trombidiformes | Trombidioidea | Trombiculidae | - |
| Lice | Phthiraptera | Anoplura | Neolinognathidae | *Neolinognathus elephantuli* |

Nine ixodid tick species, belonging to four genera as well as the tick species *Nuttaliella namaqua,* were recorded from eastern rock sengis (Table 2). Only immature stages were retrieved from the animals. Mites could only be identified to family level (Table 2). A single species of lice was identified, namely *Neolinognathus elephantuli* (Table 2). *N. elephantuli* was the only adult ectoparasite found on *E. myurus.* Considering only first captures in a trip the most common ectoparasite species was a tick species with a prevalence of 100%, namely *Rhipicephalus* (*R.*) *warburtoni* (previously referred to as *R.* sp. near *warburtoni* in Harrison *et al.* 2011) . Prevalences are included in the appendix (Appendix Figure 1) throughout the year. A second tick species, *Rhipicentor* (*Rc*.) *nuttalli* was identified with a prevalence of 38.5% (Table 3). The other eight species of ticks had a prevalence of less than 4%, with five of those species having less than 1% prevalence (Table 3). Chiggers were the second most common ectoparasite with a prevalence of 66.2% whereas the only louse species *N. elephantuli* had a prevalence of 17.8%. Prevalence and abundances of all ectoparasites found are presented in Table 3. This shows that eight of the ten species of ticks had total abundances of less than 12 and a mean abundance of less than 2.31 ± 2.95 (Table 3). In contrast, *R. warburtoni* had a total abundance of 53358 (Table 3) and a mean abundance of 259.02 ± 129.03 per animal. *Rc. nuttalli* had a total abundance of 711 with a mean abundance of 3.47± 4.31 per animal (Table 3). The abundances for chiggers and *N. elephantuli* are also presented in Table 3.

### *Short term patterns*

For abundances we found that *R. warburtoni* was significantly affected by treatment (Table 4). Treated animals had significantly lower abundances (27.263 ± 3.991) of ticks than untreated animals (60.722 ± 8.838). Abundances were also affected by capture status of an animal (Table 3). Post hoc tests revealed that new animals (270.788 ± 24.723) had significantly higher abundances of ticks than RCT/ 1 (24.099 ± 2.929, $p < 0.0001$) and RCT/2 (10.322 ±2.146, $p < 0.0001$). RCT/1 also had higher abundances of ticks than RCT/2 (LSD: $p < 0.0001$). *R. warburtoni* was also significantly affected by season (Table 4).

***Table 3*** - Population structure of ectoparasite species found on *E. myurus.*

| | **Total Abundance** | **Prevalence [%] (95%CI)** | **Mean Abundance (95% CI)** |
|---|---|---|---|
| *Amblyoma brumpti* (larvae) | 3 | 0.9 (0.00 – 0.03) | 0.01 (0.00 - 0.02) |
| *Amblyoma hebraeum* (larvae) | 8 | 0.5 (0.00 – 0.03) | 0.04 (0.00 – 0.11) |
| *Amblyoma marmoreum* (larvae) | 5 | 2.3 (0.01 – 0.05) | 0.02 (0.00 – 0.05) |
| *Haemaphysalis elliptica* (larvae) | 3 | 1.4 (0.00 – 0.04) | 0.01 (0.00 – 0.03) |
| *Haemaphysalis leche* (larvae) | 2 | 0.5 (0.00 – 0.03) | 0.01 (0.00 – 0.03) |
| *Nuttalliella namaqua* (larvae) | 32 | 0.5 (0.00 – 0.02) | 0.16 (0.00 – 0.47) |
| *Rhipicentor nuttalli* (nymphs) | 219 | 29.1 (0.23 – 0.36) | 1.03 (0.74 – 1.56) |
| *Rhipicentor nuttalli* (larvae) | 492 | 38.5 (0.32 – 0.45) | 2.31 (1.77 – 2.95) |
| *Rhipicephalus arnoldi* (nymphs) | 2 | 0.9 (0.00 – 0.03) | 0.01 (0.00 - 0.02) |
| *Rhipicephalus simus* (larvae) | 11 | 3.3 (0.01 – 0.07) | 0.05 (0.02 – 0.09) |
| *Rhipicephalus warburtoni* (nymphs) | 4915 | 99.1 (0.97 – 1.00) | 23.66 (21.54 – 25.89) |
| *Rhipicephalus warburtoni* (larvae) | 48443 | 100 (0.97 – 1.00) | 231.44 (211.16 – 253.20) |
| Trombiculidae (chigger mites) | 2944 | 66.2 (0.60 – 0.73) | 15.30 (11.97 – 19.74) |
| *Neolinognathus elephantuli* (males) | 246 | 23 (0.18 – 0.30) | 1.71 (1.20 – 2.34) |
| *Neolinognathus elephantuli* (females) | 227 | 25.5 (0.20 – 0.32) | 1.38 (0.95 – 1.93) |
| *Neolinognathus elephantuli* (nymphs) | 330 | 19.3 (0.14 – 0.25) | 1.71 (1.10 – 2.58) |

We also found a significant interaction between treatment and capture status (Table 4). Post hoc tests showed that there was no significant difference in parasite abundances between new animals that were either treated or untreated (LSD: $p = 0.205$, Figure 1a). For RCT/1 treated animals had significantly lower abundances than untreated (LSD: $p < 0.0001$, Figure 1a).

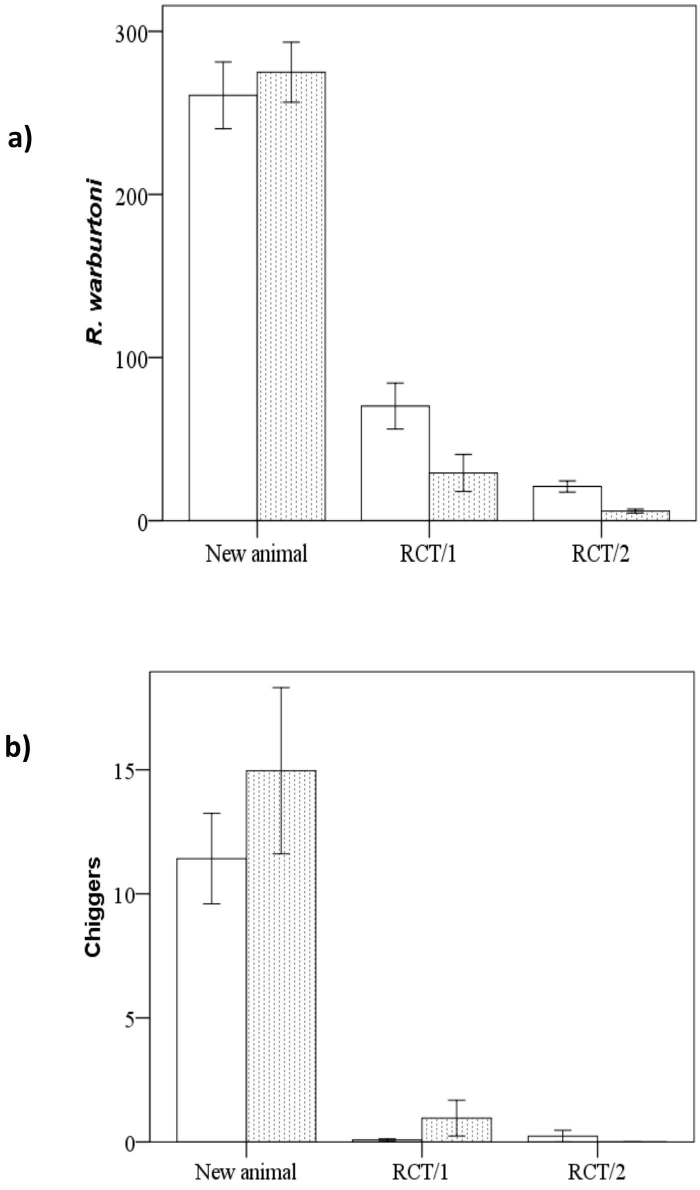

***Figure 1*** - Effects of treatment and capture status on the abundance ± SE of a) *R. warburtoni* and b) chiggers. White bars represent untreated animals and filled bars represent treated animals.

The same was found for RCT/2, namely that treated animals had significantly lower abundances, than untreated (LSD: p: 0.023, Figure 1a). None of the other variables tested or the other interaction terms were found to be significant for *R. warburtoni* (Table 4).

The abundance of *Rc. nuttalli* was significantly affected by capture status of the animals (Table 4); however post hoc tests were not significant (LSD: p= 0.546). As with *R. warburtoni* we found a significant effect of season of which the post hoc tests were similar to that of the long term data and as such will be discussed with those results (Table 4). The interaction between treatment and capture status were found to significantly affect *Rc. nuttalli* abundance but post hoc tests did not reveal any significant interaction (LSD: p = 1.000). None of the other factors or their interactions was found to be significant (Table 4).

For chiggers we found that abundances were significantly affected by treatment (Table 4) and treated (7.528 ± 2.271) animals had higher abundances of mites than untreated (1.778 ± 0.595). Abundances were also affected by capture status of the animal (Table 4) and new animals (10.851 ± 2.120) had significantly higher abundances of mites than RCT/1 (2.241 ± 0.611) and RCT/2 (2.014 ± 2.014, p < 0.0001 for both comparisons). There was no significant difference between RCT/1 and RCT/2 mite abundances (LSD: p = 0.852). Significant seasonal effects will be discussed with the long term data.

The interaction between treatment and capture status was significant (Table 4) and post hoc analysis revealed that there was no significant difference between treated and untreated animals when new (LSD: p = 0.675, Figure 1b) or when RCT/2 (LSD: p = 0.191, Figure 1b). There was however a significant effect of RCT/1 with treated animals having higher abundances than untreated (LSD: p = 0.014, Figure 1b). None of the other variables tested or their interactions were found to be significant (Table 4). *N. elephantuli* mean abundance was found to be significantly affected by season but none of the other factors investigated or their interactions (Table 4). Unlike the other ectoparasites it was found that *N. elephantuli* was not significantly affected by season (Table 4).

*Long term patterns*

Mean *R. warburtoni* abundance was significantly affected by season, but not by any other factors or interactions investigated (Table 4). The lowest mean abundance was observed in June while it was highest in October (Figure 2a).

*Table 4* - Results of GLMMs for short term and long term effects of sex, treatment, capture status and season on the abundance of the four most common ectoparasite species of *E. myurus*.

| | | | ***R. warburtoni*** | | ***Rc. Nuttalli*** | | **chiggers** | | ***N. elephantuli*** | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | **df** | **F** | **p-value** | **F** | **p-value** | **F** | **p-value** | **F** | **p-value** |
| **Short Term** | Sex | 1, 321 | 0.369 | 0.544 | 1.888 | 0.170 | 0.624 | 0.430 | 2.086 | 0.150 |
| | Treatment | 1, 321 | 15.104 | **<0.0001*** | 0.000 | 1.000 | 10.088 | **0.002*** | 1.075 | 0.301 |
| | Capture status | 2, 321 | 274.247 | **<0.0001*** | 11.110 | **<0.0001*** | 19.157 | **<0.0001*** | 6.997 | **0.001*** |
| | season | 5, 321 | 3.373 | **0.006*** | 7.438 | **<0.0001*** | 6.646 | **<0.0001*** | 0.015 | 1.000 |
| | Sex*treatment | 1, 321 | 1.324 | 0.251 | 0.654 | 0.419 | 0.046 | 0.831 | 0.098 | 0.754 |
| | Sex*capture status | 2, 321 | 0.813 | 0.444 | 0.951 | 0.387 | 0.760 | 0.468 | 1.771 | 0.172 |
| | Treatment*capture status | 2, 321 | 26.960 | **<0.0001*** | 0.3331 | **<0.0001*** | 7.172 | **0.001*** | 0.003 | 0.997 |
| | Treatment*season | 5, 321 | 0.444 | 0.817 | 1.399 | 0.224 | 0.696 | 0.627 | 0.144 | 0.982 |
| **Long Term** | Sex | 1, 193 | 0.002 | 0.967 | 7.077 | **0.008*** | 0.608 | 0.437 | 4.601 | **0.033*** |
| | Treatment | 1, 193 | 1.509 | 0.221 | 0.000 | 1.000 | 0.793 | 0.374 | 4.682 | **0.032*** |
| | Capture status | 1, 193 | 0.001 | 0.993 | 0.945 | 0.332 | 0.019 | 0.889 | 0.713 | 0.399 |
| | season | 5, 193 | 6.278 | **<0.0001*** | 4.998 | **<0.0001*** | 15.649 | **<0.0001*** | 0.150 | 0.980 |
| | Sex*treatment | 1, 193 | 0.129 | 0.720 | 7.604 | **0.006*** | 0.156 | 0.693 | 0.137 | 0.711 |
| | Sex*capture status | 1, 193 | 1.880 | 0.172 | 0.043 | 0.836 | 1.207 | 0.273 | 5.721 | **0.018*** |
| | Treatment*capture status | 1, 193 | 1.06 | 0.745 | 0.038 | 0.846 | 0.083 | 0.774 | 2.745 | 0.099 |
| | Treatment*season | 5, 193 | 0.761 | 0.579 | 0.414 | 0.838 | 1.032 | 0.400 | 0.818 | 0.538 |

***significant effects**

The lowest mean abundance was observed in June while it was highest in October (Figure 2a). In June we observed significantly lower (Figure 2a) mean abundances than in March (LSD: $p < 0.0001$), October (LSD: $p = 0.026$) January (LSD: $p = 0.016$) and March 2013 (LSD: $p = 0.045$, Figure 2a). In August we observes significantly lower (Figure 2a) mean abundances than in March (LSD: $p = 0.003$), October (LSD: $p =0.029$), January (LSD: $p = 0.036$) and March 2013 (LSD: $p = 0.005$, Figure 2a). None of the other mean abundances significantly differed between seasons.

For *Rc. nuttalli* it was found that sex significantly affected mean abundance with males (0.014 ± 44.551) having higher abundance than females (0.007 ± 22.918, Table 4). It was also found that season significantly affected mean abundance of *Rc. nuttalli* (Table 4). The lowest mean abundance was observed in January as this species was absent during this month and it was highest in March (Figure 2b). In March we found significantly higher mean abundances than in August (LSD: $p = 0.034$), October (LSD: $p = 0.001$), January (LSD: $p = 0.001$) and March 2013 (LSD: $p = 0.003$, Figure 2b). In June we observed significantly higher mean abundances than in October (LSD: $p = 0.002$), January (LSD: $p = 0.001$) and March 2013 (LSD: $p = 0.034$, Figure 2b)

We observed significantly higher mean abundances in August than in October (LSD: $p = 0.012$) and January (LSD: $p = 0.003$, Figure 2b). In January we had significantly lower mean abundances than in March 2013 (LSD: $p = 0.003$, Figure 2b). None of the other seasons varied significantly in terms of mean *Rc. nuttalli* abundance. The interaction between sex and treatment was found to be significant (Table 4) however post hoc tests did not confirm this (LSD: $p = 1.000$). None of the other factors investigated were found to be significant and neither were their interactions (Table 4). Chigger mean abundance was found to be significantly affected season (Table 4).

The highest mean abundance of chiggers was found to be in March 2013 while the lowest was found in August (Figure 2c). In March we observed significantly higher mean abundances than August (LSD: $p = 0.005$) and March 2013 (LSD: $p = 0.011$, Figure 2c). In June we found significantly higher mean abundances than August (LSD: $p = 0.003$, Figure 2c).

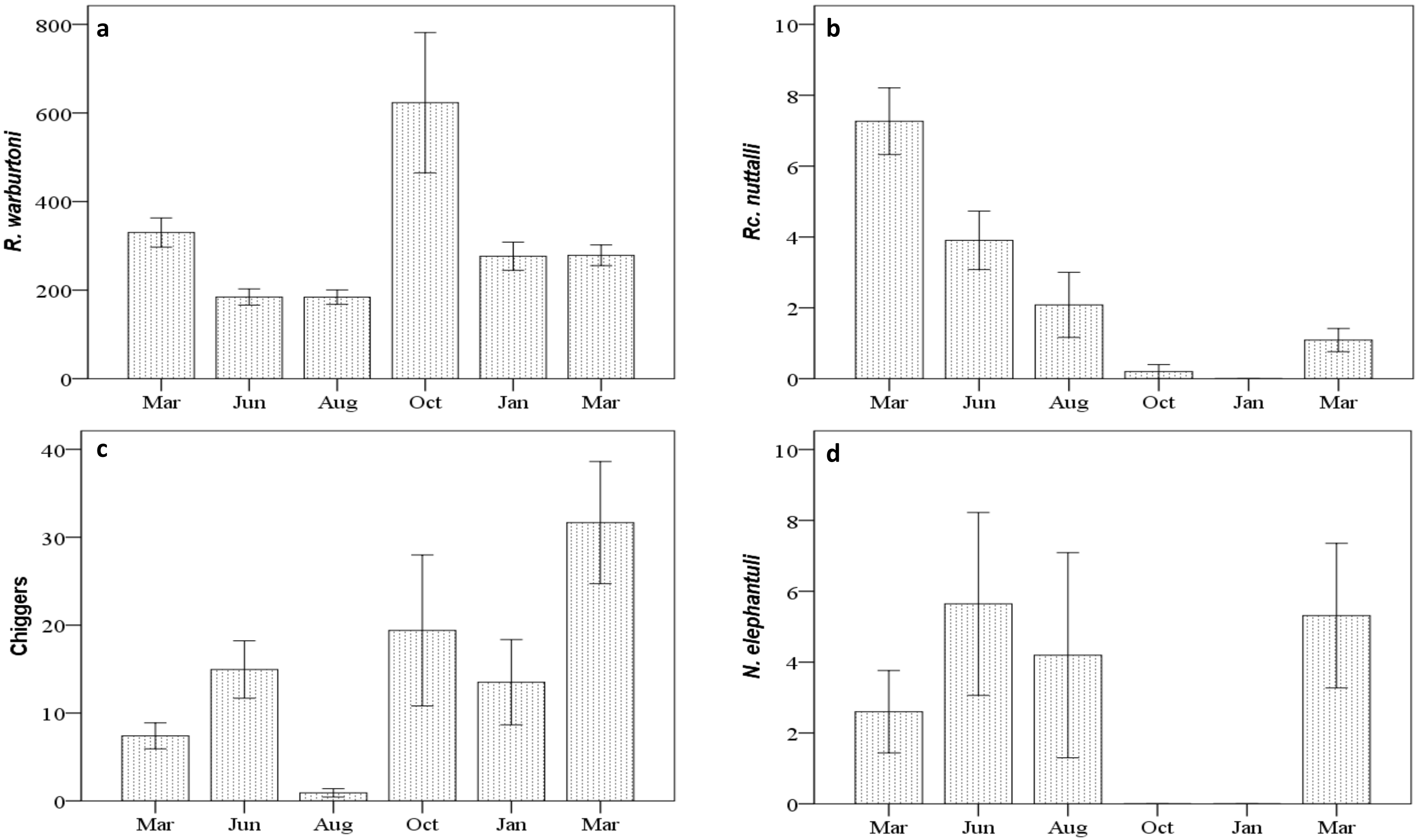

***Figure 2*** - Seasonal variation in abundance ± SE of a) *R. warburtoni*, b) *Rc. nuttalli*, c) chiggers and d) *N. elephantuli* found on *E. myurus*.

August had a significantly lower mean abundances than January (LSD: $p = 0.019$) and March 2013 (LSD: $p = 0.002$, Figure 2c). None of the other variables explored were found to be significant nor their interactions (Table 4). *N. elephantuli* mean abundance was significantly affected by sex with males (10.915 ± 6.113) having higher abundances than females (2.828 ± 1.484). In addition, treatment and the interaction between sex and capture status was significant (Table 4). However, none of the post hoc tests done showed any significant interactions. There was also no significance found with any off the other factors examined or their interactions (Table 4).

### *Body Condition*

#### *Short term patterns*

Body condition of an animal was found to be significantly affected by treatment (Table 5). Treated animals (0.892 ± 0.017) had significantly higher mean body condition than untreated animals (0.798 ± 0.017). Season was also found to significantly affect body condition (Table 5). The lowest mean body condition was observed in March while the highest body condition was found in August (Figure 3). In March animals had a significantly lower body condition than August (LSD: $p < 0.0001$), January (LSD: $p < 0.0001$) and March 2013 (LSD: $p = 0.004$, Figure 3). The body condition in June was significantly lower than in August (LSD: $p < 0.0001$), January (LSD: $p = 0.001$), and March 2013 (LSD: $p = 0.011$, Figure 3). None of the other seasons varied significantly in terms of body condition. The interaction between treatment and season was found to be significant (Table 5). For August it was found that treated animals had significantly higher body condition than untreated (LSD: $p = 0.033$, Figure 4). This was also the case for October (LSD: $p = 0.009$), January (LSD: $p < 0.0001$) and March 2013 (LSD: $p = 0.003$, Figure 4). None of the other interactions between season and treatment was significant. Similarly none of the other factors investigated were found to be significant (Table 5).

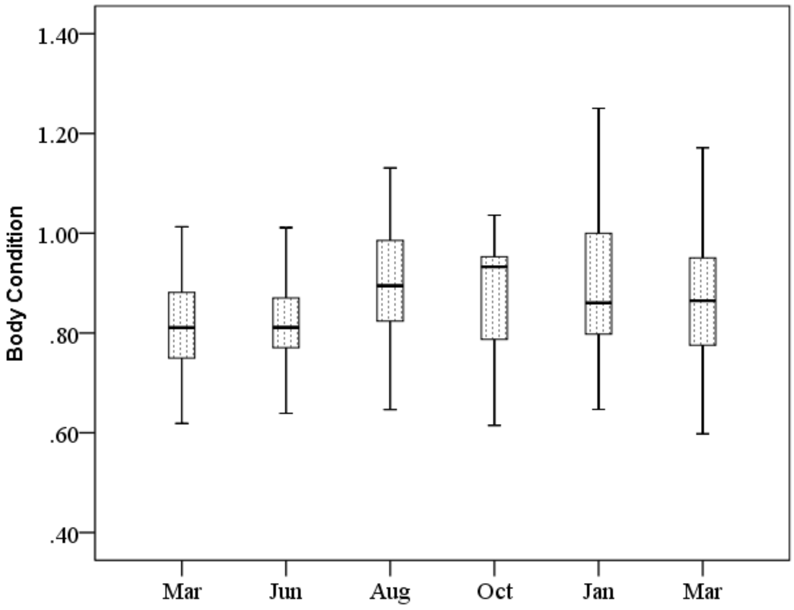

*Figure 3* – Seasonal variation of body condition based on short term data. Black horizontal lines (bands) represent medians and whiskers represent minimum and maximum values.

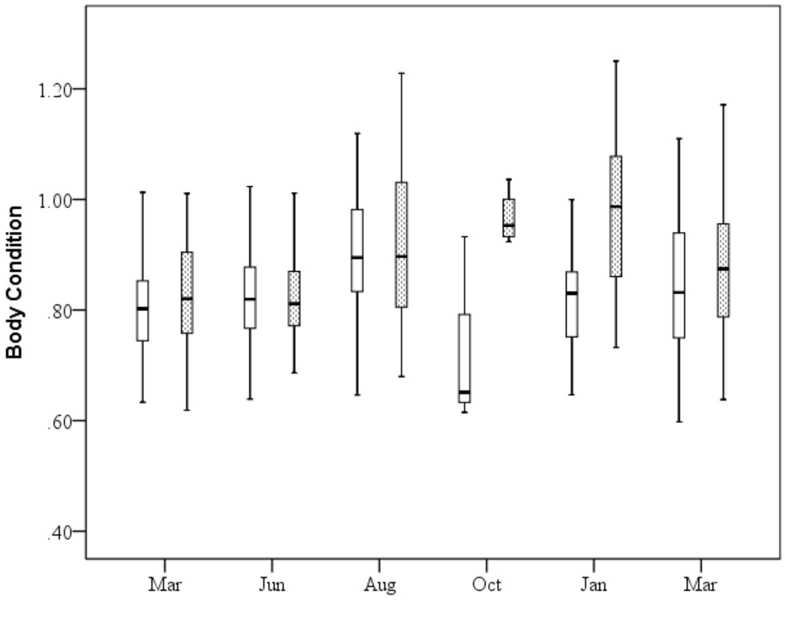

*Figure 4* – Seasonal variation of body condition of untreated (open bars) and treated (filled bars) *E. myurus* recaptured within trips. Black horizontal lines represent medians and whiskers represent minimum and maximum values.

***Table 5*** - Results of GLMMs looking at effect of sex, treatment, capture status, season and the abundance of the four most common ectoparasite species on body condition of *E. myurus*.

| | **Short term patterns** | | | **Long term patterns** | | |
|---|---|---|---|---|---|---|
| | **df** | **F** | **p-value** | df | **F** | **p-value** |
| Sex | 1, 317 | 0.382 | 0.537 | 1, 190 | 1.400 | 0.238 |
| Treatment | 1, 317 | 17.528 | **<0.0001*** | 1, 190 | 5.501 | **0.020*** |
| Capture status | 2, 317 | 1.484 | 0.228 | 1, 190 | 5.596 | **0.019*** |
| Season | 5, 317 | 7.895 | **<0.0001*** | 5, 190 | 1.507 | 0.189 |
| *R. warburtoni* | 1, 317 | 0.578 | 0.448 | 1, 190 | 1.098 | 0.296 |
| *Rc. Nuttalli* | 1, 317 | 0.039 | 0.843 | 1, 190 | 0.098 | 0.754 |
| chiggers | 1, 317 | 2.785 | 0.096 | 1, 190 | 5.480 | **0.020*** |
| *N. elephantuli* | 1, 317 | 0.251 | 0.616 | 1, 190 | 1.069 | 0.303 |
| Sex*treatment | 1, 317 | 0.060 | 0.807 | 1, 190 | 0.004 | 0.951 |
| Sex*capture status | 2, 317 | 0.022 | 0.979 | 1, 190 | 3.206 | 0.075 |
| Treatment*capture status | 2, 317 | 0.998 | 0.370 | 1, 190 | 1.138 | 0.287 |
| Treatment*season | 5, 317 | 2.878 | **0.015*** | 5, 190 | 0.763 | 0.578 |

***significant effects**

### *Long term Patterns*

Body condition was significantly affected by treatment (Table 5). Treated animals (-0.057 ± 0.008) had a significantly higher body condition than untreated animals (-0.085 ± 0.009). The body condition was also significantly affected by capture status of the animal (Table 5, Figure 5). It was found that new animals (-0.088 ± 0.009) had significantly lower body condition than recaptures (-0.066 ± 0.009) and treated animals that were recaptured had significantly higher body condition than recaptured animals that were untreated (LSD: p = 0.030, Figure 5). However new animals whether treated or untreated were not significantly different (LSD: p = 0.357, Figure 5). Chiggers were the only ectoparasite to significantly affect body condition (Table 4) and it was only found with mean abundance, not with prevalence (Appendix Table 3). It was found with increasing body condition that there was a significant increase in mean chigger abundance (Figure 6). None of the other factors investigated were found to be significant (Table 5).

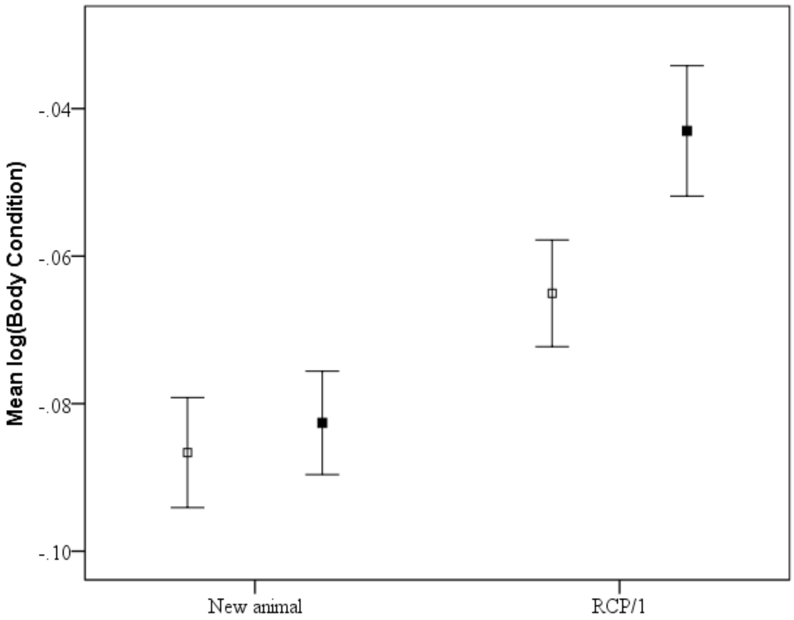

***Figure 5*** - Effects of capture status and treatment on body condition. Displayed are means ± SE.

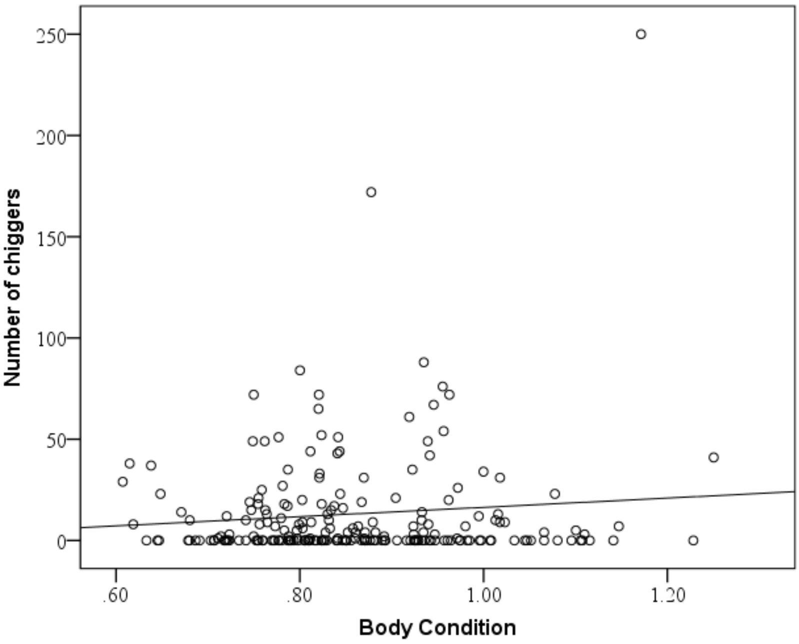

***Figure 6*** – Correlation between body condition and chigger abundance in *E. myurus*. Line through the scatters represents the relationship between the two variables.

## Discussion

In this study we examined the ectoparasite fauna infesting *E. myurus*. The most common ectoparasites found were ticks with, ten different species. Two of these occurred at high prevalence and abundance. In addition chiggers and *N. elephantuli* were found with a relatively high prevalence, although the abundance of the latter was relatively low compared to the two major tick species. The number of tick species described was within the range of those previously described for this host, although the specific species varied somewhat (Fourie *et al.* 1995; Horak *et al.* 2005). The species which had the highest abundance, *R. warburtoni*, prefers *E. myurus* as the host for its immature stages (Fourie *et al.* 1995; Harrison *et al.* 2011). Similarly, immature stages of *Rc. nuttalli* are also thought to be found on *E. myurus* although the preference seems to be hedgehogs (Fourie *et al.* 2002). Their lower abundance is likely as the main adult host of *Rc. nuttalli,* as found in other studies, is the domestic dog and leopards and there were no dogs present at the sites of our study and leopards are actively hunted on the farm. So it is possible the seasonal effect is due to changes in less preferred wild host populations for adult *Rc. nuttalli* such as hedgehogs (Horak *et al.* 2011). Also it is generally accepted that chiggers are a common ectoparasite of small mammals with a wide distribution and that most small mammals tend to have lice even if the abundances are low (Morand *et al.* 2006). The larval stages of chiggers are parasitic while the adult forms are generally free-living predatory soil mites. So chiggers are dependent on a close interaction with hosts during their vulnerable larval stage (Krantz & Walter 2009). It is possible that *N. elephantuli* make use of the host in a similar fashion, thereby allowing some protection from external climatic variables (Hopkins 1948; Morand *et al.* 2006). It is common for sucking lice to remain permanently on the host due to high host specificity and *N. elephantuli* is highly specific for sengis and has been found on several species including *E. myurus* (Hopkins 1948; Fourie *et al.* 1995). Since sengis do not make use of nests, it is likely that lice are transmitted from mother to offspring which may account for our low abundances as transferal is restricted compared to the other ectoparasites which may feed off other hosts and are able to roam.

We also investigated season by looking at the different months throughout the trapping period in which trapping was done. Although prevalence data was included only in the appendix it is interesting to note that the continued presence throughout the year of the tick *R. warburtoni* seems unusual for an ectoparasite, particularly ticks, which generally exhibit strong influences of seasonal change (Hlatshwayo *et al.* 2002; Oorebeek & Kleindorfer 2008).However Lutermann *et al.* (2012b), also found the presence of *R.* warburtoni to be year round and they attributed this to ambient temperatures being milder during winter months and as such the questing of the immature stages of *R. warburtoni* likely went uninterrupted as has been noted during hot temperatures (Benoit & Denlinger 2010). *Rc. nuttalli* was absent from October – January. The engorgement period for female *Rc. nuttalli* is longer than that of other ixodid ticks, including *R. warburtoni* (Fourie *et al.* 2002). This is likely due to the narrow host range of *R. nuttalli* and the likelihood that only a single life cycle is completed annually compared to *R. warburtoni* which appears slightly better suited to a wider range of hosts and the climate (Fourie *et al.* 2002).

Our findings on abundances of tick species corresponded with a previous study conducted on *E. myurus* in Goro Game Reserve where it was found that abundances of *R. warburtoni* were dependant on season. Lutermann *et al.* (2012b) found *R. warburtoni* abundance of both nymph and larvae to be significantly affected by rainfall and temperature which is expected as ticks in general are reliant on humidity and temperature as they are prone to desiccation (Randolph 2004). The previous study also showed that the highest abundances were found in June and July, whereas our highest abundances were in October and similarly the lowest abundances found in the previous study were found in September whereas ours was in June. However it should be noted that during October we caught only a small number of females, (n=5), most of which may have been pregnant.

This may have increased our parasite abundances as have been reported previously for the study species (Lutermann *et al.* 2012b).

However for *Rc. nuttalli,* we found that abundances tended to decrease as the trapping period continued, which was the opposite trend to *R. warburtoni* and chiggers. This also contradicted a previous study that investigated seasonality of *Rc. nuttalli*. Fourie *et al.* (2002) found that *Rc. nuttalli* were prevalent throughout the entire year with the greatest abundances during September, while the highest abundances in this study were during March. These changes may be due to the fact that Fourie *et al.* (2002) looked at ticks mainly in the Free State Province and on livestock farms. Our study area is a game reserve with exclusively game present in the trapping area. Also some studies have shown that ectoparasite abundances can be significantly affected by breeding and non-breeding difference in hosts (Viljoen *et al.* 2011). In a study by Lutermann *et al.* (2012b) it was found that tick abundances were higher during non-breeding seasons, suggesting that host responses to climatic variation can be as important as direct effects on ectoparasites.

Chiggers showed an opposite trend to the tick species, specifically *Rc. nuttalli*, in that chigger abundances seemed to increase during the wet season. This coincides with the requirements of chiggers to avoid desiccation as many ectoparasites do, due to the fact that periods of time are spent of host, making themselves susceptible to environmental factors such as rainfall (Keetch 1971; Townsend Jr. *et al.* 2006). The majority of chiggers are free-living, but in the immature stages they are saprophagous and live in close association with warm-blooded animals likely due to the protection these offer the sensitive immature stages (Spieksma 1997). Chiggers had the second highest prevalence which is likely due to the fact that it appears to be a generalist ectoparasite with a worldwide distribution and as such are relatively common in those areas where they are found (Fain & Lukoschus 1975; Nadchatram *et al.* 1980; Jones 1987; Bordes *et al.* 2010)

*N. elephantuli* showed no significant effects on abundances as seen in the other ectoparasites when considering season. Avian lice have been shown to spend their entire life cycle on the host (Clayton

& Tompkins 1995). As such lice may be more affected by host biotic factors rather than climatic variation (Abd El-Halim *et al.* 2009; Lareschi & Krasnov 2010).

Sengis are socially monogamous, with males and females coming together mainly to mate (Ribble & Perrin 2005; Rathbun & Rathbun 2006) Sengis are not sexually dimorphic which may explain the lack of an effect of sex in the variables measured. Males and females inhabit similarly sized home ranges and it is thought that roaming and social behaviours are similar (Rathbun & Rathbun 2006), one would predict that they do not exhibit different parasite abundances or body conditions. This supports results found in other studies that have investigated sexual bias in parasite burdens and found it to be weakly supported at best (Brunner & Ostfeld 2008; Kiffner *et al.* 2011). Scantlebury *et al.* (2010) showed sex bias parasite abundances in grey squirrels with males having larger loads despite there being no sexual dimorphism, contradicting the notion that differences in parasite load are strictly due to differences in size between the sexes. As a result of the Frontline® treatment applied, treated animals had substantially lower abundances of *R. warburtoni* during the short term period of re-colonization. However, the opposite was true of chiggers, with re-colonization rates being higher, hence larger abundances during the short term period for treated animals, while there was no such effect on *Rc. nuttalli* and lice. This finding shows that Frontline® is effective in combating re-colonization rates of *R. warburtoni* at least on a short term basis and that abundances can be manipulated in a wild host that is released back into the wild where re-infestation is likely to occur. However it was only *R. warburtoni* abundances that were negatively affected by treatment within captures, during the period of potential re-colonization. This suggests that in our study Frontline® altered the ectoparasite community on the host, something which due to logistical difficulties have been mainly done in lab conditions with parasites chosen specifically for responsiveness (Graham 2008). It is important to note that in accordance with the suppliers indications different ectoparasites respond differently to Frontline® with regards to time taken to die or escape the host as well as re-infestation rates of parasites onto a ‘clean’ host (Winchester *et* *al.* 2004; Diaz 2005). This suggests that removing ectoparasites and treating the animal with Frontline® may alter species composition and affect how and when certain species re-colonize their hosts which has implication for competition between species.

Most other studies have however mainly focused on single parasites when looking at host-parasite interactions and possible fitness consequences or behavioural manipulation; however most animals are infected by more than one parasite species (Petney & Andrews 1998; Cox 2001; Druilhe *et al.* 2005). Potentially the interactions between parasites could affect susceptibility to disease and increase infestation rates of one another. In a study by Druilhe et al (2005) they found that treating children for worms significantly decreased malaria incidence and other parasite densities. The opposite however may also be the case as was found by us; our data suggests that due to interspecific competition between ectoparasites once the pressures of ticks were removed, specifically *R. warburtoni*, the second most abundant ectoparasite, chiggers, were able to increase their numbers. The mechanisms driving these interactions are currently unknown but it may be due to competition for space and resources as both groups inhabit the surface of the animal and both require dermal surface area to attach (Walker *et al.* 2000; Krantz & Walter 2009). Ferrari et al (2009) found something similar when looking at yellow-necked mice, the chemical removal of the intestinal nematode *Heligmosomoides polygyrus*, using Pyrantel pamoate, increased infestation of the tick species *Ixodes ricinus.* A more recent study by Pedersen and Antonovics (2013) also demonstrated the importance of parasite community dynamics by treating deer mice and white-footed mice with Ivermectin. This reduced the prevalence of intestinal nematodes while significantly increasing cestode and coccidian prevalence. As with our study this demonstrates the importance of looking at parasites as an ecological community, which is often stressed but due to difficulty in the field, is often not investigated (Holt & Dobson 2006; Pedersen & Fenton 2007; Ferrari *et al.* 2009; Knowles *et al.* 2013).

For the long term patterns we found no effect on any of the ectoparasites except lice. The active ingredient in Frontline® is fipronil, a chemical insecticide that is effective when used against ticks and fleas in domestic animals (Diaz 2005). However, the re-infestation rates of different ectoparasites when using Frontline® is not clear. The general consensus for ticks is a period of 4 – 6 weeks where the host would be free of parasites (Dryden *et al.* 2008; De Oliveira *et al.* 2011; Kužner *et al.* 2012). Consequently, the time that elapsed between captures (2 – 10) exceeded this period and re-infestation had already occurred between trips, as has been found in other studies (Widermann 2000; Winchester *et al.* 2004).

Treatment with Frontline® significantly increased body condition of sengis within trips and between trips. This suggests that parasite burdens have significant negative effects on the host, which concur with the general consensus on parasite effects (Morand *et al.* 2006). Many studies suggest that it is mainly the combination of opportunistic parasites feeding on already immune compromised individuals that bring about this trend (Smyth 1991; Ebert & Herre 1996; Lafferty & Kuris 1999). What we found however corresponds well with wild or natural populations that have been studied (Tella *et al.* 1995; Kiffner *et al.* 2011) in that there is limited effects apparent of parasite burdens, most likely due to the co-evolution of host parasite interactions when looking at untreated animals (Medley 2002; Rigby *et al.* 2002). However once treated our data suggests that there is some cost involved to harbouring large ectoparasite abundances as has been found in *E. myurus*. The cost may not be apparent when investigating the population initially due to the strong co-evolution of hosts and parasites (Morand *et al.* 2006).

The data showing that treated animals improved body condition between and within trips suggests that the removal of the ectoparasites neutralised the negative costs usually associated with high ectoparasite abundances. It is also one of only a few studies to investigate this due to the difficulty in manipulating burdens in wild populations (Ebert *et al.* 2000; Medley 2002). The results suggest that the treated sengis may have a greater amount of resources available that could be implemented in life-history traits other than parasite defence. This effect of parasite removal is further emphasised by looking at capture status of an animal. New animals had significantly lower body condition than recaptures suggesting that removal of ectoparasites for any period of time could be beneficial to the animal. Even with re-infestation occurring, manipulation of burdens can allow animals a reprieve with which to increase resources available for other functions such as growth and reproduction. These results highlight the substantial direct cost of parasite burdens, something which is not always seen in wild hosts due to complex interactions. (Tella *et al.* 1995)

Chiggers were the only ectoparasite to increase significantly with increased body condition when looking at sengis between trips. This again is likely due to interspecific competition as a result of treatment removing *R. warburtoni* and increasing body condition as a result of this removal of the major ectoparasite. It is also possible that chiggers would increase due to animals in better condition being able to sustain larger loads of ectoparasites as has been found by other (Pulkkinen & Ebert 2004). If this were the case however it would be likely that we would see some effect of treatment on *Rc. nuttalli* and *N. elephantuli* as well, this was not the case.

Our data demonstrates that sengis can maintain a great diversity of ectoparasite species with large tick as well as mite burdens. Sex did not affect prevalence and abundances of ectoparasites. The prevalence and abundances of ticks and chiggers was significantly affected by season, although this was not the case for lice. This study also highlights the importance of looking at multiple parasites on the host and their interaction with one another as community structure of parasites may determine fitness costs to the host. The interspecific competition between parasites as demonstrated by our data also has implication for life history of the host, something which needs to be investigated further to understand underlying mechanism of this competition. In addition, we found significant effects of manipulating burdens in that body condition significantly increased for animals that had been treated with Frontline®. This could have implications for the survival and reproductive fitness of animals as an increased body condition suggesting greater resource availability. This suggests the removal of parasites can potentially affect fitness of animals. We also demonstrated that this could be seen both short and long term, something which is not always examined in studies manipulating parasite burdens. Our study suggests that it is important to consider duration and continuation of manipulation or examination as there is no simple interaction between host and parasite.

## References

**Abd El-Halim, A. S., Allam, K. A. M., Metwally, A. M. & El Boraey, A. M.** 2009. Seasonal variation of infestation rate with lice, tick and mite among rodents in certain Egyptian regions. *Journal of the Egyptian Society of Parasitology*, **39**, 617–624.

**Apfelbeck, B., Mortega, K., Kiefer, S., Kipper, S., Vellema, M., Villavicencio, C. P., Gahr, M. & Goymann, W.** 2013. Associated and disassociated patterns in hormones, song, behavior and brain receptor expression between life-cycle stages in male black redstarts, *Phoenicurus ochruros*. *General and Comparative Endocrinology*, **184**, 93–102.

**Arnaudov, D. & Antov, I.** 1977. Species and seasonal dynamics of the ixodid ticks in Smolyan Province. *Veterinarnomeditsinski nauki*, **14**, 68–73.

**Asher, R. J., Novacek, M. J. & Geisler, J. H.** 2003. Relationships of endemic African mammals and their fossil relatives based on morphological and molecular evidence. *Journal of Mammalian Evolution*, **10**, 131–194.

**Bardosh, K., Thys, S. & Ngowi, H.** 2011. *Socio-cultural research on the neglected zoonotic diseases in Africa: A review of the literature and outline for a future research agenda.* Blackwell Publishing Ltd.

**Basu, A. K. & Bandyopadhyay, P. K.** 2004. The effect of season on the incidence of ticks. *Bulletin of Animal Health and Production in Africa*, **52**, 39–42.

**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**, 1366–1376.

**Bize, P., Jeanneret, C., Klopfenstein, A. & Roulin, A.** 2008. What makes a host profitable? Parasites balance host nutritive resources against immunity. *The American Naturalist*, **171**, 107–118.

**Bordes, F., Morand, S., Krasnov, B. R. & Poulin**. 2010. Parasite diversity and latitudinal gradients in terrestrial mammals. In: *The Biogeography of Host-Parasite Interactions*, (Ed. by S. Morand & B. R. Krasnov), pp. 89–98. UK: Oxford University Press.

**Boyer, N., Réale, D., Marmet, J., Pisanu, B. & Chapuis, J.-L.** 2010. Personality, space use and tick load in an introduced population of Siberian chipmunks, *Tamias sibiricus. The Journal of Animal Ecology*, **79**, 538–47.

**Brunner, J. L. & Ostfeld, R. S.** 2008. Multiple causes of variable tick burdens on small-mammal hosts. *Ecology*, **89**, 2259–2272.

**Buczek, A.** 1999. Physiology of ticks (Ixodida) in non-parasitic phase of life cycle. *Wiadomości parazytologiczne*, **45**, 151–159.

**Bush, A. O., Lafferty, K. D., Lotz, J. M. & Shostak, A. W.** 1997. Parasitology meets ecology on its own terms: Margolis *et al.* Revisted. *The Journal of Parasitology*, **83**, 575–583.

**Carmichael, J. A., Strauss, R. E. & McIntyre, N. E.** 2007. Seasonal variation of North American form of *Gigantolaelaps mattogrossensis* (Acari: Laelapidae) on marsh rice rat in southern coastal Texas. *Journal of Medical Entomology*, **44**, 80–84.

**Clayton, D. H. & Tompkins, D. M.** 1995. Comparative effects of mites and lice on the reproductive success of rock doves (*Columba livia*). *Parasitology*, **110**, 195–206.

**Coertze, R. D.** 1986. Livestock in the social and cultural life of African communities. *South African Journal of Ethnology*, **9**, 129–135.

**Cox, F. E.** 2001. Concomitant infections, parasites and immune responses. *Parasitology*, **122**, 23–38.

**De Garine-Wichatitsky, M., Miguel, E., Mukamuri, B., Garine-Wichatitsky, E., Wencelius, J., Pfukenyi, D. M. & Caron, A.** 2012. Coexisting with wildlife in transfrontier conservation areas in

Zimbabwe: Cattle owners’ awareness of disease risks and perceptions of the role played by wildlife. *Comparative Immunology Microbiology and Infectious Diseases*, **32**, 321-332

**De Lope, F., Møller, A. P. & De La Cruz, C.** 1998. Parasitism, immune response and reproductive success in the house martin, *Delichon urbica*. *Oecologia*, **114**, 188–193.

**De Oliveira, P. R., Bechara, G. H., Denardi, S. E., Pizano, M. A. & Mathias, M. I. C.** 2011. Toxicity effect of the acaricide fipronil in semi-engorged females of the tick *Rhipicephalus sanguineus* (Latreille, 1806) (Acari: Ixodidae): preliminary determination of the minimum lethal concentration and LC(50). *Experimental Parasitology*, **127**, 418–422.

**Diaz, S. L.** 2005. Efficacy of fipronil in the treatment of pediculosis in laboratory rats. *Laboratory Animals*, **39**, 331–335.

**Dreyer, K., Fourie, L. J. & Kok, D. J.** 1997. Predation of livestock ticks by chickens as a tick-control method in a resource-poor urban environment. *The Onderstepoort Journal of Veterinary Research*, **64**, 273–276.

**Druilhe, P., Tall, A. & Sokhna, C.** 2005. Worms can worsen malaria: towards a new means to roll back malaria? *Trends in Parasitology*, **21**, 359–62.

**Dryden, M., Payne, P., 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 Research in Applied Veterinary Medicine*, **9**, 15–25.

**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**, 30-50.

**Dunne, J. A, Lafferty, K. D., Dobson, A. P., Hechinger, R. F., Kuris, A. M., Martinez, N. D., McLaughlin, J. P., Mouritsen, K. N., Poulin, R., Reise, K., Stouffer, D. B., Thieltges, D. W., Williams, R. J. & Zander, C. D.** 2013. Parasites affect food web structure primarily through increased diversity and complexity. *PLoS Biology*, **11**, e1001579.

**Durden, L. A. & DeBruyn, E. J.** 1984. Louse infestations of tree shrews (*Tupaia glis*). *Laboratory Animal Science*, **34**, 188–190.

**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.

**Estrada-Pena, A.** 2009. Tick-borne pathogens, transmission rates and climate change. *Frontiers in Bioscience a Journal and Virtual Library*, **14**, 2674–2687.

**Fain, A. & Lukoschus, F. S.** 1975. Parasitic mites of Surinam. New observations on the Genera Chirnyssoides and Notoedres from bats (Sarcoptiformes: Sarcoptidae). *Acta zoologica et pathologica Antverpiensia*, **61**, 91–118.

**Fernandes, A. J., Chiari, E., Casanova, C., Dias, J. C. P. & Romanha, A. J.** 1992. The threat of reintroduction of natural transmission of Chagas-disease in Bambui, Minas-Gerais State, Brazil, due to *Panstrongylus-megistus*. *Memórias do Instituto Oswaldo Cruz*, **87**, 285–289.

**Ferrari, N., Cattadori, I. M., Rizzoli, A & Hudson, P. J.** 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. *The American Naturalist*, **139**, 603–622.

**Fourie, L. J., Du Toit, J. S., Kok, D. J. & Horak, I. G.** 1995. Arthropod parasites of elephant-shrews, with particular reference to ticks. *Mammal Review*, **25**, 31–37.

**Fourie, L. J., Horak, I. G., Kok, D. J. & Zyl, W. V. A. N.** 2002. Hosts, seasonal occurrence and life cycle of *Rhipicentor nuttalli* (Acari : Ixodidae). *Onderstepoort Journal of Veterinary Research*, **69**, 177–187.

**Fourie, L. J., Horak, I. G. & Woodall, P. F.** 2005. Elephant shrews as hosts of immature ixodid ticks. *The Onderstepoort Journal of Veterinary Research*, **72**, 293–301.

**Ghosh, S., Azhahianambi, P. & De La Fuente, J.** 2006. Control of ticks of ruminants, with special emphasis on livestock farming systems in India: present and future possibilities for integrated control - a review. *Experimental and Applied Acarology*, **40**, 49–66.

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

**Hall, A.** 1985. Nutritional aspects of parasitic infection. *Progress in Food Nutrition Science*, **9**, 227–256.

**Harrison, A., Bown, K. J. & Horakà, I. G.** 2011. Detection of *Anaplasma bovis* in an undescribed tick species collected from the eastern rock sengi *Elephantulus myurus*. *Journal of Parasitology*, **97**, 1012–1016.

**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.

**Hlatshwayo, M., Mbati, P. A & Dipeolu, O. O.** 2002. Seasonal abundance of adult ixodid ticks infesting cattle belonging to resource-limited farmers in the north-eastern Free State Province of South Africa. *The Onderstepoort Journal of Veterinary Research*, **69**, 1–6.

**Holt, R. D. & Dobson, A. P.** 2006. Extending the principles of community ecology to address the epidemiology of host-pathogen systems. In: *Disease ecology, community structure and pathogen dynamics*, (Ed. by S. K. Collinge & C. Ray), pp. 6–27. New York: Oxford University Press.

**Hopkins, M.** 1948. The Host-asociations of the lice of mammals. *Proceedings of the Zoological Society of London*, **119**, 387 – 604.

**Horak, I. G., Fourie, L. J. & Braack, L. E. O.** 2005. Small mammals as hosts of immature ixodid ticks. *The Onderstepoort Journal of Veterinary Research*, **72**, 255–261.

**Horak, I. G., Welman, S. & Hallam, S. L.** 2011. Ticks of four-toed elephant shrews and Southern African hedgehogs. *Onderstepoort Journal of Veterinary Research*, **78**, 1–3.

**Irvine, R. J.** 2007. Parasites and the dynamics of wild mammal populations. *Animal Science*, **82**, 775-781.

**Jones, J. G.** 1987. Chiggers. *American Family Physician*, **36**, 149–152.

**Kahn, A. T., Kokko, H. & Jennions, M. D.** 2013. Adaptive sex allocation in anticipation of changes in offspring mating opportunities. *Nature Community*, **4**, 1603–1608.

**Keetch, D. P.** 1971. Ecology of the citrus red mite. *Panonychus citri* (McGregor), (Acarina: Tetranychidae) in South Africa I. The seasonal abundance of *P. citri* in an orchard under natural control. *Journal of the Entomological Society of Southern Africa*, **34**, 63–72.

**Kiffner, C., Lödige, C., Alings, M., Vor, T. & Rühe, F.** 2011. Body-mass or sex-biased tick parasitism in roe deer (*Capreolus capreolus*). A GAMLSS approach. *Medical and Veterinary Entomology*, **25**, 39–45.

**Kim, K.** 1985. *Coevolution of parasitic arthropods and mammals.* 1st edn. New York: Wiley and 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 B: Biological Sciences*, **280**, 1–9.

**Kokko, H., Jennions, M. D. & Brooks, R.** 2006. Unifying and testing models of sexual selection. *Annual Review of Ecology Evolution and Systematics*, **37**, 43–66.

**Krantz, G. W. & Walter, D. E.** 2009. *A Manual of Acarology.* 3rd edn. Lubbock: Texas Tech University Press.

**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**, 209–217.

**Kužner, J., Turk, S., Grace, S., Soni-Gupta, J., Fourie, J. J., Marchiondo, A. A. & Rugg, D.** 2012. 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. *Limonology And Oceanography*, **44**, 925–931.

**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.

**Ledger, J. A. . & Konigsmann, E.** 1980. The arthropod parasites of vertebrates in Africa south of the Sahara. Volume IV. Phthiraptera (Insecta). *Publications of the South African Institute for Medical Resaerch*, **56**, 327–330.

**Lehmann, T.** 1992. Ectoparasite impacts on *Gerbillus andersoni allenbyi* under natural conditions. *Parasitology*, **104**, 479–488.

**Li, Y., Luo, J., Guan, G., Ma, M., Liu, A., Liu, J., Ren, Q., Niu, Q., Lu, B., Gao, J., Liu, Z., Dang, Z., Tian, Z., Zhang, B., He, Z., Bai, Q. & Yin, H.** 2009. Experimental transmission of *Theileria uilenberg*i infective for small ruminants by *Haemaphysalis longicornis* and *Haemaphysalis qinghaiensis*. *Parasitology Research*, **104**, 1227–1231.

**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**, 1–9.

**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.

**Marcogliese, D. J.** 2005. Parasites of the superorganism: Are they indicators of ecosystem health? *International Journal for Parasitology*, **35**, 705–716.

**McCartan, B. M., Hunter, A. G., Pegram, R. G. & Bourne, A. S.** 1987. Tick infestations on livestock in the Yemen Arab Republic and their potential as vectors of livestock diseases. *Tropical Animal Health and Production*, **19**, 21–31.

**Medley, G. F.** 2002. The epidemiological consequences of optimisation of the individual host immune response. *Parasitology,* **125**, 61–70.

**Miller, M. R., White, A. & Boots, M.** 2006. The evolution of parasites in response to tolerance in their hosts : the good, the bad and apparent commensalism. *Evolution; International Journal of Organic Evolution*, **60**, 945–956.

**Milutinovic, M., Pavlovic, I., Kulisic, Z. & Ivovic, V.** 1996. Effect of macroclimatic factors on population dynamics of ticks (Acarina, Ixodidae) in Serbia. *Veterinarski Glasnik,* **50**, 753–759.

**Morand, S. & Krasnov, B. R.** 2006. *Micromammals and Macroparasites From Evolutionary Ecology to Management.* Japan: Springer-Verlag.

**Moyer, B. R., Drown, D. M. & Clayton, D. H.** 2002. Low humidity reduces ectoparasite pressure: implications for host life history evolution. *Oikos*, **97**, 223–228.

**Mzilikazi, N. & Lovegrove, B. G.** 2005. Daily torpor during the active phase in free-ranging rock elephant shrews (*Elephantulus myurus*). *Journal of Zoology*, **267**, 103–111.

**Nadchatram, M., Lukoschus, F. S. & Fain, A.** 1980. Malaysian parasitic mites II. Myobiidae (prostigmata) from rodents. *International Journal of Acarology,* **6**, 109–120.

**Needham, G. R. & Teel, P. D.** 1991. Off-host physiological ecology of ixodid ticks. *Annual Review of Entomology*, **36**, 659–681.

**Nicoll, M. & Rathbun, G. B.** 1990. *African Insectivora and elephant-shrews: an action plan for their conservation.* 1st edn. Gland, Switzerland: IUCN.

**Oorebeek, M. & Kleindorfer, S.** 2008. Climate or host availability: what determines the seasonal abundance of ticks? *Parasitology Research,* **103**, 871–875.

**Patz, J. A., Graczyk, T. K., Geller, N. & Vittor, A. Y.** 2000. Effects of environmental change on emerging parasitic diseases. *International Journal for Parasitology*, **30**, 1395–1405.

**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.

**Perry, B. D., Kruska, R., Lessard, P., Norval, R. A. I. & Kundert, K.** 1991. Estimating the distribution and abundance of *Rhipicephalus appendiculatus* in Africa. *Preventive Veterinary Medicine*, **11**, 261–268.

**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.

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

**Pryce, J. E., Coffey, M. P. & Simm, G.** 2001. The relationship between body condition score and reproductive performance. *Journal of Dairy Science*, **84**, 1508–1515.

**Pulkkinen, K. & Ebert, D.** 2004. Host starvation decreases parasite load and mean host size in experimental populations. *Ecology*, **85**, 823–833.

**Randolph, S. E.** 2004. Tick ecology: processes and patterns behind the epidemiological risk posed by ixodid ticks as vectors. *Parasitology*, **129**, 37–65.

**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. B.** 1979. The social structure and ecology of elephant-shrews. *Advances in Ethology*, **20**, 1–75.

**Rathbun, G. B. & Rathbun, C. D.** 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.

**Redi, C. A., Garagna, S., Zuccotti, M. & Capanna, E.** 2007. Genome size: a novel genomic signature in support of Afrotheria. *Journal of Molecular Evolution*, **64**, 484–487.

**Ribble, D. O. & Perrin, M. R.** 2005. Social organization of the eastern rock elephant-shrew (*Elephantulus myurus*) : the evidence for mate guarding. *Nature*, **135**, 167–173.

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

**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.

**Sheldon, B. C. & Verhulst, S.** 1996. Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. *Trends in Ecology & Evolution*, **11**, 317–321.

**Silverin, B.** 1998. Territorial behaviour and hormones of pied flycatchers in optimal and suboptimal habitats. *Animal behaviour*, **56**, 811–818.

**Skinner, J. D. & Chimimba, C. T.** 2005. Order: Macroscelidea. In: *The mammals of the southern African subregion*, Vol 2nd 3rd edn. (Ed. by D. van der Horst), pp. 22–34. Cape Town: Cambridge Univ Press.

**Smyth, J. D.** 1991. Parasites as biological tags. *Parasitology*, **59**, 182–185.

**Spickett, A. M., Heyne, I. H. & Williams, R.** 2011. Survey of the livestock ticks of the North West province, South Africa. *The Onderstepoort Journal of Veterinary Research*, **78**, 1–12.

**Spieksma, F. T.** 1997. Domestic mites from an acarologic perspective. *Allergy*, **52**, 360–368.

**Tella, J. L., Gortazar, C., Gajon, A. & Osacar, J. J.** 1995. Apparent lack of effects of a high louse-fly infestation (Diptera, Hippoboscidae) on adult colonial Alpine Swifts. *Ardea*, **83**, 435–439.

**Townsend Jr., V. R., Mulholland, K. A., Bradford, J. O., Proud, D. N. & Parent, K. M.** 2006. Seasonal variation in parasitism by Leptus mites (Acari, Erythraeidae) upon the harvestman, *Leiobunum formosum* (Opiliones, Sclerosomatidae). *Journal of Arachnology*, **34**, 492–494.

**Turner, W. C., Versfeld, W. D., Kilian, J. W. & Getz, W. M.** 2012. Synergistic effects of seasonal rainfall, parasites and demography on fluctuations in springbok body condition. *Journal of Animal Ecology*, **81**, 58–69.

**Ueti, M. W., Palmer, G. H., Scoles, G. A., Kappmeyer, L. S. & Knowles, D. P.** 2008. Persistently infected horses are reservoirs for intrastadial tick-borne transmission of the apicomplexan parasite *Babesia equi*. *Infection and Immunity*, **76**, 3525–3529.

**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: Cambridge University Press.

**Weiss, R. A.** 2009. Apes, lice and prehistory. *Journal of Biology,* **8**, 20–28.

**Widermann, C.** 2000. Studies on the efficacy of Fipronil against ectoparasites - II. Tick control. *Tierarztliche Umschau*, **55**, 211–216.

**Winchester, M., Farrell, B., Hayes, Y. & Bellinger, D.** 2004. The use of fipronil (Frontline) and selamectin (Revolution) for the treatment and control of parasites in mice. In: AALAS National Meeting; 2004 Oct 17–24; Tampa Bay, FL. Contemp Top Lab Anim Sci, **43**, 65.

## *Appendix*

***Table 1*** **-** Correlations between different ages and sexes of the common ectoparasite species.

| | **$R_S$** | **p-value** |
|---|---|---|
| *Rhipicentor nuttalli* larvae * *Rhipicentor nuttalli* nymphs | 0.562 | $p < 0.001$ |
| *Rhipicephalus warburtoni* larvae * *Rhipicephalus warburtoni* nymph | 0.319 | $p < 0.001$ |
| *Neolinognathus elephantuli* males * *Neolinognathus elephantuli* females | 0.629 | $p = 0.021$ |
| *Neolinognathus elephantuli* females * *Neolinognathus elephantuli* nymphs | 0.735 | $p = 0.004$ |
| *Neolinognathus elephantuli* nymphs * *Neolinognathus elephantuli* males | 0.560 | $p = 0.047$ |

***Table 2*** - Results of GLMMs for short term and long term effects of sex, treatment, capture status and season on ectoparasite prevalence on *E. myurus*.

| | | | ***R. warburtoni*** | | ***Rc. nuttalli*** | | **chiggers** | | ***N. elephantuli*** | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | **df** | **F** | **p-value** | **F** | **p-value** | **F** | **p-value** | **F** | **p-value** |
| **Short Term** | Sex | 1, 321 | 0.000 | 0.992 | 3.344 | 0.068 | 0.121 | 0.728 | 0.000 | 0.991 |
| | Treatment | 1, 321 | 4.574 | **0.033*** | 0.000 | 0.989 | 0.243 | 0.622 | 0.031 | 0.859 |
| | Capture status | 2, 321 | 5.679 | **0.004*** | 6.271 | **0.002*** | 23.836 | **<0.0001*** | 4.243 | **0.015*** |
| | season | 5, 321 | 0.383 | 0.860 | 7.066 | **<0.0001*** | 5.481 | **<0.0001*** | 1.636 | 0.150 |
| | Sex*treatment | 1, 321 | 0.885 | 0.348 | 3.461 | 0.064 | 0.031 | 0.861 | 0.126 | 0.723 |
| | Sex*capture status | 2, 321 | 0.050 | 0.951 | 0.261 | 0.770 | 0.070 | 0.932 | 0.264 | 0.768 |
| | Treatment*capture status | 2, 321 | 2.285 | 0.103 | 2.175 | 0.115 | 0.243 | 0.785 | 0.000 | 1.000 |
| | Treatment*season | 5, 321 | 0.226 | 0.951 | 0.250 | 0.940 | 0.498 | 0.778 | 0.061 | 0.998 |
| **Long Term** | Sex | 1, 193 | - | - | 3.412 | 0.066 | 0.004 | 0.947 | 0.678 | 0.411 |
| | Treatment | 1, 193 | - | - | 0.000 | 0.996 | 0.000 | 0.983 | 0.000 | 1.000 |
| | Capture status | 1, 193 | - | - | 1.081 | 0.300 | 0.171 | 0.679 | 4.527 | **0.035*** |
| | season | 5, 193 | - | - | 3.067 | **0.010*** | 5.608 | **<0.0001*** | 0.834 | 0.527 |
| | Sex*treatment | 1, 193 | - | - | 2.425 | 0.121 | 0.162 | 0.688 | 0.196 | 0.658 |
| | Sex*capture status | 1, 193 | - | - | 0.733 | 0.393 | 0.258 | 0.612 | 0.571 | 0.451 |
| | Treatment*capture status | 1, 193 | - | - | 1.513 | 0.220 | 0.018 | 0.894 | 0.072 | 0.789 |
| | Treatment*season | 5, 193 | - | - | 0.566 | 0.726 | 0.170 | 0.973 | 0.231 | 0.949 |

***significant effects**

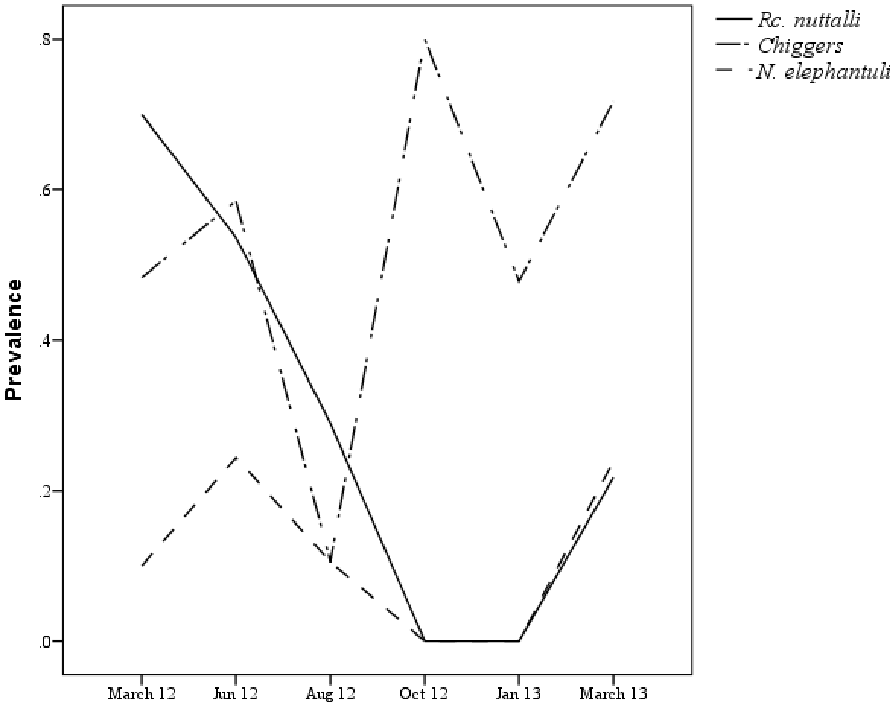

***Figure* 1** - Seasonal variation in the prevalence of the three major ectoparasite groups found on *E. myurus*. *R. warburtoni* was found to be prevalent throughout the year and as such was not included in the figure.

***Table 3*** - Results of GLMMs looking at short term and long term effects of sex, treatment, capture status, season and ectoparasite prevalence on body condition of *E. myurus.*

| | **Short term patterns** | | | **Long term patterns** | | |
|---|---|---|---|---|---|---|
| | **df** | **F** | **p-value** | **df** | **F** | **p-value** |
| Sex | 1, 317 | 0.262 | 0.609 | 1, 190 | 1.779 | 0.184 |
| Treatment | 1, 317 | 17.648 | **<0.0001*** | 1, 190 | 4.388 | **0.038*** |
| Capture status | 2, 317 | 0.670 | 0.513 | 1, 190 | 4.198 | **0.042*** |
| Season | 5, 317 | 7.666 | **<0.0001*** | 5, 190 | 2.000 | 0.080 |
| *R. warburtoni* | 1, 317 | 0.608 | 0.436 | 1, 190 | - | - |
| *Rc. nuttalli* | 1, 317 | 0.084 | 0.773 | 1, 190 | 0.602 | 0.439 |
| chiggers | 1, 317 | 1.752 | 0.187 | 1, 190 | 1.757 | 0.187 |
| *N. elephantuli* | 1, 317 | 1.026 | 0.312 | 1, 190 | 1.526 | 0.218 |
| Sex*treatment | 1, 317 | 0.078 | 0.780 | 1, 190 | 0.004 | 0.951 |
| Sex*capture status | 2, 317 | 0.024 | 0.297 | 1, 190 | 3.206 | 0.075 |
| Treatment*capture status | 2, 317 | 1.218 | 0.297 | 1, 190 | 1.138 | 0.287 |
| Treatment*season | 5, 317 | 2.951 | **0.013*** | 5, 190 | 0.763 | 0.578 |

***significant effects**

# Chapter 3

## Personality and parasites of the eastern rock sengi (*Elephantulus myurus*)

### Abstract

Many studies have shown that consistent behavioural differences (also termed personality) between individuals in a population may significantly affect the way in which an individual interacts with its environment. More exploratory, aggressive and bold (i.e. proactive) individuals may increase the quantity and/or quality of the food they consume and in turn increase their body condition. At the same time they may increase their exposure to parasite by roaming wider areas than reactive (i.e. less exploratory, more submissive and shyer) individuals. We tested both of these hypotheses in a living population of eastern rock sengis (*Elephantulus myurus*) captured between March 2012 and April 2013 in Limpopo Province, South Africa. We were able to assess the behaviour of 125 sengis between one to five times and found behaviours to be correlated across context (i.e. they exhibited a behavioural syndrome). The personality measures were highly repeatable during subsequent captures. Animals in poorer body condition were more proactive and less reactive. Only one of the four ectoparasite species considered was found to correlate with personality with more reactive animals having higher abundances of the tick *Rc. nuttalli.* We suggest that differences in the interaction between personality and parasite burdens may be a composite result of a parasite's abundance in the environment, its life-cycle and the host's personality.

## Introduction

The ability of an animal to change its behavioural responses across different circumstances and throughout time makes sense from the perspective of adaption. However, the individual differences that have been found to remain consistent are harder to explain (Sih *et al.* 2004; Dall *et al.* 2004; Dingemanse & Réale 2005). These consistent individual differences in behaviour have been alternatively called temperament, behavioural types or personality (Archer 1973; Bolig *et al.* 1992) and we will adopt the latter term throughout this chapter. There has been a rapid increase in personality research from a range of fields including evolutionary ecology (Réale *et al.* 2007) through to conservation and rehabilitation (Metcalfe *et al.* 2003; Cote *et al.* 2010). Many studies have shown that personality may significantly affect the way individuals interact with their environment (Dall *et al.* 2004; Boon *et al.* 2008; Smith & Blumstein 2008; Fucikova *et al.* 2009). Something that used to be considered as merely a bias around the mean has come to explain much of the variation we see in populations (Svartberg & Forkman 2002).

Personality has been studied in diverse taxa, with much of the initial work being focused on rodents (Archer 1973; Boyer *et al.* 2010), canids (Svartberg & Forkman 2002) and fish (Wilson *et al.* 1994; Toms *et al.* 2010). This has given support to the hypothesis that many animals vary consistently in their behavioural responses (Wilson *et al.* 1994; Dingemanse & Réale 2005). Most commonly personality in animals is measured on a scale similar to human personality gradients such as measureable levels of boldness, aggression and exploratory behaviours (Gosling 2001). This often leads to behaviours also being grouped, i.e. animals that are considered bolder, more aggressive and more exploratory are often labelled as proactive while animals showing opposite behaviour's tend to be called reactive (Koolhaas *et al.* 1999; Bell 2007). Personality in animals has been shown to affect diet, predation rate and dispersal of an individual to mention but a few central interactions (Yeo *et al.* 1997; Blumstein *et al.* 2006; Cote *et al.* 2010). Wilson *et al.* (1994) showed that bold individuals consumed a much better diet than shy individuals in the population and as such could potentially have a better body condition which would increase their fitness. Similarly it has been shown in cichlid fish (*Amatitlania nigrofasciata*) that individuals with greater exploratory behaviour also improve their chances to obtain larger territories and more abundant food sources. However, this was linked to a slower response when faced with a predator and increased chances of an untimely death (Jones & Godin 2010). This would suggest a trade of between different personalities within a population as there are rewards and risks associated with each which affects individual fitness (Dall *et al.* 2004; Dingemanse & Réale 2005; Coppens *et al.* 2010).

Links between behavioural traits and parasites are also likely. There are many ways in which parasites can potentially affect life history strategies and fitness of the animal such as by causing long term stress or inducing behavioural manipulation (Barber & Dingemanse 2010; Montiglio *et al.* 2012). The link between behavioural manipulations in animal host and parasite infestation has been well studied in parasites with complex life-cycles (such as cestodes or trematodes) that cause the host to endanger itself to ensure that the parasite can complete its life cycle (Biron *et al.* 2005; Lefèvre *et al.* 2009; van Houte *et al.* 2013). Less studied is the potential link between burdens of parasites and personality of an animal (Hammond-Tooke *et al.* 2012). Host personality can explain differences in parasite burdens of a population as some behaviours, such as roaming or aggressiveness, can increase the risk of infestation (Boyer *et al.* 2010; Dunn *et al.* 2011). However, few studies have investigated this; Boyer *et al* (2010) found that there was an indirect effect of personality of Siberian chipmunks (*Tamias sibiricus*) on tick load through activity. They used trappability and trap diversity as a measure of inter-individual difference of exploration and activity in their study animal and found that males with increased activity patterns had higher tick loads than females. Although not specifically investigated it would be more likely for parasite species that sit and wait for their hosts, or actively quest for them, such as ticks, to be affected by personality. As such we would expect to not necessarily find such correlations with parasites that spend their entire life cycle on the host, such as lice, as transmission is not encounter-dependant in this case.

This suggests that personality types within a population may be maintained and affected by the different life-history trade-offs that individuals with different personality types may experience.

Often it is only a single parasite species or genus that is investigated when looking at how individual variation in behaviour may affect parasite load of the individual host, not necessarily the full range of parasites potentially present in or on the host and possible interactions between these different parasites and host behaviour (Dunn *et al.* 2011; Koprivnikar *et al.* 2012; Poulin 2013). The current study investigates possible effects of personality on the ectoparasite community of the eastern rock sengi (*Elephantulus myurus*) that is endemic to southern Africa (Skinner & Chimimba 2005). Sengis inhabit rocky outcrops and have precocial young which are capable of following their mother within a few hours of birth (Rathbun 1979). They are sexually monomorphic, socially monogamous with males and females inhabiting overlapping territories (Ribble & Perrin 2005). They have mostly been investigated in terms of thermoregulation (Roxburgh & Perrin 1994; Lovegrove *et al.* 1999; Mzilikazi & Lovegrove 2005) In addition; a number of studies have focussed on the ticks they carry as they can harbour substantial burdens (Fourie *et al.* 1995; Horak *et al.* 2011). Despite the large tick burden these animals carry in the wild (Lutermann *et al.* 2012a), few studies have investigated the potential reasons for the great variance in tick abundances seen between individuals. Some have investigated sex and body length as a possible causes and also changes during breeding season although these do not quite explain individual variation but highlight important trends (Lutermann *et al.* 2012a, 2012b). Coupled with the lack of research in wild populations, sengis pose an interesting model to measure personality and the subsequent effects on ectoparasite burden.

This study was one of the first to include all the major ectoparasites present on *E. myurus* in the study area and their subsequent effects on the host. Although sengis may harbour a great diversity of ectoparasites (see previous chapter) we found only four main ectoparasites on our study animal; namely two tick species, *Rhipicephalus warburtoni* (100%) and *Rhipicentor nuttalli* (38.5%), chigger mites (Family: Trombiculidae, 66.2%) and the louse *Neolinognathus elephantuli* (25.5%). While *R. warburtoni* and chiggers are present at high abundances throughout the year (259.05 ± 129.03 and 15.40 ± 28.94 respectively, Lutermann *et al.* 2012, previous chapter), *Rc. nuttalli* and *N. elephantuli* occur at low abundance (3.47 ± 4.31 and 3.80 ± 13.04 respectively) and are absent during spring and summer (see previous chapter).We also found that the removal of parasites by treating the hosts with Frontline® substantially improved long term and short term body condition. However, this treatment did have no long term effect on parasite burden.

This study aims to investigate personalities of eastern rock sengis and their possible effects on ectoparasite burdens in a wild population. The short term (1 month) consistency of personality traits in sengis have been confirmed in a laboratory study (Hoffmann 2011). The current study is, however, the first to investigate long term consistency and repeatability of personality in sengis. We predicted that animals would display varying personality and a behavioural syndrome due to the correlation of bold, aggressive and exploratory behaviours as has been found for sengis under laboratory conditions (Hoffmann 2011). Furthermore, we predicted that due to the lack of sexual dimorphic characteristics of sengis we would not see any difference in personality between sexes. In addition, we hypothesised that animals in better body condition would be the more proactive individuals in the population. We also then predicted that treating animals with Frontline® would result in less pronounced changes in personality in proactive individuals but possibly there would be changes in reactive individuals due to improvements in body condition due to the short term effects of this treatment reported in the previous chapter. Furthermore, we investigated the relationship between personality and ectoparasite abundances of sengis. We predicted that the more proactive individuals would have larger abundances for those ectoparasites, such as ticks, that spend time off the host but that for lice (*N. elephantuli*) this might not be the case as these have a close associations with the host and spend no time off host(Hopkins 1948)(Hopkins 1948)(Hopkins 1948)(Hopkins 1948)(Hopkins, 1948).

## Materials and methods

### *Study Animals*

Sengis were collected from Goro Game Reserve in the Limpopo Province, South Africa (22°58’S; 29°25’E) from March 2012 - April 2013. Sherman traps (H. B. Sherman Traps, Inc. Tallahassee, Florida, U.S.A.) were used to capture animals and these traps were baited with a mixture of peanut butter, sardines and oats. Animals were collected during six different trips occurring every other month during the capture period. Animals were collected from eight sites scattered throughout the reserve. Sites were between 300 meters and 3 km apart from each other. The sites varied roughly 75 meters in altitude. In each site two parallel lines approximately 10 metres apart and with 10 steps between traps. 150 traps were laid out in the early afternoon and collected the following morning for each trapping session.

Animals were caught under the permit number 001-CPM401-0002 from the Department of Environmental Affairs, Limpopo Province.

### *Personality Assessments*

The personality assessments involved three tests that were done sequentially in a single run-through for each individual *E. myurus*. This was to reduce the amount of handling of the animals in order to decrease stress. The assessment consisted of an exploratory test, an aggressive response test and a boldness test (Archer 1973). The assessment took place in a plastic container (57x 30 x 40cm) with the sides painted white to prevent animals from seeing the observer when removing dividers. A section was marked with gridlines on the bottom so that distances could be measured (Figure 1).

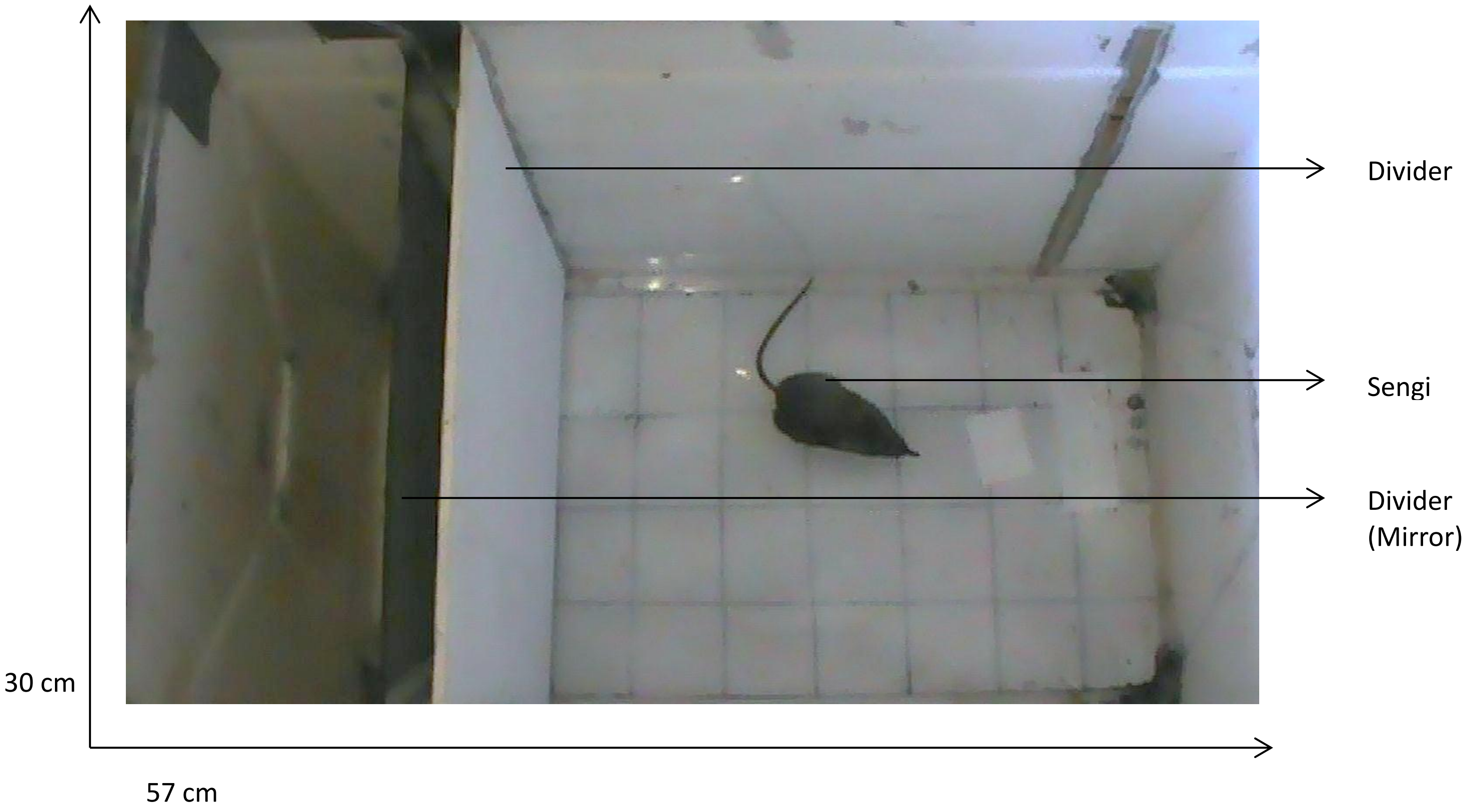

*Figure 1* - Experimental setup used for the personality assessments of eastern rock sengis. A novel object is behind the divider marked as mirror and dividers are removed through the slots. Animal here is shown in the section used for the exploratory test

For the exploratory assessment the animal was placed in the marked part of the container and allowed to become accustomed to the new environment for two minutes before any measurement were taken. Once the two minutes had elapsed a divider was removed and the animal was left to explore the first compartment (43 x 30 cm) for five minutes. After five minutes had elapsed, the next divider was removed and the animal was exposed to a mirror (35 x 40 cm) for an additional five minutes. For the last five minutes the animal was then exposed to the novel object on the other side of the last divider. Behavioural measures used in the analysis consisted of three behaviours per test and the behaviours considered are displayed in (Table 1).

***Table 1*** - Behaviours measured during the video observations.

| **Behaviour** | **Description** |
|---|---|
| Time Spent Exploring (E) | How much time the animal spends exploring the plastic container |
| Rear Up (E) | When an animal goes onto its back legs to investigate |
| Latency Escape (E) | Time taken before an animal tries to escape |
| Pacing (M) | When an animal moves rapidly up and down in the container in front of the mirror |
| Foot Drumming (M) | Time spent foot drumming |
| Cowering (M) | When an animal presses itself against the sides of the container and remains motionless |
| Latency to interact (N) | Time taken before an animal interacts with the novel object |
| Closest distance to object (N) | Closest distance between the animal and the novel object |
| Total number physical interactions (N) | Total number of interactions where the animal physically touches the object. |

**E: exploratory behaviours, M: aggressive responsive behaviours, N: boldness measures.**

The personality assessments resulted in 15 minute videos for each animal recorded with a video recorder (Panasonic SDR-S50, MV Tronics, Midrand, South Africa) suspended above the container on a tripod. The personality assessments were conducted once during each trip. A new novel object was introduced for each trip. These were an orange tennis ball (Spar ©, Dog toy Brand, Kwazulu-Natal, South Africa), blue plastic rugby ball, plastic zebra and a plastic giraffe (Crazy Store Toys ©, Cape Town, South Africa), ceramic orange piggy bank (S. Hoffmann personal item) and a purple plush teddy bear (S. Hoffmann personal item). Novel objects were picked in such a way that they had different textures, were made of different materials, and had different colours but were of similar sizes. Observations were made from the recorded footage from the video camera and the behavioural measures were quantified using The Observer XT 11 (Noldus, 2012).

### *Parasite assessment and body condition*

Once captured, animals were brought back to the camp and processed. Processing consisted of weighing the animals using a digital scale (Scout Pro SPU123; Ohaus Corporation, USA) and sexing. Animals then underwent personality assessments before being examined for ectoparasites. This was done to prevent possible stress from handling to affect the personality assessments. After the personality assessments, ectoparasites were removed from the animals manually and stored in 70% ethanol. For further details of this procedure see previous chapter. After the ectoparasites were removed, animals were given unique ear-clips for identification during subsequent field trips. Body length was measured from the back of the neck to the base of the tail using electronic callipers (INSIZE Co., Ltd). This measure was used, along with mass, to determine the body condition, i.e. length divided by mass. Half the animals were then treated with Frontline® using the same procedure as outlined in the previous chapter. After processing and assessments, the animals were released in the afternoon at their site of capture.

### *Statistical Analysis*

We tested for consistency across behavioural contexts by extracting a single component for each test (exploration, aggressive response and boldness) using a principal component analysis (PCA) and tested for correlations across different tests with a Spearman's Rank Correlation. Since the principal components (PC) of the three different tests were significantly correlated ($p \leq 0.05$), we combined all behavioural categories for a subsequent PCA.

Due to the personality measures extracted from the PCA being non-parametric (Shapiro-Wilk Test: $p < 0.001$) and the fact that log transformations did not affect normality, or lack thereof, repeatability of personality measures was assessed with a Wilcoxon Rank-Signed test taking into account the different measures taken each time an animal was caught i.e. whether it was the first, second, third, fourth or fifth capture (Table 4). Interval categories which had less than three animals were not included in this analysis. This approach was adapted from a pairwise comparison t-test used to investigate changes between measures at varying times (Hays 1973).

A GLMM with a gamma probability distribution with a log-link function was used to analyse the effects of sex, season, treatment (i.e. whether it was treated with Frontline® or not) and capture status (i.e. new or recaptured) on personality measures. Body condition was added as a covariate to the model.

Trappability (%) was calculated as defined by Hilborn *et al.* (1976) which measures minimum trappability. This is calculated as the number of actual captures for an individual minus two, divided by the number of possible captures for that individual minus two, and expressed as percentage. Two is subtracted to prevent animals that have been captured only twice in subsequent trips from obtaining unrealistically high scores. This was measured using all possible captures within and between trips for the entire study period as this was the recommended procedure for improved robustness (Krebs & Boonstra 1984). Possible captures refers to the number of trapping events, e.g. nights per site, that the animals could have potentially been caught. Trappability was not normally distributed (Shapiro-Wilk Test: $p< 0.001$). Consequently, a GLMM was run using a gamma probability distribution with a log-link function with sex, and treatment added as fixed effects. Personality components were added as covariates to the model.

We investigated the effect of personality measures on parasite prevalence and abundances as well. For prevalence a GLMM was run using a binomial distribution with a logit link with the same fixed effects as previously mentioned and the personality measures and body condition added as covariates. A GLMM also was run for each of the abundances of the four main parasite species using a negative binomial regression with the same fixed effects as above and the personality measures and body condition measures also added as covariates.

## Results

### *Personality repeatability and overall determinants of personality*

Out of the 125 captures (68 ♂, 57 ♀); 53 animals were captured at least one other time throughout the study. A total of 24 animals were caught three times, seven were caught four times and one animal was caught five times. Detailed capture data for the sexes and seasons are shown in Table 2.

***Table 2*** - Capture results for sengis trapped throughout the study period.

| | | **Males** | | **Females** |
|---|---|---|---|---|
| **Season** | **New** | **Recaptures** | **New** | **Recaptures** |
| **March** | 34 | 0 | 26 | 0 |
| **June** | 11 | 14 | 8 | 8 |
| **August** | 3 | 15 | 4 | 12 |
| **October** | 0 | 0 | 1 | 4 |
| **January** | 4 | 5 | 8 | 4 |
| **March 13** | 15 | 7 | 10 | 12 |

The first two components extracted from the PCA explained over 50% of the variance while the third component only added an additional 16.9 % (Table 3). Hence we only included the first two components in the analysis. Principal component one (PC1) was positively loaded with reactive behaviours, such as taking longer to approach object, and principal component two (PC 2) was positively loaded with proactive behaviours, such as spending a larger amount of time exploring the container. A correlation analysis confirmed that the two components were significantly negatively correlated. Consequently, both components were included in the subsequent analysis as one component alone was not deemed sufficient to obtain accurate resolution in models.

We found no significant difference for personality measures (both for PC 1and PC 2) taken during successive trips (Table 4). Hence we used only the first measurement of PC 1 and PC 2 of each animal for subsequent analyses.

***Table 3*** - Results of the principal component analysis for the behaviours measured during the personality assessments of eastern rock sengis.

| | **Principal Component** | | |
|---|---|---|---|
| | **1** | **2** | **3** |
| Time Spent Exploring | -0.364 | 0.631 | 0.120 |
| Rear Up | 0.077 | 0.466 | 0.094 |
| Latency Escape | -0.207 | 0.601 | 0.549 |
| Pacing | -0.477 | 0.151 | -0.317 |
| Foot Drumming | -0.180 | 0.454 | -0.509 |
| Cowering | 0.307 | -0.164 | 0.666 |
| Latency to interact | 0.886 | 0.218 | -0.025 |
| Closest distance to object | 0.859 | -0.203 | 0.180 |
| Total number Interactions | -0.849 | 0.168 | -0.113 |
| **Eigenvalues** | **2.063** | **1.230** | **1.016** |
| **variance explained %** | **34.387** | **20.492** | **16.940** |
| **Cumulative variance explained %** | **34.387** | **54.878** | **71.819** |

We investigated overall factors that could affect personality measures but we found no significant effect of sex, treatment, capture status or season on PC 1 (Table 5).

***Table 4*** - Repeatability analyses of subsequent measures of personality.

| | **PC 1** | | | **PC 2** | | |
|---|---|---|---|---|---|---|
| | **Z** | **df** | **p-value** | **Z** | **df** | **p-value** |
| **1st measure – 2nd measure** | -0.919 | 1, 52 | 0.358 | -0.231 | 1, 52 | 0.817 |
| **1st measure – 3rd measure** | -0.276 | 1, 23 | 0.783 | -1.899 | 1, 23 | 0.058 |
| **1st measure – 4th measure** | -0.169 | 1, 6 | 0.866 | -0.338 | 1, 6 | 0.735 |
| **2nd measure – 3rd measure** | -1.483 | 1, 22 | 0.285 | -2.099 | 1, 22 | 0.093 |
| **2nd measure – 4th measure** | -0.105 | 1, 6 | 0.917 | -0.135 | 1, 6 | 0.893 |
| **3rd measure – 4th measure** | -0.535 | 1, 6 | 0.0.593 | -0.943 | 1, 6 | 0.345 |

***Table 5*** - Results of the GLMM evaluating the effects of sex, treatment, capture status and season on PC 1 and PC 2 of eastern rock sengis.

| | **PC 1** | | | **PC 2** | | |
|---|---|---|---|---|---|---|
| | **F** | **df** | **p - value** | **F** | **df** | **p - value** |
| Sex | 0.255 | 1 | 0.636 | 0.391 | 1 | 0.533 |
| Treatment | 0.003 | 1 | 0.957 | 0.021 | 1 | 0.886 |
| Capture Status | 0.269 | 1 | 0.604 | 0.003 | 1 | 0.957 |
| Season | 0.811 | 5 | 0.543 | 0.956 | 5 | 0.446 |
| Body Condition | 4.018 | 1 | **0.046*** | 6.385 | 1 | **0.012*** |
| Sex*treatment | 0.084 | 1 | 0.772 | 1.299 | 1 | 0.256 |
| Sex*capture | 0.767 | 1 | 0.382 | 0.558 | 1 | 0.456 |
| Treatment*capture | 0.325 | 1 | 0.569 | 0.933 | 1 | 0.335 |
| Treatment*season | 1.144 | 5 | 0.338 | 0.611 | 5 | 0.691 |

*** significant effects**

However, we did find a significant effect of body condition on PC 1 and reactivity increased with body condition (Figure 2).

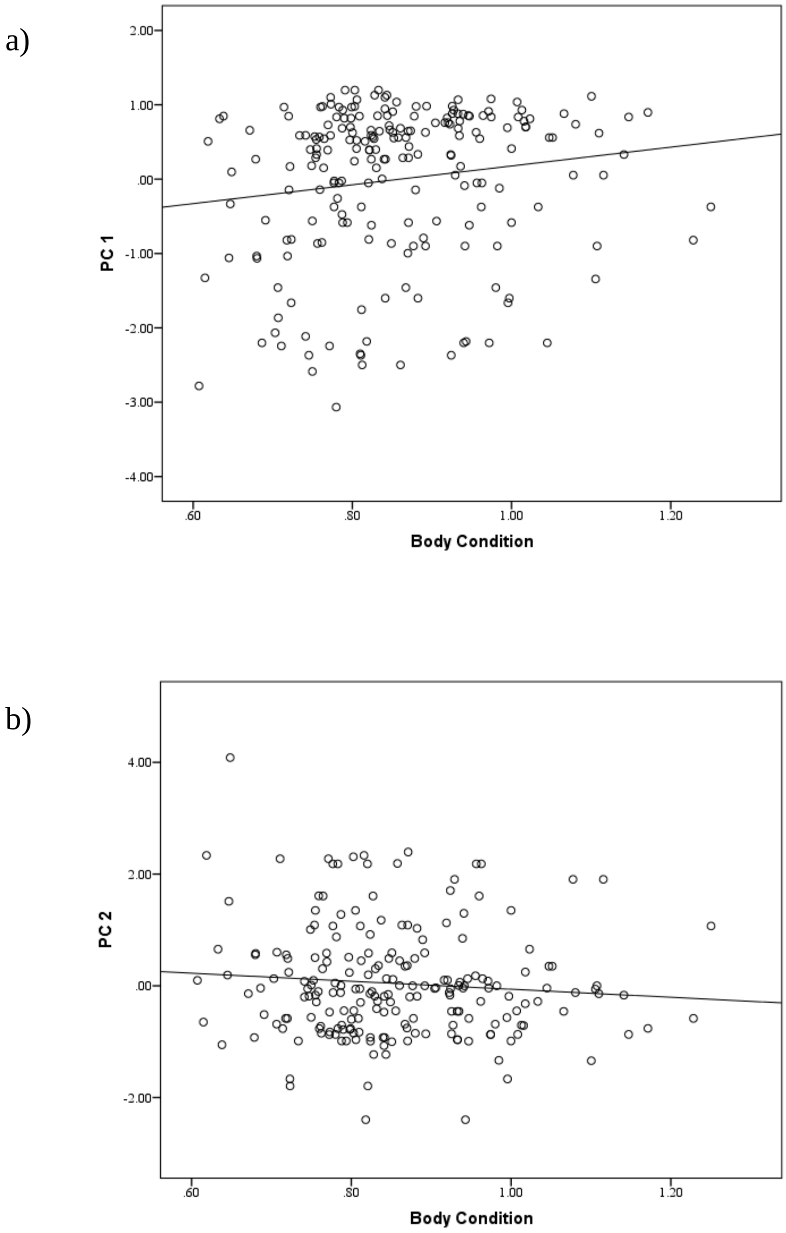

***Figure 2*** - Correlations of body condition and a) the reactive personality measure (PC1) and b) the proactive personality measure (PC2). Lines through the scatters represent the relationship between the two variables

None of the two-way interaction was significant (Table 5). For PC 2 we found no significant effect of sex, treatment, capture status, or season (Table 5). This was also the case for two-way interactions (Table 5). However, similar to PC 1, we did find a significant effect of body condition on PC 2 and proactivity decreased with increasing body condition (Figure 2).

### *Trappability*

We found no significant effects of sex, season or interaction terms on trappability (Table 6). Similarly, the trappability of an animal was not significantly affected by either PC 1, PC 2 or body condition (Table 6).

***Table 6*** - Results of the GLMM evaluating the effects of sex, treatment, season and personality measures on trappability of an animal.

| | Trappability | | |
|---|---|---|---|
| | F | df | p - value |
| Sex | 0.028 | 1 | 0.868 |
| Treatment | 0.124 | 1 | 0.726 |
| PC 1 | 0.083 | 1 | 0.773 |
| PC 2 | 0.138 | 1 | 0.711 |
| Sex*treatment | 0.117 | 1 | 0.732 |

### *Parasite burden and personality*

The observed patterns of the prevalence and abundance of the four main ectoparasite species did not change significantly from the previous chapter when PC 1 and PC 2 were added as covariates to the model. For prevalence of the four main parasites we found that season remained a significant factor for *Rc. nuttalli* and chiggers but not *N. elephantuli* (Table 7). Capture status significantly affected *N. elephantuli* as previously found and gender significantly affected *Rc. nuttalli* (Table 7).

The only difference from the previous chapter was that the interaction between sex and treatment became significant for *Rc. nuttalli* with non-treated males (0.568 ± 0.204) having a significantly lower prevalence than non-treated females (0.849 ± 0.105, Table 7). Similarly, for abundances of ectoparasites we found no significant changes in the main effects when PC 1, PC 2 and trappability were added as covariates to the model. Season remained a significant factor for *R. warburtoni*, *Rc. nuttalli*, and chiggers but not *N. elephantuli* (Table 7). The only other difference was that for *N. elephantuli* abundance the interaction between treatment and capture status became significant (Table 7). However, post hoc analysis did not confirm this significance (p> 0.05). For the chigger abundance one difference was that, the interaction between sex and capture status became significant when personality measures were included in the model. However, post hoc tests did not reveal any significant differences (p>0.05 for all).

When looking at personality measures as covariates in our parasite abundance models PC 1 significantly affected the abundance of *Rc. nuttalli* (Table 7). *Rhipicentor nuttalli* abundance increased significantly with increased values of PC 1 (Coefficient: 0.227, p = 0.025, Figure 3). In contrast, PC 2 and trappability had no significant effect on any of the factors measured (Table 7). Sex still affected *Rc. nuttalli* and *N. elephantuli* but not the other parasite abundances measured (Table 7). *Neolinognathus elephantuli* remained the only ectoparasite for which treatment significantly affected abundances (Table 7).

***Table 7* -** Effects of sex, treatment, capture status, season, body condition and personality measures on the prevalence and abundance of common sengi ectoparasites. Prevalence for *R. warburtoni* was not included in a model as it had a prevalence of 100%.

| | | | ***R. warburtoni*** | | ***Rc. nuttalli*** | | **chiggers** | | ***N. elephantuli*** | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | **df** | **F** | **p-value** | **F** | **p-value** | **F** | **p-value** | **F** | **p-value** |
| **prevalence** | Sex | 1, 190 | - | - | 4.834 | **0.029*** | 0.056 | 0.814 | 0.976 | 0.324 |
| | Treatment | 1, 190 | - | - | 0.591 | 0.443 | 0.000 | 0.988 | 0.000 | 1.000 |
| | Capture status | 1, 190 | - | - | 1.808 | 0.180 | 0.290 | 0.591 | 4.803 | **0.030*** |
| | Season | 1, 190 | - | - | 5.177 | **<0.0001*** | 5.249 | **<0.0001*** | 0.950 | 0.450 |
| | Sex*treatment | 1, 190 | - | - | 4.343 | **0.038*** | 0.000 | 0.986 | 0.030 | 0.863 |
| | Sex*capture status | 1, 190 | - | - | 0.296 | 0.587 | 0.046 | 0.831 | 0.833 | 0.363 |
| | Treatment*capture status | 1, 190 | - | - | 0.843 | 0.360 | 0.017 | 0.895 | 0.100 | 0.752 |
| | Treatment*season | 1, 190 | - | - | 0.760 | 0.579 | 0.170 | 0.973 | 0.318 | 0.902 |
| | PC 1 | 1, 190 | - | - | 0.002 | 0.966 | 0.130 | 0.719 | 0.621 | 0.432 |
| | PC 2 | 1, 190 | - | - | 2.086 | 0.150 | 3.492 | 0.063 | 1.668 | 0.198 |
| | Trappability | 1, 105 | - | - | 0.508 | 0.478 | 2.554 | 0.113 | 0.335 | 0.564 |
| | Body Condition | 1, 190 | - | - | 0.171 | 0.680 | 2.164 | 0.143 | 1.415 | 0.236 |
| **abundance** | Sex | 1, 190 | 0.041 | 0.840 | 5.715 | **0.018*** | 2.098 | 0.149 | 6.115 | **0.014*** |
| | Treatment | 1, 190 | 1.492 | 0.223 | 3.302 | 0.071 | 0.054 | 0.816 | 5.227 | **0.023*** |
| | Capture status | 1, 190 | 0.044 | 0.834 | 1.454 | 0.229 | 0.459 | 0.499 | 1.034 | 0.310 |
| | Season | 1, 190 | 5.067 | **<0.0001*** | 7.684 | **<0.0001*** | 14.237 | **<0.0001*** | 0.137 | 0.984 |
| | Sex*treatment | 1, 190 | 0.399 | 0.528 | 9.142 | **0.003*** | 0.047 | 0.829 | 0.000 | 0.989 |
| | Sex*capture status | 1, 190 | 1.007 | 0.317 | 0.089 | 0.766 | 7.039 | **0.009*** | 6.144 | **0.014*** |
| | Treatment*capture status | 1, 190 | 0.923 | 0.338 | 0.696 | 0.405 | 0.311 | 0.578 | 4.312 | **0.039*** |
| | Treatment*season | 1, 190 | 0.751 | 0.587 | 0.547 | 0.741 | 1.273 | 0.277 | 0.947 | 0.452 |
| | PC 1 | 1, 190 | 0.198 | 0.657 | 5.124 | **0.025*** | 0.049 | 0.825 | 1.153 | 0.284 |
| | PC 2 | 1, 190 | 0.637 | 0.426 | 3.657 | 0.057 | 0.604 | 0.438 | 0.620 | 0.432 |
| | Trappability | 1, 105 | 0.246 | 0.622 | 2.942 | 0.089 | 0.075 | 0.785 | 1.437 | 0.233 |
| | Body Condition | 1, 190 | 1.798 | 0.182 | 2.323 | 0.129 | 11.869 | **0.001*** | 0.046 | 0.830 |

*** significant effects**

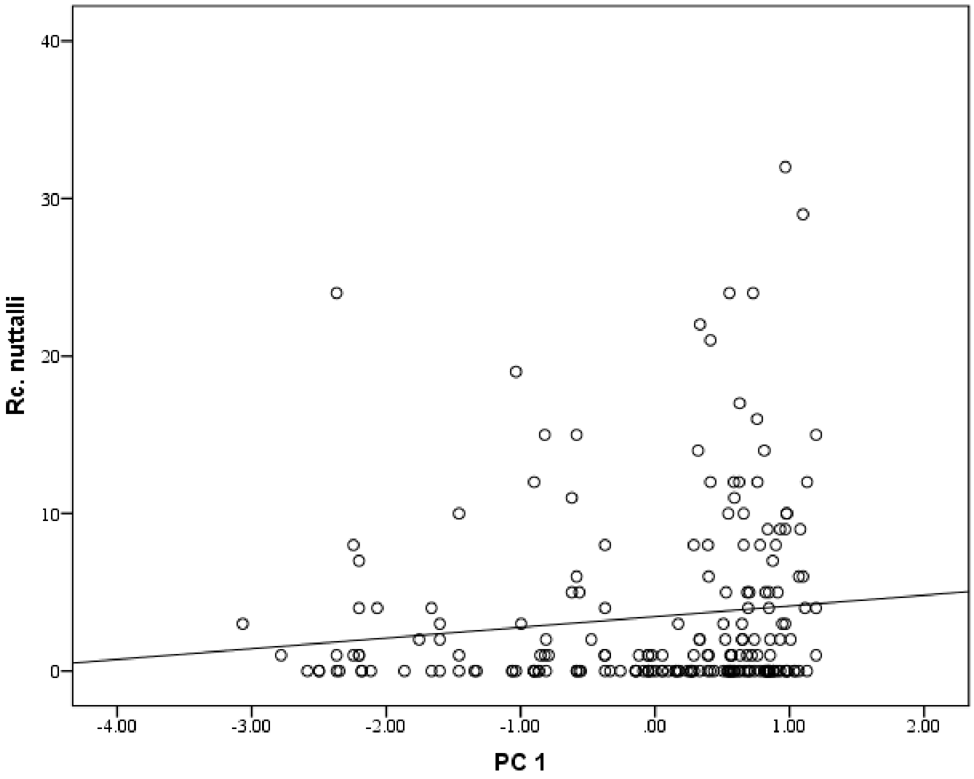

***Figure 3*** - Correlation between PC 1 (reactive behaviours) and *Rc. nuttalli* abundance. Line through data points show relationship between variables

## Discussion

The significant correlation of our different behaviours across the different assessments is indicative of a behavioural syndrome. PC 1 was positively loaded with reactive behaviours i.e. behaviours associated with animals that were less exploratory, less aggressive and shyer while PC 2 was positively loaded with proactive behaviours which show the opposite trend. This is similar to what we found in a previous study investigating personality in captive sengis (Hoffmann 2011). There is some thought that behaviours evolve together in parcels (Dingemanse & Réale 2005; Kiesel *et al.* 2012). What this implies is that there is the possibility of suboptimal behaviours in certain contexts. Usually studied with risk behaviours, where cautious individuals may fare better when facing potential predator risk although bolder individuals may obtain more food foraging in these high risk scenarios but are more likely to be preyed upon (Jones & Godin 2010; Dammhahn 2012).

No significant differences of the personality measures were found between the various testing periods of the animals. More proactive animals remained so, while more reactive animals also stayed the same. We also found no seasonal effects on PC 1 and PC 2 which confirm the repeatability of our measures. Intra-individual variability (IIV) is a term coined from human studies (Stamps *et al.* 2012) that refers to changes in behaviours of an individual that is measured recurrently in the same context. Despite its inherent importance in defining human personalities, IIV is not as well studied in animals due to the fact that few studies have repeated measures of personality. Some studies have suggested that the time between testing periods could affect how an animal performs (Stamps *et al.* 2012). The limited behavioural flexibility observed in our study species may be linked to its phylogenetic origin. Sengis belong to the ancient group Afrotheria, one of the oldest known groups of mammals (Skinner & Chimimba 2005). The Afrotheria evolved in relative isolation in what is today known as Africa and as such it is thought that sengis specifically were relatively immune to competition and invasion due to their specialized adaptations and phylogenetic inertia (Rathbun 2009). This may also explain the lack of plasticity and subsequent consistency of measures across time and explain why capture status of the animals did not significantly affect personality measures. However, this hypothesis is currently only speculative and requires further study.

Gender did not affect personality and this has been found in many other studies (Dingemanse & Réale 2005; Boyer *et al.* 2010; Dunn *et al.* 2011; Tremmel & Müller 2012). In those studies that have found personality differences between sexes it is often found in group-living, highly social animals with sexual dimorphism present (Bolig *et al.* 1992; Schurch & Heg 2010; Heg *et al.* 2011; Ensminger & Westneat 2012). For our study species it is to be expected however that gender does not affect personality, due to the non-sexually dimorphic nature of eastern rock sengis and their similarities in activity (Ribble & Perrin 2005). Both males and females maintain home ranges within larger territories and do not differ significantly in body size (Skinner & Chimimba 2005). We found no direct significant effect of treatment on personality measures. In the previous chapter we found however, that treatment affected body condition and personality was significantly affected by body condition. Consequently, our treatment might have had some indirect effects. However, the consistency of our personality measures despite the treatment effects on body condition suggest that this might be due to innate individual differences in quality rather than being flexible.

Several studies have suggested that size, often related to nutrition, and aggressiveness are strongly correlated; but mostly this applies to the larger individuals and size is usually associated with more aggressive, bolder personalities (Griffen *et al.* 2012; Pruitt *et al.* 2012). Our study results suggest that animals in poorer condition are more exploratory and more aggressive due to the need to find potential mates and food, rather than having a secure territory (Wong *et al.* 2012). As suggested in a study by Wong *et al.* (2012) the smaller animals may have less to lose and behave accordingly due to the potential benefit of behaving more proactively rather than waiting for the subsequent breeding season to put on mass. Our results would suggest something similar, where animals in better body condition are less proactive and more reactive, possibly due to having better access to food due to different foraging strategies, and greater mating opportunities due to well situated territories (Kurvers *et al.* 2010; Betini & Norris 2012; David *et al.* 2012; Pruitt *et al.* 2012) .

It has been suggested that mammals captured by trapping, may in fact be the bolder personality types of a population (Carter *et al.* 2012). The fact that we found no significant effect of either reactive or proactive personality components on the trappability of the animals may suggest that we were possibly capturing only the boldest individuals. However, due to the large range in the loadings of behaviours associated with reactive behaviours, such as latency to move (Réale *et al.* 2007), it seems more likely that the lack of significant interaction of trappability is due to the fact that a whole range of animals were caught from all personality types throughout the trapping period. The lack of correlation of trappability to PC1 and PC2 could suggest that it should be considered as an independent measure of personality as was done by Boyer *et al.* (2010) and Patterson & Schulte-Hostedde (2011).

Only one of the four ectoparasite species considered was affected by our personality measures. The abundance of *Rc. nuttalli* increased significantly with an increasingly reactive personality score. This suggests that results for the relationship between personality and parasites differ with the focal parasite species. This is currently underappreciated and many studies only consider a single parasite species. Potentially this means that future studies should take into account what species is being investigated and how the set of taxa or species could change results. The increase in *Rc. nuttalli* abundances in more proactive individuals does not corroborate the hypothesis, that more proactive individuals have larger parasite burdens (Barber & Dingemanse 2010; Boyer *et al.* 2010). Because an animal when it is proactive is more likely to roam further, it is appealing that potentially the animal would come into contact with a wider range and number of ectoparasites, risking larger infestation loads. *R. warburtoni* has been identified as a tick species that remains consistently present throughout the year, with no seasonal variation in prevalence (Fourie *et al.* 2005; Lutermann *et al.* 2012a). It is possible that *R. warburtoni* has greater questing activity potentially due to a lowered risk of desiccation due to a perceived less sensitivity to heat (Fourie *et al.* 1992, 2005; Hlatshwayo *et al.* 2002). As such it is expected that *Rc. nuttalli* would be more dependent on the chance meeting of the host *E. myurus* rather than the active questing as done by *R. warburtoni* (Fourie *et al.* 2002; Lutermann *et al.* 2012a). In this context it would make sense that reactive animals would have a higher abundance of *Rc. nuttalli* as more reactive sengis potentially make use of cracks and crevices more readily to hide from perceived threats (Trompeter & Langkilde 2011), thereby coming into greater contact with this tick species that may similarly use the cracks and crevices to protect themselves from the unfavourable conditions in their environment (Fourie *et al.* 2002). Also *R. warburtoni* are common and abundant in areas that they inhabit (Fourie *et al.* 2005;

Lutermann *et al.* 2012a, 2012b) which may mean that personality of an animal may be a lesser factor for determining abundance and prevalence of this species due to generally high encounter rates. A similar mechanism could account for the lack of personality effects on chigger prevalence and abundance that is generally high for the study species (see previous chapter). In contrast, lice are usually less prevalent and abundant on small mammals. This also applies to our study species and *N. elephantuli* appears furthermore to specialise on sengis (Fourie *et al.* 1995, see previous chapter). In addition, lice have a close association with the host as the entire life-cycle is spent on a single individual (Hopkins 1948; Clayton & Tompkins 1995). As such we would not expect that different personalities would dictate prevalence and abundance as once infested the animals are likely to remain infested regardless of personality. The low abundances and low prevalence, when compared to the other main parasites, also suggests that coming into contact with the parasite has more to do with the grouping of hosts in sites (Whiteman & Parker 2004) rather than individual behaviour. Due to the monogamous nature of our study species however it is likely that transmission mostly occurs between mother and offspring during suckling.

In conclusion this study found a strong correlation of behaviours across different contexts, which is evidence for behavioural syndromes in the *E. myurus*. Personality was highly repeatable within the population of *E. myurus* captured over a long term period. Contrary to a common hypothesis individuals with greater body condition were less proactive and more reactive which suggest differences in feeding strategies and opportunities between the different personalities. Only one of the four commonly sustained ectoparasite species was affected by personality. This may indicate that interactions between personality and parasites might depend on the general abundance of a parasite species in the environment as well as its life-history.

## References

**Archer, J.** 1973. Tests for emotionality in rats and mice: a review. *Animal Behaviour*, **21**, 205–235.

**Barber, I. & Dingemanse, N. J.** 2010. Parasitism and the evolutionary ecology of animal personality. *Philosophical Transaction of the Royal Society B,* **365**, 4077–4088.

**Bell, A. M.** 2007. Future directions in behavioural syndromes research. *Proceedings of the Royal Society B: Biological Sciences,* **274**, 755–61.

**Betini, G. S. & Norris, D. R.** 2012. The relationship between personality and plasticity in tree swallow aggression and the consequences for reproductive success. *Animal Behaviour,* **83**, 137–143.

**Biron, D. G., Marché, L., Ponton, F., Loxdale, H. D., Galéotti, N., Renault, L., Joly, C. & Thomas, F.** 2005. Behavioural manipulation in a grasshopper harbouring hairworm: a proteomics approach. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 2117–2126.

**Blumstein, D. T., Holland, B.-D. & Daniel, J. C.** 2006. Predator discrimination and “personality” in captive Vancouver Island marmots (*Marmota vancouverensis*). *Animal Conservation*, **9**, 274–282.

**Bolig, R., Price, C. S., Neill, P. L. O. & Suomi, S. J.** 1992. Subjective assessment of reactivity level and personality traits of rhesus monkeys. *International Journal of Primatology*, **13**, 287–306.

**Boon, A. K., Réale, D. & Boutin, S.** 2008. Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*. *Oikos*, **117**, 1321–1328.

**Boyer, N., Réale, D., Marmet, J., Pisanu, B. & Chapuis, J.-L.** 2010. Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus*. *The Journal of Animal Ecology*, **79**, 538–47.

**Carter, A. J., Heinsohn, R., Goldizen, A. W. & Biro, P. a.** 2012. Boldness, trappability and sampling bias in wild lizards. *Animal Behaviour*, **83**, 1051–1058.

**Clayton, D. H. & Tompkins, D. M.** 1995. Comparative effects of mites and lice on the reproductive success of rock doves (*Columba livia*). *Parasitology*, **110**, 195–206.

**Coppens, C. M., de Boer, S. F. & Koolhaas, J. M.** 2010. Coping styles and behavioural flexibility: towards underlying mechanisms. *Philosophical Transaction of the Royal Society B*, **365**, 4021–4028.

**Cote, J., Clobert, J., Brodin, T., Fogarty, S. & Sih, A.** 2010. Personality-dependent dispersal : characterization , ontogeny and consequences for spatially structured populations. *Philosophical Transaction of the Royal Society B*, **365**, 4065–4076.

**Dall, S. R. X., Houston, A. I. & McNamara, J. M.** 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, **7**, 734–739.

**Dammhahn, M.** 2012. Are personality differences in a small iteroparous mammal maintained by a life-history trade-off? *Proceedings of the Royal Society B: Biological Sciences*, **279**, 2645–2651.

**David, M., Auclair, Y., Giraldeau, L. & Cezilly, F.** 2012. Personality and body condition have additive effects on motivation to feed in Zebra Finches Taeniopygia guttata. *Ibis*, **154**, 372–378.

**Dingemanse, N. J. & Réale, D.** 2005. Natural selection and animal personality. *Behaviour*, **142**, 1159–1184.

**Dunn, J. C., Cole, E. F. & Quinn, J. L.** 2011. Personality and parasites: sex-dependent associations between avian malaria infection and multiple behavioural traits. *Behavioral Ecology and Sociobiology*, **65**, 1459–1471.

**Ensminger, A. L. & Westneat, D. F.** 2012. Individual and sex differences in habituation and neophobia in house sparrows (*Passer domesticus*). *Ethology*, **118**, 1085–1095.

**Fourie, L. J., Horak, I. G. & van den Heever, J. J.** 1992. The relative importance of rock elephant shrews *Elephantulus myurus* and Namaqua rock mice *Aethomys namaquensis* for economically important ticks. *South African Journal of Zoology*, **27**, 108–114.

**Fourie, L. J., Du Toit, J. S., Kok, D. J. & Horak, I. G.** 1995. Arthropod parasites of elephant-shrews , with particular reference to ticks. *Mammal Review*, **25**, 31–37.

**Fourie, L. J., Horak, I. G., Kok, D. J. & Zyl, W. V. A. N.** 2002. Hosts , seasonal occurrence and life cycle of *Rhipicentor nuttalli* ( Acari : Ixodidae ). *Onderstepoort Journal of Veterinary Research*, **69**, 177–187.

**Fourie, L. J., Horak, I. G. & Woodall, P. F.** 2005. Elephant shrews as hosts of immature ixodid ticks. *The Onderstepoort Journal of Veterinary Research*, **72**, 293–301.

**Fucikova, E., Drent, P. J., Smits, N. & van Oers, K.** 2009. Handling stress as a measurement of personality in great tit nestlings (*Parus major*). *Ethology*, **115**, 366–374.

**Gosling, S. D.** 2001. From mice to men: what can we learn about personality from animal research? *Psychological Bulletin*, **127**, 45–86.

**Griffen, B. D., Toscano, B. J. & Gatto, J.** 2012. The role of individual behavior type in mediating indirect interactions. *Ecology*, **93**, 1935–1943.

**Hammond-Tooke, C. A., Nakagawa, S. & Poulin, R.** 2012. Parasitism and behavioural syndromes in the fish *Gobiomorphus cotidianus*. *Behaviour*, **149**, 601–622.

**Hays, W. L.** 1973. *Statistics for the social sciences.* 2nd edn. New York: Holt, Rinehart and Winston Fort Worth : Harcourt Brace Jovanovich,.

**Heg, D., Schurch, R. & Rothenberger, S.** 2011. Behavioral type and growth rate in a cichlid fish. *Behavioral Ecology*, **22**, 1227–1233.

**Hilborn, R., Redfield, J. A. & Krebs, C. J.** 1976. On the reliability of enumeration for mark and recapture census of voles. *Canadian Journal of Zoology,* **54**, 1019–1024.

**Hlatshwayo, M., Mbati, P. A. & Dipeolu, O. O.** 2002. Seasonal abundance of adult ixodid ticks infesting cattle belonging to resource-limited farmers in the north-eastern Free State Province of South Africa. *The Onderstepoort Journal of Veterinary Research*, **69**, 1–6.

**Hoffmann, S.** 2011. The effects of captivity, environmental enrichment and personality on memory and spatial learning in the eastern rock elephant shrew (*Elephantulus myurus*). University of Pretoria.

**Hopkins, M.** 1948. The Host-asociations of the lice of mammals. *Proceedings of the Zoological Society of London*, **119**, 387 – 604.

**Horak, I. G., Welman, S., Hallam, S. L., Lutermann, H. & Mzilikazi, N.** 2011. Ticks of four-toed elephant shrews and Southern African hedgehogs. *Onderstepoort Journal of Veterinary Research,* **78**, 1–3.

**Jones, K. A. & Godin, J.-G. J.** 2010. Are fast explorers slow reactors? Linking personality type and anti-predator behaviour. *Proceedings of the Royal Society B: Biological Sciences,* **277**, 625–632.

**Kiesel, A. L., Snekser, J. L., Ruhl, N. & McRobert, S. P.** 2012. Behavioural syndromes and shoaling: connections between aggression , boldness and social behaviour in three different Danios. *Behaviour,* **149**, 1155–1175.

**Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. & Blokhuis, H. J.** 1999. Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience and Biobehavioral Reviews,* **23**, 925–935.

**Koprivnikar, J., Gibson, C. H. & Redfern, J. C.** 2012. Infectious personalities: behavioural syndromes and disease risk in larval amphibians. *Proceedings of the Royal Society B: Biological Sciences,* **279**, 1544–1550.

**Krebs, C. J. & Boonstra, R.** 1984. Trappability estimates for mark-recapture data. *Canadian Journal of Zoology,* **62**, 2440–2444.

**Kurvers, R. H. J. M., Prins, H. H. T., van Wieren, S. E., van Oers, K., Nolet, B. a & Ydenberg, R. C.** 2010. The effect of personality on social foraging: shy barnacle geese scrounge more. *Proceedings of the Royal Society B: Biological Sciences,* **277**, 601–8.

**Lefèvre, T., Adamo, S. A., Biron, D. G., Missé, D., Hughes, D. & Thomas, F.** 2009. Invasion of the body snatchers: the diversity and evolution of manipulative strategies in host-parasite interactions. *Advances in Parasitology,* **68**, 45–83.

**Lovegrove, B. G., Lawes, M. J. & Roxburgh, L.** 1999. Confirmation of pleisiomorphic daily torpor in mammals: the round-eared elephant shrew *Macroscelides proboscideus* (Macroscelidea). *Journal of Comparative Physiology B,* **169**, 453–460.

**Lutermann, H., Medger, K. & Horak, I. G.** 2012a. Abiotic and biotic determi1nants of tick burdens in the eastern rock sengi (*Elephantulus myurus*). *Medical and Veterinary Entomology*, **26**, 1–9.

**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.

**Metcalfe, N. B., Valdimarsson, S. K. & Morgan, I. J.** 2003. The relative roles of domestication, rearing environment, prior residence and body size in deciding territorial contests between hatchery and wild juvenile salmon. *Journal of Applied Ecology*, **40**, 535–544.

**Montiglio, P., Garant, D., Pelletier, F. & Réale, D.** 2012. Personality differences are related to long-term stress reactivity in a population of wild eastern chipmunks, *Tamias striatus*. *Animal Behaviour*, **84**, 1071–1079.

**Mzilikazi, N. & Lovegrove, B. G.** 2005. Daily torpor during the active phase in free-ranging rock elephant shrews (*Elephantulus myurus*). *Journal of Zoology*, **267**, 103–111.

**Poulin, R.** 2013. Parasite manipulation of host personality and behavioural syndromes. *The Journal of Experimental Biology*, **216**, 18–26.

**Pruitt, J. N., Burghardt, G. M. & Riechert, S. E.** 2012. Non-conceptive sexual behavior in spiders: a form of play associated with body condition, personality type, and male intrasexual selection. *Ethology*, **118**, 33–40.

**Rathbun, G. B.** 1979. *The social structure and ecology of elephant-shrews.* Berlin: Parey.

**Rathbun, G. B.** 2009. Why is there discordant diversity in sengi (Mammalia : Afrotheria : Macroscelidea) taxonomy and ecology ? *African Journal of Ecology*, **47**, 1–13.

**Réale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J.** 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews of the Cambridge Philosophical Society*, **82**, 291–318.

**Ribble, D. O. & Perrin, M. R.** 2005. Social organization of the Eastern Rock Elephant-shrew (*Elephantulus myurus*): the evidence for mate guarding. *Nature*, **135**, 167–173.

**Roxburgh, L. & Perrin, M. R.** 1994. Temperature regulation and activity pattern of the round-eared elephant shrew *Macroscelides proboscideus*. *Journal of Thermal Biology*, **19**, 13–20.

**Schurch, R. & Heg, D.** 2010. Life history and behavioral type in the highly social cichlid *Neolamprologus pulcher*. *Behavioral Ecology*, **21**, 588–598.

**Sih, A., Bell, A. & Johnson, J. C.** 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, **19**, 372–378.

**Skinner, J. D. & Chimimba, C. T.** 2005. Order: Macroscelidea. In: *The mammals of the southern African subregion*, Vol 2nd 3rd edn. (Ed. by D. van der Horst), pp. 22–34. Cape Town: Cambridge Univ Press.

**Smith, B. R. & Blumstein, D. T.** 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, **19**, 448–455.

**Stamps, J. A., Briffa, M. & Biro, P. A.** 2012. Unpredictable animals: individual differences in intraindividual variability ( IIV ). *Animal Behaviour*, **83**, 1325–1334.

**Svartberg, K. & Forkman, B.** 2002. Personality traits in the domestic dog (*Canis familiaris*). *Applied Animal Behaviour Science*, **79**, 133–155.

**Toms, C. N., Echevarria, D. J. & Jouandot, D. J.** 2010. A methodological review of personality-related studies in fish: focus on the shy-bold axis of behavior. *International Journal of Comparative Psychology*, **23**, 1–25.

**Tremmel, M. & Muller, C.** 2012. Insect personality depends on environmental conditions. *Behavioral Ecology*, **24**, 386–392.

**Trompeter, W. P. & Langkilde, T.** 2011. Invader danger: lizards faced with novel predators exhibit an altered behavioral response to stress. *Hormones and Behavior*, **60**, 152–158.

**Van Houte, S., Ros, V. I. D. & van Oers, M. M.** 2013. Walking with insects: molecular mechanisms behind parasitic manipulation of host behaviour. *Molecular Ecology*, **22**, 3458–3475.

**Whiteman, N. K. & Parker, P. G.** 2004. Effects of host sociality on ectoparasite population biology. *The Journal of Parasitology*, **90**, 939–947.

**Wilson, D. S., Clark, A., Coleman, K. & Dearstyne, T.** 1994. Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, **9**, 442–446.

**Wong, B. B. M., Svensson, P. A. & Lehtonen, T. K.** 2012. A high aggression strategy for smaller males. *PLoS ONE*, **7**, e43121.

**Yeo, M., Treloar, S., Marks, G., Heath, A. & Martin, N. G.** 1997. What are the causes of individual differences in food consumption and are they modified by personality? *Journal of Personality and Individual Difference*, **23**, 535–542.

# Chapter 4

## Links between personality, parasite abundances and the physiology of *Elephantulus myurus*

### Abstract

Individuals of the same species may differ remarkably in their individual hormone concentrations. In recent years, the knowledge that animals differ inherently in their behaviour from one another on an individual level, or personality, has become widely accepted and this may be correlated with endocrinological differences, particularly steroid hormones. At the same time steroid hormones may be modulated by parasitic infestation. In this study we investigated the relationship between two steroid hormones (cortisol and testosterone), personality and ectoparasite burden of eastern rock sengis (*Elephantulus myurus*). We monitored urinary cortisol and testosterone concentrations of 66 eastern rock sengis collected during the period March 2012 to March 2013 from a game reserve in the Limpopo Province, South Africa. All animals caught were assessed for their personality, ectoparasite burden of the four most prevalent ectoparasite species (two ticks, one chigger mite and one louse species) and urine was collected for the determination of cortisol and testosterone. We found little seasonal fluctuation of either hormone, but cortisol levels were exceptionally high while testosterone tended to be low. No significant effects of either hormone on the personality of the sengis could be detected, but females had significantly higher levels of testosterone than males. This is most likely linked to the monogamous mating system of the study species in which both sexes defend home ranges year-round. In contrast, the cortisol levels may be a result of the year-round high abundances of the tick, *Rhipicephalus warburtoni* as well as chiggers. For a second tick, *Rhipicentor nuttalli*, which is equally prevalent, but much less abundant, abundance, was contrary to the predictions of the immunocompetence handicap. Our findings suggest that mating system should be taken into account in the study of the endocrinology and animal personality. In addition,

the prevalence and abundance as well as the life-cycle of a parasite should be considered when making predictions about animal personality, endocrinology and parasites burdens.

## Introduction

Individuals of the same species may differ remarkably in their circulating hormone concentrations (While *et al.* 2010). Often these differences may be attributed to variation in sex and/or reproductive effort/ability of the individual (Finch & Rose 1995; Hau 2007). For example in dark eyed-juncos (*Junco hyemalis*) repeatability in individual differences in hormones is linked to variation in aggression which has been found to have significant effects on individual fitness (Neal *et al.* 2008; Gerlach & Ketterson 2013). Many studies have focussed on the variation of seasonal breeding efforts in relation to hormone concentrations in those animals that reproduce on a seasonal cycle (Faulkes & Abbott 1991; Ziegler *et al.* 2000). For example Medger *et al.* (2012) found in eastern rock sengis (*Elephantulus myurus*) that plasma testosterone concentrations in males were undetectable for six months of the year, peaking only during the breeding season.

In recent years it has been increasingly recognised that animals differ consistently in behaviour from one another on an individual level, also termed personality. Personality has been found to influence the learning abilities of animals (Hoffmann 2011), food choice and quality (Wilson *et al.* 1994), as well as habituation to stressful situations (Seltmann *et al.* 2012) to mention but a few. It has been proposed that personality may correlate with varying hormone concentrations of an individual (Coppens *et al.* 2010; While *et al.* 2010). Animals that are considered to be more reactive (i.e. shyer, less aggressive and less bold) may have higher concentrations of corticosteroids whereas those that are more proactive may exhibit higher concentrations of testosterone (Cote *et al.* 2010; Montiglio *et al.* 2012). However, most studies investigating hormones and behaviour tend to focus on lab studies with animals chosen specifically for their physiological traits. Consequently, correlations between hormones and tested factors may not be surprising for these models (Metcalfe *et al.* 2003; Brillaud *et al.* 2005; Archard & Braithwaite 2010; Meijer *et al.* 2010).

Corticosteroids are hormones produced in response to stress in animals. They are produced by the adrenal cortex and released in response to elevated levels of stress (Bayazit 2009). Corticosterone is the main corticoid hormone produced in bird species and reptiles (DeNardo & Sinervo 1994; Wikelski *et al.* 1999; Fairhurst *et al.* 2011; Hews & Abell Baniki 2013; Ouyang *et al.* 2013) while cortisol is the main glucocorticoid in fish and some mammals (Reburn & Wynne-Edwards 2000; Bayazit 2009; Hoffman *et al.* 2010; José *et al.* 2012; O'Connor *et al.* 2012). The rise in corticoid secretion to the increase in elevated levels of stressors can be either pronounced with a sudden (within a few minutes) increase in hormone concentration (José *et al.* 2012) or it could be generally elevated due to chronic stressors such as parasite infestation (Haond *et al.* 2003). Reproduction is also costly and requires that an animal invest resources in reproduction that could otherwise be used for maintenance of the organism and as a result it is often found that breeding females have higher cortisol concentrations than non-breeding females (Finkler & Terkel 2010; Koren *et al.* 2012). Huber *et al.* (2003) also found that in response to the low availability of deciduous plants, which are major food sources during winter for several small mammal species in temperate regions, glucocorticoids may be released to aid survival through these periods. However, the majority of seasonal peaks in glucocorticoids are associated with the breeding season (Romero 2002). In social primates Ostner *et al.* (2008) and Clough *et al.* (2009) found that cortisol increases during the mating season. The pattern of secretion in other small mammals is less clear although some studies have shown that cortisol either peaks prior to or after the breeding season but not always during it (Boswell *et al.* 1994; Place & Kenagy 2000; Soto-Gamboa *et al.* 2005). Often animals with sustained higher levels of cortisol are found to be in poor body condition due to the trade off in resources (Esch & Hazen 1980; Barton *et al.* 1987; Kitaysky *et al.* 1999). In essence this is due to glucocorticoids, being secreted via the hypothalamic-pituitary-adrenal (HPA) axis in response to external stressors, such as an attack from a predator (Sapolsky *et al.* 1986; Romero 2004).

Corticosteroids direct energy away from non-essential processes and make it available for escaping the potential predation. For example, more glucose would be released to provide energy for use by the muscle of the animal with increased corticosteroid levels (Sapolsky 1990).

A variation in the patterns of circulating hormone could also vary with the degree of parasite burdens (Dunn *et al.* 2013). Corticosteroids may act as an immune suppressant in some cases, which may increase the incidence and transmission of parasite infections and diseases (Da Silva 1999; Martin 2009). As such, increased levels of corticosteroids for extended periods of time are negatively associated with the longevity and fitness of the animal, which can be linked to hosts harbouring large abundances of parasites (Morand *et al.* 2006; Ezenwa *et al.* 2012; Dunn *et al.* 2013). Seasonal variation and fluctuations of parasite burdens in small mammals has been shown in both northern and southern hemispheres (Hopkins 1948; Fourie *et al.* 2002; Marcogliese 2005; Lutermann *et al.* 2012a) and consequently parasite induced changes in corticosteroid levels may vary seasonally. This adds to the complexity of seasonal patterns of glucocorticoid production and the underlying mechanisms are not fully understood (Romero 2002).

Similarly, testosterone has been linked to immune suppression in animals, more specifically in males. Testosterone is thought to suppress the immune system as posited in the immunocompetence handicap hypothesis. This hypothesis proposes that males with higher testosterone levels, for the development and maintenance of secondary sexual characteristics, should have decreased immune function due to testosterone acting as an immune suppressor and consequently carry larger parasite burdens (Folstad & Karter 1992). Seivwright *et al.* (2005) working on red grouse (*Lagopus lagopus scoticus*) found that males implanted with testosterone had significantly higher levels of the caecal nematode, *Trichostrongylus tenuis*. This theory has been contested however, specifically in avian studies, since the basic assumption that testosterone suppresses immune function does not always apply (Owen *et al.* 2004). However, in mammals there is evidence that testosterone suppresses immune function (Ansar Ahmed *et al.* 1985; Schuurs & Verheul 1990; Nelson & Demas 2013).

One of the most important components in studies investigating the role of testosterone in animals is the interaction of this hormone with respect to reproduction when considering factors such as territoriality and aggressive behaviours. Higher testosterone concentrations have been found to correlate significantly with increases in aggressive behaviours of animals (Moore 1984; Wingfield *et al.* 1990; Cavigelli & Pereira 2000; Cain & Ketterson 2013). Similarly, positive links have been found with testosterone and increased activity and territoriality of animals (Sinervo *et al.* 2000; Ezenwa *et al.* 2012; Gerlach & Ketterson 2013). Sinervo *et al.* (2000) working on side-blotched lizard, *Uta stansburiana*, established that males with bright orange throats had higher levels of plasma testosterone which coincided with greater endurance, activity, home range size and gaining greater control over female home ranges than that of blue- or yellow-throated males with much lower testosterone levels. In fact many studies measuring testosterone in males have found increased reproductive output of males with higher levels of testosterone through greater matings success either through mate guarding or greater chances of meeting females through exploration (DeNardo & Sinervo 1994; Negro *et al.* 2010). Most studies of this nature have been carried out in promiscuous species which exhibit a sexual dimorphism where elevated testosterone in males is associated with increased male body size and behavioural differences such as greater home ranges (Chandler *et al.* 1994; Grear *et al.* 2009). In contrast, comparative studies in species with a monogamous mating system are largely lacking. In addition, the significance of testosterone may not apply exclusively to male intra-sexual competition and female testosterone levels have rarely been considered (Shargal *et al.* 2008; Lutermann *et al.* 2013).

Sengis of the ancient order Macroscelidea, are endemic to Southern Africa (Skinner & Chimimba 2005, Rathbun 2009). All 17 members of this order are thought to be monogamous (Rathbun 2009) and some have shown to exhibit mate guarding (Schubert *et al.* 2011). All species are also found to lack any sexual dimorphism. In rufous sengis, *Elephantulus rufescens*, pairs construct and maintain complex trail systems that they defend sex-specifically and young are chased of by the parents once mature (Rathbun & Redford 1981). Other sengi species have also been shown to inhabit overlapping territories between males and females with a pair excluding other conspecifics (Ribble & Perrin 2005; Rathbun & Rathbun 2006). Little is known about steroid hormones in sengis but glucocorticoids have been investigated in the round eared sengi, *Macroscelides proboscideus,* (Schubert *et al.* 2012). In eastern rock sengis, *Elephantulus myurus*, some work has been done on plasma androgens with regards to seasonal reproduction (Medger *et al.* 2012). The latter study showed that males exhibit seasonal variation in testosterone levels with a peak in July. All of these traits make sengis a promising model group to test the hypotheses and predictions laid out above in a monogamous system. For the current study we chose *Elephantulus myurus,* the eastern rock sengi, as our study species as it is probably the best studied sengi species with regards to their ectoparasites. They inhabit rocky outcrops in arid areas which experience seasonal variation in rainfall. However, despite this they are known to have a long breeding season lasting from August to March (Skinner & Chimimba 2005; Medger *et al.* 2012). Although monogamy in animals is often attributed to the need for parental care of young by both sexes in our study species the precocial young are cared for primarily by the mother although this appears to be limited to nursing (Fitzgibbon 1997; Ribble & Perrin 2005). In eastern rock sengis there is no significant difference between males and females in terms of parasite abundance, size or personality type (see previous chapters). This makes eastern rock sengis an interesting animal to investigate the effects of host factors and external stressors on hormone concentrations.

The aim of this study was to measure the circulating urinary hormone profiles of wild male and female *E. myurus* with specific reference to the hormones cortisol and testosterone and to document their seasonal fluctuations. We also intended to validate the solid-phase radioimmunoassay for measuring urinary cortisol and testosterone in *E. myurus*. Furthermore we aimed to evaluate possible links between of hormones and personality of an individual. Lastly, we intended to investigate how fluctuations in hormones may be linked to their parasite burdens.

## Materials and Methods

Sengis were captured from the Goro Game reserve, Limpopo Province, South Africa (22°58'S; 29°25'E). Animals were trapped six times from March 2012 – April 2013 using Sherman traps (H. B. Sherman Traps, Inc. Tallahassee, Florida, U.S.A.) baited with oats, peanut butter and sardines. On each trapping site 150 traps were laid out in parallel lines during the afternoon and collected the following morning. Lines were approximately ten metres apart with ten paces between traps. Animals were trapped at eight different sites situated throughout the reserve roughly 300 metres apart with the two furthest sites being 3 km apart. Captures were conducted under the permit number 001-CPM401-0002 from the Department of Environment Affairs, Limpopo Province. Captured animals were sexed and weighed using a digital scale (Scout Pro SPU123; Ohaus Corporation, USA). Animals underwent personality assessments comprising of an exploratory test, an aggressive response test and a boldness test. The three assessments were done consecutively for each individual animal. Assessments were recorded using a digital video recorder (Panasonic SDR-S50, MV Tronics, Midrand, South Africa) which resulted in 15 minute videos for each individual, five minutes per test. This procedure is explained in more detail in the previous chapter. Using principal component analysis two principal components (PC 1 and PC 2) corresponding to reactive and proactive behavioural traits, respectively, were extracted (for further details see previous chapter).

After the personality assessments, the ectoparasites were removed from the animals using tweezers while being restrained by hand and stored in 70 % ethanol. In the study site *E. myurus* harbours only four ectoparasite species in substantial numbers: two tick species (*Rhipicephalus warburtoni* and *Rhipicentor nuttalli*), chigger mites of the family Trombiculidae and one species of lice (*Neolinognathus elephantuli*) (see chapter 2) and only these were considered for analyses. After the ectoparasites were removed, a unique ear-clip was given to each animal for identification during successive field trips. Half of the animals were treated using Frontline®, a chemical insecticide, to manipulate parasite burdens as it prevents reinfestation of ectoparasites such as ticks and mites. Frontline® was applied as described in the first chapter. The body length of an individual was then measured using electronic callipers (INSIZE Co., Ltd) from the back of the neck to the base of the tail. The mass of the animal was divided by this body measure to determine body condition.

After the personality assessments and removal of ectoparasites from the individual animals were placed in a urine collection chamber (26cm x 17cm x 12cm). Animals were checked every hour for a period of roughly six hours, until animals were taken back to the spot of capture and released. Animals were fed water (using a pipette) before placement in the chambers and a slice of apple was provided during the sampling period. Urine samples were collected with plastic pipettes and kept in Eppendorf tubes, placed in the freezer as they were collected. We chose urinary collection for this study as eastern rock sengis are difficult to bleed in the field and it is not easy to obtain sufficient blood to measure hormone levels (S. Hoffmann pers. obs.) It has furthermore the benefit of a more delayed corticosteroid response than plasma, which can show increases in glucocorticoids from handling as rapidly as one to five minutes after experiencing a stressor (Reburn & Wynne-Edwards 2000).

### *Hormone determination*

For the hormone assays urine samples were defrosted 2 hours prior to commencement and mixed in a vortexer (VM-1000, Digisystem Laboratory system, Taiwan) to ensure that the samples were homogenous. Coat-A-Count® hormone kits (Siemens Medical Solutions Diagnostic Products Corporation, Los Angeles, USA) were used to measure cortisol (C) and testosterone (T) concentrations in the urine of both male and female sengis. This is a solid-phase radioimmunoassay based on a radioactive labelled hormone which then competes for antibody binding space in the test tubes provided by the manufacturer. The assay does not require any extraction or chromatography. Both kits are highly specific for their respective steroid hormone (sensitivity for cortisol, 5.5nmol/l;

testosterone, 0.14nmol/l). For cortisol, the cross-reactivity of the antibody was below 1% except for prednisone (2.6%), 11- deoxycortisol (11.4%) and prednisolone (76%). Cross-reactivity of the antibody for testosterone was also below 1% with the exception of methyltestosterone (1.7%), 5α-dihydrotestosterone (<3.5%), 11-ketotestosterone (16%) and 19-nortestosterone (22%).

After a period of incubation (3 hours for C and 45 min for T) the amount of bound radioactive labelled hormone in the tube was measured using a gamma counter. A curve was calibrated using the known samples of hormone provided by the manufacturer. The gradients of the serial dilution curves compared to the calibration curves of the two hormones measured were analysed for parallelism with a general linear model (GLM) after log-logit-transformation (Chard, 1978) to validate the assay for hormone concentrations of both C and T in urine of *E. myurus*. The different curves, i.e. the standard curve and the curve produced from the sengi sample, were employed as a random factor and the dilutions added as covariates in the model.

The assay measuring urinary C concentrations (nmol/L) was validated for *E. myurus* as there was no significant difference between serial dilution curves for both urinary C and the calibration curve ($F_{1, 5}$ = 0.861, n = 3, p = 0.369). The sensitivity of the assay was 0.36 nmol/L and the intra-assay coefficient of variation for repeated determination of quality control was between 2.9% and 4.7% for the different assays. The inter-assay coefficient of variation was found to be 8.8%.

Similarly the urinary T concentration assay was validated for *E. myurus* as there was no significant difference between the serial dilution curve of urinary T and the calibration curve ($F_{1, 7}$ = 1.341, n = 5, p = 0.285). The intra-assay coefficient of variation for repeated determination of quality control was between 6.7% and 7.8% for the different assays and the inter-assay coefficient was found to be 6.1%.

Urinary creatinine (Cr) was measured to account for different dilutions of urine samples (Bonney *et al.* 1982). The assay was carried out in micro plates for use in plate readers and 7 µl of standards, samples and quality control samples (i.e. high and low concentration samples) were pipetted into micro plate wells. Then working picrate reagent was added to each well and left to develop progressively over 2 to 3 hours. The amount of light able to penetrate the liquid mixture was then measured on plate reader at 420 nm. After the level of Cr was determined per sample (mg/ml) it was used to determine the true hormone levels in the urine by correcting for the dilution.

### *Statistical Analysis*

Data were analysed in IBM SPSS v.21. The concentration of C was normally distributed Shapiro-Wilk Test: $p = 0.054$). In contrast T concentrations and personality measures and parasite abundances were not normally distributed (Shapiro-Wilk Test: $p < 0.001$). Consequently a generalized linear mixed model (GLMM) with a linear distribution with an identity link function was used to analyse the effects of sex, season, treatment (i.e. treated or not) and capture status (new or recaptured) on C concentrations. It should be noted that treatment refers to the secondary treatment of applying Frontline® to half of the animals. All possible two-way interactions were included in the model. Due to limited sample sizes in the interactions between sex or treatment and season could not be included in the model. Both PC 1 and PC 2 were added as co-variates in the models. For T concentration the same model was run with a gamma distribution with a log link function. We investigated the effect of hormone concentrations on parasite abundances as well. A GLMM was run for each of the abundances of the four main parasite species using a negative binomial regression with a log link function with T and C concentration as covariates as well as personality measures and body condition. The effects of sex, season, treatment and capture status was also included in the model as fixed effects. Similar analyses were conducted for parasite prevalence. However, since we found that there was no significant effect of any of the factors investigated these analyses were not included in the results.

## Results

From a total of 125 individuals a sufficiently large urine sample was collected only once for 66 animals, twice for 14 animals and three times for two animals. Out of the number of samples collected 43 were collected from animals that were caught for the first time, while 39 samples were collected from recaptures, although this does not mean the animal necessarily urinated the first time it was caught. Samples were collected from 18 new animals in the first month of trapping (March 2012) then for the successive trapping months there were fewer samples collected from new animals and more collected from recaptures (Table 1). The C concentrations were found to be high and urine samples were diluted 10, 20 or 30 times to obtain measurable concentrations of this hormone. This was not necessary for T. Due to limitations in the urine volume that could be collected we were left with 67 samples for T and 74 samples for C and 60 measures for animals for which we had both T and C measures.

***Table 1*** - Urine samples collected for sengis throughout the study period.

| | **Males** | | **Females** | |
|---|---|---|---|---|
| **Season** | **New** | **Recapture** | **New** | **Recapture** |
| **March** | 7 | 0 | 11 | 0 |
| **June** | 3 | 6 | 2 | 5 |
| **August** | 2 | 11 | 2 | 6 |
| **October** | 0 | 0 | 0 | 0 |
| **January** | 1 | 3 | 3 | 2 |
| **March 13** | 8 | 1 | 4 | 5 |

The concentration of C was not significantly affected by gender, season, treatment or capture status (Table 2). The two-way interactions were also not significant, nor did it significantly covary with body condition or PC 1 and PC 2 (Table 2). In contrast T concentrations was significantly affected by gender (Table 2), with females (0.634 ± 0.085 µg.mgCr$^{-1}$) having higher T concentrations than males (0.414 ± 0.053 µg.mgCr$^{-1}$). In addition, T varied significantly with season (Table 2).

Post hoc analysis revealed that animals caught in March 2013 had significantly higher T concentrations than all the other seasons where urine was collected ($p < 0.005$ for all, Figure 1). There was no significant difference between T concentrations of any of the other seasons ($p \geq 0.05$ for all, Figure 1).

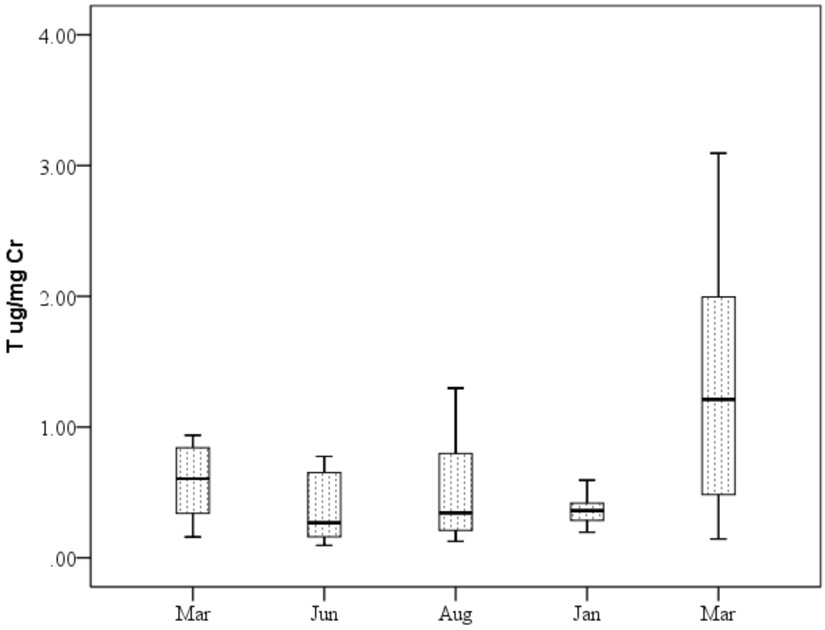

***Figure 1*** **-** Seasonal variation in testosterone throughout the trapping period for *E. myurus*. Black horizontal lines represent medians and whiskers represent minimum and maximum values.

Similarly, there was no significant effect of either treatment or capture status on T concentrations (Table 2). In addition, none of the two-way interactions were significant (Table 2). Neither PC1 nor PC2 significantly affected T concentrations (Table 2)

As reported in chapter 2 the abundance of *R. warburtoni* varied significantly with season (Table 3) and post hoc analysis confirmed the patterns reported in chapter 2. We also found a significant effect of body condition (Table 2) with sengis with a greater body condition having significantly fewer *R. warburtoni* (Figure 2). Neither steroid hormone nor any of the other factors investigated, nor their two-way interactions did significantly affect *R. warburtoni* abundance.

***Table 2*** - Results of the GLMMs investigating the effects of sex, treatment, capture status, season, personality measures (PC1 and 2) and body condition on the urinary hormone concentrations of *E. myurus*.

| | | **Cortisol** | | **Testosterone** | |
|---|---|---|---|---|---|
| | df | F | p-value | F | p-value |
| Sex | 1, 45 | 0.683 | 0.412 | 5.181 | **0.027*** |
| Treatment | 1, 45 | 0.894 | 0.348 | 0.298 | 0.588 |
| Capture status | 1, 45 | 0.087 | 0.769 | 0.007 | 0.936 |
| Season | 1, 45 | 0.896 | 0.472 | 8.145 | **<0.0001*** |
| PC 1 | 1, 45 | 0.025 | 0.552 | 0.030 | 0.426 |
| PC 2 | 1, 45 | 0.751 | 0.875 | 0.154 | 0.864 |
| Body Condition | 1, 45 | 0.358 | 0.390 | 0.644 | 0.696 |
| Sex*treatment | 1, 45 | 0.015 | 0.901 | 0.152 | 0.698 |
| Sex*capture status | 1, 45 | 3.654 | 0.061 | 0.164 | 0.687 |
| Treatment*capture status | 1, 45 | 0.044 | 0.834 | 0.014 | 0.906 |

***significant effects**

The abundance of *Rc. nuttalli* was significantly affected by the concentration of T but not C with the abundance of *Rc. nuttalli* decreased with increasing T (Table 3, Figure 3). None of the remaining factors significantly affected the abundance of *Rc. nuttalli* (Table 3). For the abundance of chiggers we found a significant effect of season (Table 3) and this pattern, as with *R. warburtoni* was found to be the same as previously reported in chapter 2. Neither urinary C nor T concentration or the personality measures affected the abundance of chiggers and none of the other factors included in the model were significant (Table 3). None of the factors considered had a significant effect on the abundance of *N. elephantuli* (Table 3).

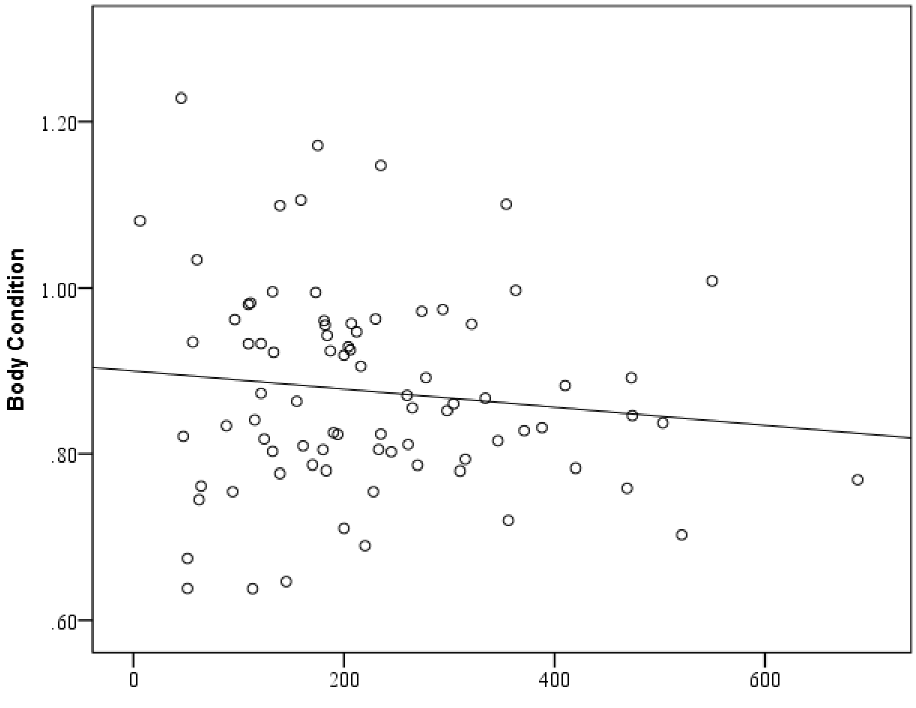

***Figure 2*** - Correlation between body condition and *R. warburtoni* abundance for *E. myurus*. Line through data points represents relationship between the variables

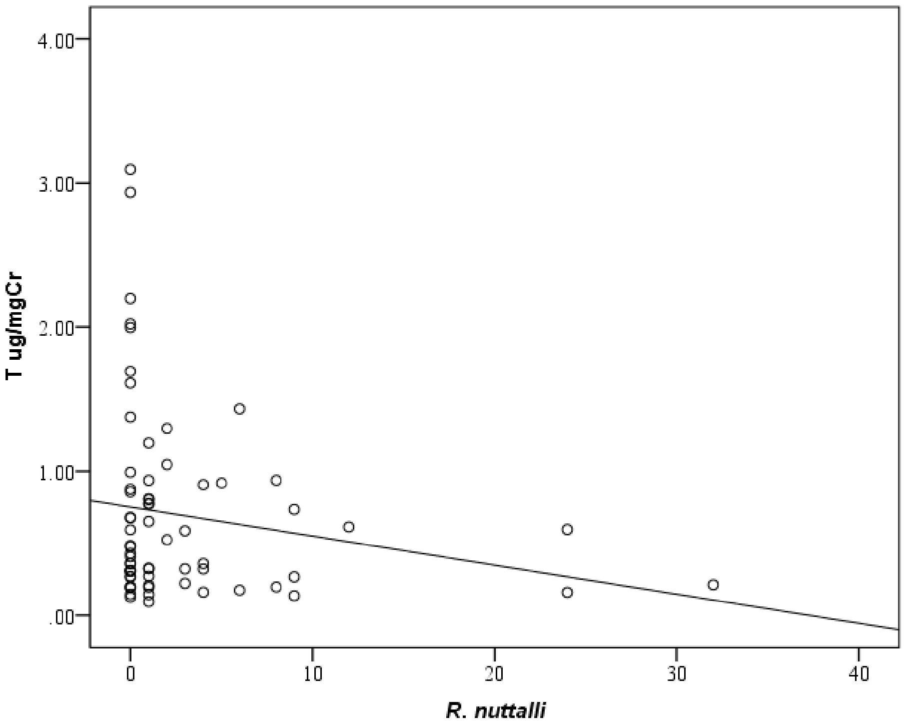

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***Figure 3*** - Correlation between urinary testosterone concentration and *Rc. nuttalli* abundance for E. myurus captured throughout the study period. Line through the scatters shows the relationship between the variables.

***Table 3*** **-** Results of the GLMMs investigating the effects of sex, treatment, capture status, season, personality measures (PC1 and 2) and body condition and urinary hormone concentrations on parasite abundances of *E. myurus.*

| | | ***R. warburtoni*** | | ***Rc. nuttalli*** | | **chiggers** | | ***N. elephantuli*** | |
|---|---|---|---|---|---|---|---|---|---|
| | **df** | **F** | **p-value** | **F** | **p-value** | **F** | **p-value** | **F** | **p-value** |
| Sex | 1, 44 | 0.790 | 0.379 | 0.010 | 0.920 | 2.047 | 0.160 | 0.544 | 0.465 |
| Treatment | 1, 44 | 0.957 | 0.333 | 0.004 | 0.947 | 3.554 | 0.066 | 1.471 | 0.232 |
| Capture status | 1, 44 | 4.025 | 0.051 | 0.061 | 0.806 | 0.198 | 0.658 | 0.225 | 0.637 |
| Season | 4, 44 | 4.025 | **0.007** | 1.785 | 0.149 | 3.452 | **0.015** | 0.650 | 0.630 |
| Sex*treatment | 1, 44 | 3.178 | 0.082 | 2.379 | 0.130 | 2.354 | 0.132 | 0.500 | 0.483 |
| Sex*capture status | 1, 44 | 3.062 | 0.087 | 0.556 | 0.460 | 0.005 | 0.942 | 0.355 | 0.554 |
| Treatment*capture status | 1, 44 | 2.206 | 0.145 | 0.125 | 0.726 | 0.099 | 0.754 | 1.715 | 0.197 |
| PC 1 | 1, 44 | 0.957 | 0.333 | 2.384 | 0.130 | 1.451 | 0.235 | 1.578 | 0.216 |
| PC 2 | 1, 44 | 1.717 | 0.197 | 2.165 | 0.148 | 0.874 | 0.355 | 0.195 | 0.661 |
| Cortisol | 1, 44 | 0.103 | 0.750 | 0.045 | 0.833 | 0.236 | 0.629 | 0.232 | 0.633 |
| Testosterone | 1, 44 | 1.934 | 0.171 | 5.018 | **0.030** | 0.275 | 0.603 | 0.114 | 0.738 |
| Body Condition | 1, 44 | 6.545 | **0.014** | 1.914 | 0.173 | 0.778 | 0.383 | 2.078 | 0.157 |

## Discussion

In this study C concentrations were generally high throughout the year. This contrasts with the findings of Schubert *et al.* (2012) that measured free corticosterone concentrations in the urine of the round-eared sengi, *Macroscelides proboscideus*, as well as glucocorticoid metabolites in faeces prior to and after an aggressive encounter with same-sex conspecifics. The concentrations of corticosterone measured in the urine (34 ng/ml) are much lower than those concentrations of cortisol (2939 ng/ml) found in this study which suggests that cortisol may be the principle glucocorticoid in sengis. Compared to other small African mammals such as the highveld mole-rat (*Cryptomys hottentotus pretoriae*) eastern rock sengis possess much higher concentrations of urinary cortisol. Lutermann *et al.* (2012b) reports the mean cortisol concentrations of highveld mole-rats to be around 200 nmol/l while that found in our study was 9460 nmol/l prior to creatinine corrections. These generally high concentrations may also have masked any possible correlations with the other factors considered in our analysis.

The continually elevated concentrations of C in sengis may in part have been due to the stress of being captured and the processing for parasites prior to urine collection. Handling has been found to be an acute stressor for many different taxa of animals (Hargreaves & Hutson 1990; Heinrichs & Koob 2006; Bayazit 2009; Narayan *et al.* 2013). Acute stress can result in C manifesting itself within minutes and can remain in circulation, at least in the plasma, for many hours or until the animal is stressed again (Espelid *et al.* 1996; Reburn & Wynne-Edwards 2000; Cockrem 2013). However, for urinary cortisol there is a much longer delay in measurable levels of increases than for plasma, from a few hours (> 12) to a day or two's delay for the increase to be noted (Bayazit 2009; Schubert *et al.* 2012; Fanson *et al.* 2013). This suggests that it is unlikely for capture and handling stress to be solely responsible for the high cortisol levels in our species. Instead, the high parasite burdens may have contributed to the high C concentrations and lack of variation. In general persistently high concentrations of glucocorticoids are associated with a large number of negative effects (Sapolsky *et al.* 2000; Romero 2004). When taken into account that hosts and their parasites co-evolve, it makes sense that hosts must adapt to infestation (Combes 2001; Morand *et al.* 2006). Therefore it could be reasoned that it would be evolutionary unstable for the host to develop physiological responses that are likely to cause damage to itself, even in response to something perceived as negative. Consequently natural levels of parasitic infestation may not directly correlate with chronic secretions or increases of glucocorticoids, as demonstrated in a study by Lutermann *et al.* (2012b) who investigated highveld mole-rats. They found that natural infections already present in captured mole-rats did not correlate to host cortisol concentrations. Eastern rock sengis harbour a large number of ectoparasites naturally in wild populations (see chapter 2) and this persistent stressor may account for the consistently elevated cortisol levels observed. This could explain the lack of a direct significant interaction with cortisol and parasite abundances as well as the non-significant effects on C in general. Other studies have found high concentrations of cortisol with parasite abundances (Wilson *et al.* 1993; Da Silva 1999; Miller *et al.* 2006). As such, increased concentrations of cortisol for extended periods of time are negatively associated with the longevity and fitness of the animal, which has been found to be associated with animals harbouring large abundances of parasites (Morand *et al.* 2006; Hoby *et al.* 2006; Clough *et al.* 2010). Previous data for the study area suggest that individuals in the study population rarely live beyond one year while sengis can reach substantially higher ages in captivity (Medger *et al.* 2102, S. Hoffmann, pers. obs.) possibly indicating some costs to the continuously elevated cortisol levels in the study population. In addition but not mutually exclusive, other factors may also have contributed to the high C concentrations observed. Reproduction is one of the most energetically costly life-history traits and as such there is the potential for increases in glucocorticoids in response to reproductive investment (Kubokawa *et al.* 1999; Lynch *et al.* 2002; Manire *et al.* 2007; Hews & Abell Baniki 2013). Due to the long breeding period in eastern rock sengis (8 months as defined by Medger *et al.* 2012). It is possible that the C concentrations of the females may have remained elevated due to the costs of a long gestation and lactation period which could also have masked any personality effects.

For T we found a significant effect of sex and season. We found females to have higher T concentrations than males. Most studies that investigate T concentrations tend to use only males and as such direct comparisons between sexes are not usually made (Faulkes & Abbott 1991; Chandler *et al.* 1994; Saino & Møller 1994; Peters 2000; Schulte-Hostedde & Patterson 2011; Medger *et al.* 2011; Apfelbeck *et al.* 2013). This stems mainly from the assumption that T is more important in males due to the development and maintenance of secondary sexual traits such as brightly coloured plumage and larger antlers (Folstad & Karter 1992; Zuk & McKean 1996). However, there are those that investigate female T concentrations in relation to their males and one such animal under scrutiny is the hyrax (*Procavia capensis*), a phylogenetically related small mammal to our study species. Koren *et al.* 2006 found that female hyraxes have either similar or higher T concentrations than males and the social group of a single male with a harem of females was dominated by a female or two although the reasons for this remain obscure. What is an exciting thought to entertain is the possibility of a phylogenetic link to females having higher T than males in ours and related species although more study is required to determine for which species of Afrotheria this relationship may hold true.

Sengis are monogamous and have a longer breeding period than many small mammals which could account for males not having higher T concentrations as suggested in the challenge hypothesis (Wingfield *et al.* 1990). In the challenge hypothesis, Wingfield *et al.* (1990) proposed a correlation between testosterone, intra-sexual competition and aggression in adult male animals. Territory defence is a behavioural trait usually associated with higher T in males; who traditionally guard territories and their mates more aggressively (Moore 1984; Salvador *et al.* 1997; Seivwright *et al.* 2005). Wingfield *et al.* (1990) also made the distinction however that T concentrations are likely linked to the mating system. Although some evidence for increased aggression and testosterone has been found in mammals, such as ring-tailed lemurs, *Lemur catta* (Cavigelli & Pereira 2000) it was mainly proposed on the review of polygynous seasonal breeders in bird, reptiles and fish studies. Higher T levels, however, may also interfere with paternal care, hence why increased T and aggression is more often correlated in polygynous species during breeding seasons than might be expected for monogamous species (Wingfield *et al.* 1990). Territory defence in sengis has been noted for females in the golden-rumped sengi, *Rhynchocyn chrysopygu*s*,* as well as the males (Rathbun 1978; Fitzgibbon 1997) which may explain the elevated concentrations of T in a species where females are required to defend young and resources from other females. Sengis exhibit a parental care system in which the female leaves the young for extended periods of time, coming back only occasionally to feed which is a trait shared amongst all species of sengi (Rathbun 1979; Ribble & Perrin 2005). Alternatively, but not mutually exclusive, the low male T levels are probably a result of the monogamous mating system of our study species, which is different to most studies investigating the challenge hypothesis (Wingfield *et al.* 1990; Cavigelli & Pereira 2000) and may account for the higher T concentrations in female sengis.

As with the C concentrations, the T concentrations remained remarkably stable throughout the study period and we only found a significant increase in T during March/April 2013. This would coincide with young animals leaving their mother's territory and attempting to establish their own home ranges (Fitzgibbon 1997). Sengis have a long breeding season which typically occurs during the wet season in our study area (September – March, Medger *et al.* 2012) and we expected T to peak during or just before the breeding season as the general consensus is that testosterone supports physiological and behavioural adaptations to heighten fecundity in males (Hau *et al.* 2010). Male sengis have plasma T concentrations which peak in July (Medger *et al.* 2012) and are immeasurable for the large parts of the year. The seasonal pattern observed in the current study may be a result of increased survival of treated individuals due to their improved body condition (see chapter 2). If the improved body condition translated in higher survival of treated individuals fewer vacancies would have been available when young were recruited into the population in March 2013. This would result in a greater amount of interaction between conspecifics and a concomitant increase in aggressive behaviours between animals, both of which has been linked to elevated T as mentioned previously (Silverin 1998; Höjesjö *et al.* 2004; Boon *et al.* 2007; Cote *et al.* 2010). A possible reason for not observing this same peak during our initial trapping period, also March of the previous year, could be that animals had not been treated with Frontline® yet. This hypothesis should be addressed in future studies.

We found no significant effect of personality on either C or T concentration. Few studies have investigated whether a link between personality and steroid hormones exists although theoretically it is predicted that this may be the case (Coppens *et al.* 2010; While *et al.* 2010). Most research to date on this topic has been done on fish and birds, but much less so in mammals (reviewed in Cote *et al.* 2010; Mashburn *et al.* 2012; Montiglio *et al.* 2012; Seltmann *et al.* 2012). In wild eastern chipmunks, *Tamias striatus*, Montiglio *et al.* (2012) found that personality was only weakly correlated with variability of cortisol concentrations in their animals and was not linked to mean cortisol concentrations over the study period. If a comparable pattern exists in sengis as well this may explain the lack of significance in our study since we looked at mean cortisol concentrations and not individual variation which, with further investigation, may demonstrate different patterns. In addition, the factors discussed earlier (i.e. consistently high parasite burdens and extended reproductive investment) may have affected the C levels in the study animals and masked any possible correlations between personality and C concentrations.

The levels of T have been linked to aggressive and dispersal behaviours in a large number of studies however, these have been mostly carried out in birds and reptiles (Silverin 1980, 1998; Koolhaas *et al.* 1999; Silverin *et al.* 2004; Boon *et al.* 2007; Cote *et al.* 2010), while comparatively few studies have looked at this correlation in mammals. We did not find the same significant correlation with increased T and aggressive personality measures as has been suggested by others. A large number of studies on varying T concentrations and associated aggressive behavioural responses are done on species where breeding is restricted to short periods of times and males need only fight for or guard females while sexually receptive (Moore 1984; Wingfield *et al.* 1990; Cavigelli & Pereira 2000; Schurch & Heg 2010; Zipser *et al.* 2013). Consequently, male T levels may generally be low while year-round territoriality is associated with high T levels because frequent elevations in both sexes in response to territorial interactions may be mediated by hormones other than T (Levin & Wingfield 1992). The extended period where males need to defend mates and territories, as well as females being required to obtain food for reproduction may have resulted in less variation in T and therefore showed no significant effect on personality. Only the second most prevalent and abundant tick species was significantly affected by T concentration. *Rc. nuttalli* decreased with increasing T which is the opposite trend as would be suggested by the immunocompetence handicap hypothesis (Folstad & Karter 1992). However, the immunocompetence handicap hypothesis has received mixed support from investigations on wild populations of animals with many non-avian animals showing no significant effect of T on parasite load (Salvador *et al.* 1997; Oppliger *et al.* 2004; Owen *et al.* 2004; Ezenwa *et al.* 2012). The lack of effect of T on the abundant ectoparasite species may be due to the high load of these ectoparasites the animals are continuously exposed to. As suggested by Morand *et al.* (2006) and discussed in chapters 1 and 2, due to the co-evolution of parasites and their hosts it would make sense from an adaptive point of view that both are able to co-exist due to continued exposure to one another and the need parasites have for their hosts. This may also explain the lack of significant results of T on louse abundance as *N. elephantuli* appears to prefer *Elephantulus* spp. exclusively (Durden & Musser 1994; Fourie *et al.* 1995).

Overall for parasite abundances we found that the effect of season to remain for *R. warburtoni* and chiggers which is to be expected based on our previous chapters. Seasonality and other factors affecting parasite abundances will not be discussed in great detail as this has been covered in our previous chapters. We did however find a significant effect of *R. warburtoni* on body condition which was not present in the first chapter. This could be due to a smaller sample size being used in this part of the study as opposed to the sample being used in the first chapter. That being said though *R. warburtoni* followed the pattern expected in that larger abundances of ticks was found on sengis with poorer body condition (Morand *et al.* 2006; Turner *et al.* 2012). This can often translate into an animal with a large parasite burden having decreased body condition compared to less parasitized hosts in the population (Turner *et al.* 2012). By looking at the entire ectoparasite community this study showed that it is necessary to differentiate between parasites and investigate more than one species when addressing questions with regards to the complex interactions between T and parasite burdens. Depending on the ectoparasite we looked at we found different results and this is a factor often overlooked in many studies.

In conclusion we found little seasonal variation in either C or T concentrations but C concentrations were remarkably high while the opposite was true for T. The cause of this elevated C is not clear although the high abundances of ectoparasites throughout the year coupled with the long breeding season of this species may account for this observation. In contrast, higher T concentrations in female compared to male sengis may be linked to the monogamous mating system as well as the year-round territorial defence by both sexes. The latter may also account for the increased levels of T during the last capture period if our anti-parasite treatment resulted in improved survival and a reduced number of vacant territories for dispersing offspring. This as well as the large parasite burdens may furthermore account for the lack of correlations between personality measures and steroid hormone concentrations and studies in other monogamous species should address this possibility. Only one of the four parasite species considered showed a correlation with the T levels highlighting the need to consider more than one parasite species. Overall we found little support for the frequently hypothesised relationships between personality, parasites and steroid hormones and suggest that future studies explicitly consider mating system as well as multiple parasite species when addressing similar questions.

## References

**Ansar Ahmed, S., Penhale, W. J. & Talal, N.** 1985. Sex hormones, immune responses, and autoimmune diseases. *The American Journal of Pathology*, **121**, 531–551.

**Apfelbeck, B., Mortega, K., Kiefer, S., Kipper, S., Vellema, M., Villavicencio, C. P., Gahr, M. & Goymann, W.** 2013. Associated and disassociated patterns in hormones, song, behavior and brain receptor expression between life-cycle stages in male black redstarts, *Phoenicurus ochruros*. *General and Comparative Endocrinology*, **184**, 93–102.

**Archard, G. A. & Braithwaite, V. A.** 2010. The importance of wild populations in studies of animal temperament. *Journal of Zoology*, **281**,

**Barton, B. A., Schreck, C. B. & Barton, L. D.** 1987. Effects of chronic cortisol administration and daily acute stress on growth, physiological conditions, and stress responses in juvenile rainbow trout. *Diseases of Aquatic Organisms*, **2**, 173–185.

**Bayazit, V.** 2009. Evaluation of cortisol and stress in captive animals. *Australian Journal of Basic and Applied Sciences*, **3**, 1022–1031.

**Boon, A. K., Réale, D. & Boutin, S.** 2007. The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecology Letters*, **10**, 1094–1104.

**Boswell, T., Woods, S. C. & Kenagy, G. J.** 1994. Seasonal changes in body mass, insulin, and glucocorticoids of free-living golden-mantled ground squirrels. *General and Comparative Endocrinology*, **96**, 339–346.

**Brillaud, E., Morillion, D. & De Seze, R.** 2005. Modest environmental enrichment: effect on a radial maze validation and well being of rats. *Brain Research*, **1054**, 174–182.

**Cain, K. E. & Ketterson, E. D.** 2013. Costs and benefits of competitive traits in females : aggression, maternal care and reproductive success. *PLoS ONE*, **8**, e77816.

**Cavigelli, S. A. & Pereira, M. E.** 2000. Mating season aggression and fecal testosterone levels in male ring-tailed lemurs (*Lemur catta*). *Hormones and Behavior*, **37**, 246–255.

**Chandler, C. R., Ketterson, E. D., Nolan Jr, V. & Ziegenfus, C.** 1994. Effects of testosterone on spatial activity in free-ranging male dark-eyed juncos, *Junco hyemalis*. *Animal Behaviour*, **47**, 1445–1455.

**Clough, D., Heistermann, M. & Kappeler, P. M.** 2009. Individual facial coloration in male *Eulemur fulvus rufus*: a condition-dependent ornament? *International Journal of Primatology*, **30**, 859–875.

**Clough, D., Heistermann, M. & Kappeler, P. M.** 2010. Host intrinsic determinants and potential consequences of parasite infection in free-ranging red-fronted lemurs (*Eulemur fulvus rufus*). *American Journal of Physical Anthropology*, **142**, 441–52.

**Cockrem, J. F.** 2013. Corticosterone responses and personality in birds: individual variation and the ability to cope with environmental changes due to climate change. *General and Comparative Endocrinology*, **190**, 156–163.

**Combes, C.** 2001. *Parasitism: The ecology and evolution of intimate interactions.* USA: University of Chicago Press.

**Coppens, C. M., de Boer, S. F. & Koolhaas, J. M.** 2010. Coping styles and behavioural flexibility: towards underlying mechanisms. *Philosophical Transaction of the Royal Society B*, **365**, 4021–4028.

**Cote, J., Clobert, J., Brodin, T., Fogarty, S. & Sih, A.** 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transaction of the Royal Society B*, **365**, 4065–4076.

**Da Silva, J. A. P.** 1999. Sex hormones and gluocorticoids: interactions with the immune system. *Annals of the New York Academy of Sciences*, **876**, 102–118.

**DeNardo, D. F. & Sinervo, B.** 1994. Effects of steroid hormone interaction on activity and home-range size of male lizards. *Hormones and Behavior*, **28**, 273–287.

**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**, 30–50.

**Durden, L. A. & Musser, G. G.** 1994. The mammalian hosts of the sucking lice (Anoplura) of the world: a host-parasite list. *Bull Soc Vect Ecol*, **19**, 130–168.

**Esch, G. W. & Hazen, T. C.** 1980. Stress and body condition in a population of largemouth bass: implications for red-sore disease. *Transactions of the American Fisheries Society*, **109**, 532–536.

**Espelid, S., Lokken, G. B., Steiro, K. & Bogwald, J.** 1996. Effects of cortisol and stress on the immune system in Atlantic salmon (*Salmo salar L.*). *Fish and Shellfish Immunology*, **6**, 95–110.

**Ezenwa, V. O., Stefan Ekernas, L. & Creel, S.** 2012. Unravelling complex associations between testosterone and parasite infection in the wild. *Functional Ecology*, **26**, 123–133.

**Fairhurst, G. D., Frey, M. D., Reichert, J. F., Szelest, I., Kelly, D. M. & Bortolotti, G. R.** 2011. Does environmental enrichment reduce stress? An integrated measure of corticosterone from feathers provides a novel perspective. *PLoS ONE*, **6**, e17663.

**Fanson, K. V, Lynch, M., Vogelnest, L., Miller, G. & Keeley, T.** 2013. Response to long-distance relaocation in Asian elephants (*Elephas maximus*): monitering adrenocortical activity via serum, urine, and feces. *European Journal of Wildlife Research*, **59**, 655–664.

**Faulkes, C. G. & Abbott, D. H.** 1991. Social control of reproduction in breeding and non-breeding male naked mole-rats (*Heterocephalus glaber*). *Journal of Reproduction and Fertility*, **93**, 427–435.

**Finch, C. E. & Rose, M. R.** 1995. Hormones and the physiological architecture of life history evolution. *The Quarterly Review of Biology*, **70**, 1–52.

**Finkler, H. & Terkel, J.** 2010. Cortisol levels and aggression in neutered and intact free-roaming female cats living in urban social groups. *Physiology & Behavior*, **99**, 343–347.

**Fitzgibbon, D.** 1997. The adaptive significance of monogamy in the golden-rumped elephant-shrew. *The Zoological Society of London*, **242**, 167–177.

**Folstad, I. & Karter, A. J.** 1992. Parasites, bright males, and the immunocompetence handicap. *The American Naturalist*, **139**, 603–622.

**Fourie, L. J., Du Toit, J. S., Kok, D. J. & Horak, I. G.** 1995. Arthropod parasites of elephant-shrews, with particular reference to ticks. *Mammal Review*, **25**, 31–37.

**Fourie, L. J., Horak, I. G., Kok, D. J. & Zyl, W. V. A. N.** 2002. Hosts, seasonal occurrence and life cycle of *Rhipicentor nuttalli* (Acari : Ixodidae). *Onderstepoort Journal of Veterinary Research*, **69**, 177–187.

**Gerlach, N. M. & Ketterson, E. D.** 2013. Experimental elevation of testosterone lowers fitness in female dark-eyed juncos. *Hormones and Behavior*, **63**, 782–790.

**Grear, D. A., Perkins, S. E. & Hudson, P. J.** 2009. Does elevated testosterone result in increased exposure and transmission of parasites? *Ecology Letters*, **12**, 528–37.

**Haond, C., Nolan, D. T., Ruane, N. M., Rotllant, J. & Wendelaar Bonga, S. E.** 2003. Cortisol influences the host-parasite interaction between the rainbow trout (*Oncorhynchus mykiss*) and the crustacean ectoparasite Argulus japonicus. *Parasitology*, **127**, 551–560.

**Hargreaves, A. L. & Hutson, G. D.** 1990. The stress response in sheep during routine handling procedures. *Applied Animal Behaviour Science*, **26**, 83–90.

**Hau, M.** 2007. Regulation of male traits by testosterone: implications for the evolution of vertebrate life histories. *BioEssays : News and Reviews in Molecular, Cellular and Developmental Biology*, **29**, 133–144.

**Hau, M., Ricklefs, R. E., Wikelski, M., Lee, K. a & Brawn, J. D.** 2010. Corticosterone, testosterone and life-history strategies of birds. *Proceedingsof The Royal Society B: Biological Sciences*, **277**, 3203–12.

**Heinrichs, S. C. & Koob, G. F.** 2006. Application of experimental stressors in laboratory rodents. *Current Protocols in Neuroscience*, **Chapter 8**, 8–4.

**Hews, D. K. & Abell Baniki, A. J.** 2013. The breeding season duration hypothesis : acute handling stress and total plasma concentrations of corticosterone and androgens in male and female striped plateau lizards (*Sceloporus virgatus*). *Journal of Comparative Physiology B*, **183**, 933–946.

**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.

**Hoffman, C. L., Ayala, J. E., Mas-Rivera, A. & Maestripieri, D.** 2010. Effects of reproductive condition and dominance rank on cortisol responsiveness to stress in free-ranging female rhesus macaques. *American Journal of Primatology*, **72**, 559–565.

**Hoffmann, S.** 2011. The effects of captivity, environmental enrichment and personality on memory and spatial learning in the eastern rock elephant shrew (*Elephantulus myurus*). University of Pretoria.

**Höjesjö, J., Johnsson, J. & Bohlin, T.** 2004. Habitat complexity reduces the growth of aggresive and dominant brown trout (*Salmo trutta*) relative to subordinates. *Behavioral Ecology and Sociobiology*, **56**, 286–289.

**Hopkins, M.** 1948. The host-asociations of the lice of mammals. *Proceedings of the Zoological Society of London*, **119**, 387 – 604.

**Huber, S., Palme, R. & Arnold, W.** 2003. Effects of season, sex, and sample collection on concentrations of fecal cortisol metabolites in red deer (*Cervus elaphus*). *General and Comparative Endocrinology*, **130**, 48–54.

**José, L., Barcellos, G., Carlos, L., Koakoski, G., Acosta, T., Gabriel, J. & Fagundes, M.** 2012. Fish age, instead of weight and size, as a determining factor for time course differences in cortisol response to stress. *Physiology & Behavior*, **107**, 397–400.

**Kitaysky, A. S., Wingfield, J. C. & Piatt, J. F.** 1999. Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. *Functional Ecology*, **13**, 577–584.

**Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. & Blokhuis, H. J.** 1999. Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience and Biobehavioral Reviews*, **23**, 925–935.

**Koren, L., Mokady, O. & Geffen, E.** 2006. Elevated testosterone levels and social ranks in female rock hyrax. *Hormones and Behavior*, **49**, 470–477.

**Koren, L., Nakagawa, S., Burke, T., Soma, K. K., Wynne-Edwards, K. E. & Geffen, E.** 2012. Non-breeding feather concentrations of testosterone, corticosterone and cortisol are associated with subsequent survival in wild house sparrows. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 1560–1566.

**Kubokawa, K., Watanabe, T., Yoshioka, M. & Iwata, M.** 1999. Effects of acute stress on plasma cortisol, sex steroid hormone and glucose levels in male and female sockeye salmon during the breeding season. *Aquaculture,* **172**, 335–349.

**Levin, R. N. & Wingfield, J. C.** 1992. The hormonal control of territorial aggression in tropical birds. *Ornis Scandinavica*, **23**, 284–291.

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

**Lutermann, H., Bodenstein, C. & Bennett, N. C.** 2012b. Natural parasite infection affects the tolerance but not the response to a simulated secondary parasite infection. *PloS ONE,* **7**, e52077.

**Lutermann, H., Young, A. J. & Bennett, N. C.** 2013. Reproductive status and testosterone among females in cooperative mole-rat societies. *General and Comparative Endocrinology*, **187**, 60–65.

**Lynch, J. W., Ziegler, T. E. & Strier, K. B.** 2002. Individual and seasonal variation in fecal testosterone and cortisol levels of wild male tufted capuchin monkeys, *Cebus apella nigritus*. *Hormones and Behavior*, **41**, 275–287.

**Manire, C. A., Rasmussen, L. E. L., Maruska, K. P. & Tricas, T. C.** 2007. Sex, seasonal, and stress-related variations in elasmobranch corticosterone concentrations. *Comparative Biochemistry and Physiology-Part A: Molecular & Integrative physiology*, **148**, 926–935.

**Marcogliese, D. J.** 2005. Parasites of the superorganism: Are they indicators of ecosystem health? *International Journal for Parasitology*, **35**, 705–716.

**Martin, L. B.** 2009. Stress and immunity in wild vertebrates: timing is everything. *General and Comparative Endocrinology*, **163**, 70–76.

**Medger, K., Chimimba, C. T. & Bennett, N. C.** 2011. Reproductive photoresponsiveness in male spiny mice from South Africa. *Journal of Zoology*, **1**, 1–7.

**Medger, K., Chimimba, C. T. & Bennett, N. C.** 2012. Seasonal reproduction in the eastern rock elephant-shrew: influenced by rainfall and ambient temperature? *Journal of Zoology*, **288**, 283–293.

**Meijer, M. K., Lemmens, A. G., Zutphen, B. F. M. Van & Baumans, V.** 2010. Urinary corticosterone levels in mice in response to intraperitoneal injections with saline. *Journal of Applied Animal Welfare Science*, **8**, 279–283.

**Metcalfe, N. B., Valdimarsson, S. K. & Morgan, I. J.** 2003. The relative roles of domestication, rearing environment, prior residence and body size in deciding territorial contests between hatchery and wild juvenile salmon. *Journal of Applied Ecology*, **40**, 535–544.

**Miller, M. R., White, A. & Boots, M.** 2006. The evolution of parasites in response to tolerance in their hosts: the good, the bad and apparent commensalism. *Evolution*, **60**, 945–956.

**Montiglio, P., Garant, D., Pelletier, F. & Réale, D.** 2012. Personality differences are related to long-term stress reactivity in a population of wild eastern chipmunks, *Tamias striatus*. *Animal Behaviour*, **84**, 1071–1079.

**Moore, M. C.** 1984. Changes in territorial defense produced by changes in circulating levels of testosterone: a possible hormonal basis for mate-guarding behavior in white-crowned sparrows. *Behaviour*, **88**, 215–226.

**Morand, S., Krasnov, B. R. & Poulin, R.** 2006. *Micromammals and Macroparasites From Evolutionary Ecology to Management.* Japan: Springer.

**Narayan, E. J., Cockrem, J. & Hero, J.** 2013. Changes in serum and urinary corticosterone and testosterone during short-term capture and handling in the cane toad (*Rhinella marina*). *General and Comparative Endocrinology*, **191**, 225–230.

**Neal, D. M. O., Reichard, D. G., Pavilis, K. & Ketterson, E. D.** 2008. Experimentally-elevated testosterone, female parental care, and reproductive success in a songbird, the dark-eyed Junco (*Junco hyemalis*). *Hormones and Behavior*, **54**, 571–578.

**Negro, S. S., Caudron, A. K., Dubois, M., Delahaut, P. & Gemmell, N. J.** 2010. Correlation between male social status, testosterone levels, and parasitism in a dimorphic polygynous mammal. *PloS ONE*, **5**, e12507.

**Nelson, R. & Demas, G. E.** 2013. Seasonal changes in immune function. *The Qaurterly Review of Biology*, **71**, 511–548.

**O'Connor, C. M., Nannini, M., Wahl, D. H., Wilson, S. M., Gilmour, K. M. & Cooke, S. J.** 2012. Sex-specific consequences of experimental cortisol elevation in pre-reproductive wild largemouth bass. *Journal of Experimental Zoology*, **319**, 23–31.

**Oppliger, A., Giorgi, M. S., Conelli, A. & Nembrini, M.** 2004. Effect of testosterone on immunocompetence, parasite load, and metabolism in the common wall lizard (*Podarcis muralis*). *Canadian Journal of Zoology*, **82**, 1713–1719.

**Ostner, J., Heistermann, M. & Schülke, O.** 2008. Dominance, aggression and physiological stress in wild male Assamese macaques (*Macaca assamensis*). *Hormones and Behavior*, **54**, 613–619.

**Ouyang, J. Q., Muturi, M., Quetting, M. & Hau, M.** 2013. Small increases in corticosterone before the breeding season increase parental investment but not fitness in a wild passerine bird. *Hormones and Behavior*, **63**, 776–781.

**Owen, N. T., Hasselquist, D., Wingfield, J. C. & Owen-ashley, N. T.** 2004. Androgens and the immunocompetence handicap hypothesis: unraveling direct and indirect pathways of immunosuppression in song sparrows. *The American Naturalist*, **164**, 490–505.

**Patterson, L. D. & Schulte-Hostedde, A. I.** 2011. Behavioural correlates of parasitism and reproductive success in male eastern chipmunks, *Tamias striatus*. *Animal Behaviour*, **81**, 1129–1137.

**Peters, A.** 2000. Testosterone treatment is immunosuppressive in superb fairy-wrens, yet free-living males with high testosterone are more immunocompetent. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 883–889.

**Place, N. J. & Kenagy, G. J.** 2000. Seasonal changes in plasma testosterone and glucocorticosteroids in free-living male yellow-pine chipmunks and the response to capture and handling. *Journal of Comparative Physiology B*, **170**, 245–251.

**Rathbun, G. B.** 1978. Evolution of the rump region in the golden-rumped elephant-shrew. *Bulletin of Carnegie Museum of Natural History*, **6**, 11–19.

**Rathbun, G. B.** 1979. *The social structure and ecology of elephant-shrews.* Berlin: Parey.

**Rathbun, G. B. & Redford, K.** 1981. Pedal scent-marking in the rufous elephant-shrew, *Elephantulus rufescens*. *Journal of Mammalogy*, **62**, 635–637.

**Rathbun, G. B. & Rathbun, C. D.** 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.

**Rathbun, G. B.** 2009. Why is there discordant diversity in sengi (Mammalia : Afrotheria : Macroscelidea) taxonomy and ecology? *African Journal of Ecology*, **47**, 1–13.

**Reburn, C. J. & Wynne-Edwards, K. E.** 2000. Cortisol and prolactin concentrations during repeated blood sample collection from freely moving, mouse-sized mammals (*Phodopus* spp.). *Comparative Medicine*, **50**, 184–198.

**Ribble, D. O. & Perrin, M. R.** 2005. Social organization of the eastern rock elephant-shrew (*Elephantulus myurus*): the evidence for mate guarding. *Nature*, **135**, 167–173.

**Romero, L. M.** 2002. Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. *General and Comparative Endocrinology*, **128**, 1–24.

**Romero, L. M.** 2004. Physiological stress in ecology: lessons from biomedical research. *Trends in Ecology & Evolution*, **19**, 249–255.

**Saino, N. & Møller, A. P.** 1994. Secondary sexual characters, parasites and testosterone in the barn swallow, *Hirundo rustica*. *Animal Behaviour*, **48**, 1325–1333.

**Salvador, A., Veiga, J. P., Martín, J. & López, P.** 1997. Testosterone supplementation in subordinate, small male lizards: consequences for aggressiveness, color development, and parasite load. *Behavioral Ecology*, **8**, 135–139.

**Sapolsky, R. M., Krey, L. C. & McEwen, B. S.** 1986. The neuroendocrinology of stress and aging: the glucocorticoid cascade hypothesis. *Endocrine Reviews*, **7**, 284–301.

**Sapolsky, R. M.** 1990. Stress in the wild. *Scientific American*, **1**, 11–1236.

**Sapolsky, R. M., Romero, L. M. & Munck, A. U.** 2000. How do glucocorticoids influence stress responses? Preparative actions. *Endocrine Reviews*, **21**, 55–89.

**Schubert, M.** 2011. A summary of the social system of the round-eared sengi. *Afrotherian Conservation*, **8**, 12–13.

**Schubert, M., Ro ¨del, H. G., Pillay, N. & Holst, D. Von**. 2012. Promiscuous tendencies in the round-eared sengi: a male’s perspective. *Journal of Ethology*, **30**, 43–51.

**Schurch, R. & Heg, D.** 2010. Life history and behavioral type in the highly social cichlid *Neolamprologus pulcher*. *Behavioral Ecology*, **21**, 588–598.

**Schuurs, A. H. W. M. & Verheul, H. A. M.** 1990. Effects of gender and sex steroids immune response. *Journal of Steroid Biochemistry*, **35**, 157–172.

**Seivwright, L. J., Redpath, S. M., Mougeot, F., Leckie, F. & Hudson, P. J.** 2005. Interactions between intrinsic and extrinsic mechanisms in a cyclic species: testosterone increases parasite infection in red grouse. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 2299–2304.

**Seltmann, M. W., Öst, M., Jaatinen, K., Atkinson, S., Mashburn, K. & Hollmén, T.** 2012. Stress responsiveness, age and body condition interactively affect flight initiation distance in breeding female eiders. *Animal Behaviour*, **84**, 889–896.

**Shargal, D., Shore, L., Roteri, N., Terkel, A., Zorovsky, Y., Shemesh, M. & Steinberger, Y.** 2008. Fecal testosterone is elevated in high ranking female ibexes (*Capra nubiana*) and associated with increased aggression and a preponderance of male offspring. *Theriogenology*, **69**, 673–680.

**Silverin, B.** 1980. Effects of long-acting testosterone treatment on freeliving pied flycatchers, *Ficedula hypoleuca*, during the breeding period. *Animal Behaviour,* **28**, 906–912.

**Silverin, B.** 1998. Territorial behaviour and hormones of pied flycatchers in optimal and suboptimal habitats. *Animal Behaviour*, **56**, 811–818.

**Silverin, B., Baillien, M. & Balthazart, J.** 2004. Territorial aggression, circulating levels of testosterone, and brain aromatase activity in free-living pied flycatchers. *Hormones and behavior*, **45**, 225–234.

**Sinervo, B., Miles, D. B., Frankino, W. A., Klukowski, M. & DeNardo, D. F.** 2000. Testosterone, endurance, and Darwinian fitness: natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. *Hormones and Behavior,* **38**, 222–33.

**Skinner, J. D. & Chimimba, C. T.** 2005. Order: Macroscelidea. In: *The mammals of the southern African subregion*, Vol 2nd 3rd edn. (Ed. by D. van der Horst), pp. 22–34. Cape Town: Cambridge Univ Press.

**Soto-Gamboa, M., Villalón, M. & Bozinovic, F.** 2005. Social cues and hormone levels in male *Octodon degus* (Rodentia): a field test of the Challenge Hypothesis. *Hormones and Behavior*, **47**, 311–318.

**Turner, W. C., Versfeld, W. D., Kilian, J. W. & Getz, W. M.** 2012. Synergistic effects of seasonal rainfall, parasites and demography on fluctuations in springbok body condition. *Journal of Animal Ecology,* **81**, 58–69.

**While, G. M., Isaksson, C., McEvoy, J., Sinn, D. L., Komdeur, J., Wapstra, E. & Groothuis, T. G. G.** 2010. Repeatable intra-individual variation in plasma testosterone concentration and its sex-specific link to aggression in a social lizard. *Hormones and Behavior*, **58**, 208–213.

**Wikelski, M., Lynn, S., Breuner, C. & Wingfield C., J.** 1999. Energy metabolism, testosterone and corticosterone in white-crowned sparrows. *Journal of Comparative Physiology A,* **185**, 463–470.

**Wilson, D. S., Coleman, K., Clark, A. B. & Biederman, L.** 1993. Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology*, **107**, 250–260.

**Wilson, D. S., Clark, A., Coleman, K. & Dearstyne, T.** 1994. Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, **9**, 442–446.

**Wingfield, J. C., Hegner, R. E., Dufty Jr, A. M. & Ball, G. F.** 1990. The "Challenge Hypothesis": theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *The American Naturalist*, **136**, 829–846.

**Wingfield, J. C.** 1994. Hormone-behaviour interactions and mating systems in male and female birds. In: *The Differences Between the Sexes*, First edn. (Ed. by R. V Short & E. Balaban), pp. 469. Cambridge: Cambridge University Press.

**Ziegler, T., Hodges, K., Winkler, P. & Heistermann, M.** 2000. Hormonal correlates of reproductive seasonality in wild female hanuman langurs (*Presbytis entellus*). *American Journal of Primatology*, **51**, 119–134.

**Zipser, B., Kaiser, S. & Sachser, N.** 2013. Dimensions of animal personalities in guinea pigs. *International Journal of Behavioural biology*, **119**, 970–982.

**Zuk, M. & McKean, K. A.** 1996. Sex differences in parasite infections: patterns and processes. *International Journal for Parasitology*, **26**, 1009–1023.

# Chapter 5

## General Discussion

Personality has come to be an accepted term for the study of behavioural idiosyncrasies in non-human animals and something that used to be considered as merely a bias around the mean has come to explain much of the variation we see in populations of organisms (Svartberg & Forkman 2002). There has been an exponential rise in the number of studies investigating this phenomenon in numerous organisms, yet most studies have focussed on laboratory organisms or are done under laboratory conditions (Kurvers *et al.* 2009; Schurch & Heg 2010; Butler *et al.* 2012; Pruitt *et al.* 2012). There is also still some discord as to how to measure personality in study organisms (Carter *et al.* 2013). Many studies have relied on only a single measure for behaviour or do not have repeated measures and these are important factors to consider when evaluating and categorising the personality of an animal (Dingemanse & Wolf 2010; Stamps *et al.* 2012; Carter *et al.* 2013). In this study, three behaviours per behavioural context were used and all nine behaviours were combined to obtain a more rounded and descriptive personality measure. It was felt that this was a suitable approach since a strong relationship of behaviours across different contexts was observed, which implies distinct behavioural syndromes in the study species (Bergmüller 2010) and is often not tested. Personality was also repeatable within individuals of the population of *E. myurus* captured over a long term period. Few personality studies have determined the repeatability of their behavioural measures and those that have were either under controlled conditions or again used only single measures to explain personality in their study animal (Fucikova *et al.* 2009; Boyer *et al.* 2010). This is also one of the few studies to have measured personality in a wild population and one of the first measuring personality for a mammal in the southern hemisphere. Carter *et al.* (2012) demonstrated the importance of measuring personality in a wild population of agamas in Namibia, *Agama planiceps*, and as with this study highlights the importance of investigating different animals, not only laboratory bred individuals, using multiple behaviours. Wild populations are often overlooked due to logistics in obtaining animals and repeating measures. However much can be learnt from investigating how animals respond under natural conditions as studies have shown that laboratory conditions and habituation to novel environments may alter the natural responses of animals and give a different view of the population (Stoinski *et al.* 2003; Metcalfe *et al.* 2003) Many studies have shown that personality may significantly affect the way individuals interact with their environment and suggested that this may affect their fitness (Dall *et al.* 2004; Boon *et al.* 2008; Smith & Blumstein 2008; Fucikova *et al.* 2009). Wilson *et al.* (1994) showed that bold individuals consumed a much better diet than shy individuals in a population of pumpkin seed fish, *Lepomis gibbosus,* and as such could potentially increase their fitness. A better quality diet could increase body condition of the individual which in turn could translate into greater reproductive investment or increased growth as the animal has more resources available (Kitaysky *et al.* 1999, Tremmel & Müller 2012). We found support for a relationship between body condition and personality but not necessarily in the direction that has been suggested. The predominant hypothesis is that animals in greater body condition would be the more proactive individuals of a population (Seltmann *et al.* 2012 and references within). Conversely, we found that less proactive animals had a greater body condition. This study species is in no way the exception, since, Tremmel & Müller (2012) showed in mustard leaf beetles, *Phaedon cochleariae*, that animals with lower body masses were also bolder. The repeatability of personality measures despite being treated against parasites, suggests that it is not the influence of parasites which defines the relationship between personality and body condition, even though parasites affected body condition. Hence this suggests there is still more work that needs to be done in terms of empirical studies to find support for the theories on personality and body condition.

Another way in which personality may affect fitness is through parasite burdens. There are many ways in which parasites can potentially affect life history decisions and fitness of an individual such as by causing long term stress or inducing behavioural manipulation (Barber & Dingemanse 2010; Montiglio *et al.* 2012). The sengis in our study harbour a wide diversity of ectoparasite species, with tick as well as mite burdens constituting the greatest abundance and species richness for the study species. To date, links between personality and parasites have rarely been studied in (Boyer *et al.* 2010; Patterson & Schulte-Hostedde 2011) although it is a commonly held concept that more exploratory, bolder individuals should have greater parasite loads (reviewed in Sih *et al.* 2012). Boyer *et al.* (2010) showed that more exploratory Siberian chipmunks, *Tamias sibiricus,* had higher tick loads although the relationship was statistically weak. They used a single measure, trappability, to define exploratory personality measures and looked only at a single tick species. In contrast, I looked at the entire ectoparasite community which may account for the lack of strong relationships within our study animal. I highlighted the importance of studying the complete ectoparasite fauna on the host and their interaction with one another since community structure of parasites may determine both behavioural affects and fitness costs to the host. The apparent interspecific competition between ticks and mites as demonstrated by my data also has implication for life history of the host which is not always looked at in other studies (Rigby *et al.* 2002). Parasites affect one another and changes in community structure bring about change in costs to the host and this could explain the more complex interactions between host condition, or the lack thereof (Morand *et al.* 2006). Potentially the reason for the limited evidence for a relationship between personality and parasite burden may be linked to life-history traits of the parasite species in question. Some parasites, such as ticks, may spend time of host (Randolph 2004) altering the abundances while parasites, such as lice, may spend the entire life cycle on the host (Hopkins 1948) and interact differently with other ectoparasites. This constant change in dynamics may make a relationship harder to demonstrate. Differences in abundances or the intraspecific interactions between species are factors that are rarely taken into account.

As with individual differences in behaviour individuals within the same species may differ in their circulating hormone profiles (While *et al.* 2010). Hence it has been proposed that personality can potentially be shaped by these circulating hormone concentrations (Cote *et al.* 2010; Montiglio *et al.* 2012). Most studies to date have focussed on corticosteroids (cortisol and corticosterone); specifically in animals selected for their stress responses such as lab rodents, tits and salmon (Archer 1973; Barton *et al.* 1987; Dingemanse & Réale 2005; Grear *et al.* 2009; Carere *et al.* 2010). The evidence for testosterone is scarce with few studies investigating this hormone outside of manipulation studies, such as artificial increases using hormone implants (Moore 1984; Salvador *et al.* 1997; Clotfelter *et al.* 2004). Most studies have also been mainly conducted in the northern hemisphere on species which are promiscuous or polygynous seasonal breeders which could explain the strong correlations with increases in circulating hormones and increased aggression or avoidance behaviour during the breeding season specifically (Wilson *et al.* 1993; Cavigelli & Pereira 2000; Guinn Sellers *et al.* 2007; While *et al.* 2010; Mashburn *et al.* 2012). This study on the other hand found very little variation in the urinary glucocorticoids of the sengis. The cortisol (C) levels were consistently high amongst the entire population. This may be due to the chronic parasite infestations sustained by *E. myurus.* Given the heavy parasite burdens found by myself and others (Lutermann *et al.* 2011; Harrison *et al.* 2013) these parasites can be expected to have a significant effect as demonstrated by the observed changes since controlling for parasite burdens affected the body condition of *E. myurus*. My current findings on parasite abundances and circulating C revealed similar trends in studies by Grutter & Pankhurst (2000); Lutermann *et al.* (2012) and Archer (2013). The long held common assumption that large parasite abundance should be associated with increased levels of C in those individuals with higher abundances is not always the case. Similarly, the testosterone (T) levels showed little variation with regards to personality and parasites. A contributing factor may be the unique and different mating system employed by eastern rock sengis compared to most species used in studies investigating the relationship between parasite burden and T. Whereas most studies demonstrate correlations with regards to seasonal aggression linked specifically to breeding season in polygynous or promiscuous animals, our study species is monogamous and both males and females defend home ranges year round (Ribble & Perrin 2005). Their breeding season is also longer than that of most small mammals studied in the northern hemisphere. This suggests that studies should take note of the mating systems when looking at such correlations as these may determine the likelihood of strong relationships being found, leading to the incorrect assumption that the pattern holds for all species.

This study also highlighted the importance of re-evaluating T as a male-specific hormone as we found that female sengis had higher levels of T than their male counterparts. Many studies which have measured T either measure only male T levels (Faulkes & Abbott 1991; Salvador *et al.* 1997; Oppliger *et al.* 2004; Seivwright *et al.* 2005; Negro *et al.* 2010) or manipulate female testosterone levels (Clotfelter *et al.* 2004; Neal *et al.* 2008; Gerlach & Ketterson 2013). This suggests that there is a lack of research on naturally occurring levels of T in wild populations and the implications thereof for individuals. Many studies focus on those species which have clear differences in mating expectations of the difference sexes and their territoriality. Our study shows that restricting measurements of T to males or artificially elevating female T levels may not be the only relevant approach when determining personality effects.

Overall this study challenged some of the heavily promoted hypotheses in terms of personality and its implications. This may be partially due to the unique study model used in the current study. The lack of studies on southern African mammals and monogamous wild populations in general also highlights that there is still much to be gleaned from investigating this concept in exotic species outside of controlled laboratory conditions. Also our study species is an ancient order, Macroscelidea, belonging in the supergroup Afrotheria. They may reveal insight into early patterns in mammal evolution with regards to personality and may shed light on the evolutionary forces that have shaped the evolution of behavioural traits in phylogenetically younger mammal species. Personality is a new and exciting field in animal behaviour and is being applied more and more to a range of research fields. This study adds to our current knowledge on the concept and highlights a number of areas which have been understudied as well as commenting on both the theoretical framework and data collection methods which may need adjustments based on the life-history of the animal.

## References

**Archer, J.** 1973. Tests for emotionality in rats and mice: a review. *Animal Behaviour*, **21**, 205–235.

**Archer, E.** 2013. The effects of rainfall and sociality on host-parasite dynamics in the common mole-rat, *Cryptomys hottentotus hottentotus* (Lesson 1812). Masters Thesis, University of Pretoria.

**Barber, I. & Dingemanse, N. J.** 2010. Parasitism and the evolutionary ecology of animal personality. *Philisophical Transaction of the Royal Society B: Biological Sciences*, **365**, 4077–4088.

**Barton, B. A., Schreck, C. B. & Barton, L. D.** 1987. Effects of chronic cortisol administration and daily acute stress on growth, physiological conditions, and stress responses in juvenile rainbow trout. *Diseases of Aquatic Organisms*, **2**, 173–185.

**Bergmüller, R.** 2010. Animal personality and behavioural syndromes. In: *Animal Behaviour - Evolution and Mechanisms*, 1st edn. (Ed. by Peter Kappeler), pp. 587–621. Berlin Heidelberg: Springer.

**Boon, A. K., Réale, D. & Boutin, S.** 2008. Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*. *Oikos*, **117**, 1321–1328.

**Boyer, N., Réale, D., Marmet, J., Pisanu, B. & Chapuis, J. L.** 2010. Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus*. *Journal of Animal Ecology*, **79**, 538–47.

**Butler, M. W., Toomey, M. B., Rowe, M. & McGraw, K. J.** 2012. Ontogenetic immune challenges shape adult personality in mallard ducks. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 326–333.

**Carere, C., Caramaschi, D. & Fawcett, T. W.** 2010. Covariation between personalities and individual differences in coping with stress : Converging evidence and hypotheses. *Current Zoology*, **56**, 728–740.

**Carter, A. J., Heinsohn, R., Goldizen, A. W. & Biro, P. A.** 2012. Boldness, trappability and sampling bias in wild lizards. *Animal Behaviour*, **83**, 1051–1058.

**Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlishaw, G. & Heinsohn, R.** 2013. Animal personality: what are behavioural ecologists measuring? *Biological Reviews of the Cambridge Philosophical Society*, **88**, 465–75.

**Cavigelli, S. A. & Pereira, M. E.** 2000. Mating season aggression and fecal testosterone levels in male ring-tailed lemurs (*Lemur catta*). *Hormones and Behavior*, **37**, 246–255.

**Clotfelter, E. D., O'Neal, D. M., Gaudioso, J. M., Casto, J. M., Parker-Renga, I. M., Snajdr, E. A., Duffy, D. L., Jr, V. N. & Ketterson, E. D.** 2004. Consequences of elevating plasma testosterone in females of a socially monogamous songbird: evidence of constraints on male evolution? *Hormones and Behavior*, **46**, 171–178.

**Cote, J., Clobert, J., Brodin, T., Fogarty, S. & Sih, A.** 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philisophical Transaction of the Royal Society B: Biological Sciences*, **365**, 4065–4076.

**Dall, S. R. X., Houston, A. I. & McNamara, J. M.** 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, **7**, 734–739.

**Dingemanse, N. J. & Réale, D.** 2005. Natural selection and animal personality. *Behaviour*, **142**, 1159–1184.

**Dingemanse, N. J. & Wolf, M.** 2010. Recent models for adaptive personality differences: a review. *Philisophical Transaction of the Royal Society B: Biological Sciences*, **365**, 3947–3958.

**Faulkes, C. G. & Abbott, D. H.** 1991. Social control of reproduction in breeding and non-breeding male naked mole-rats (*Heterocephalus glaber*). *Journal of Reproduction and Fertility*, **93**, 427–435.

**Fourie, L. J., Horak, I. G. & van den Heever, J. J.** 1992. The relative importance of rock elephant shrews *Elephantulus myurus* and Namaqua rock mice *Aethomys namaquensis* for economically important ticks. *South African Journal of Zoology*, **27**, 108–114.

**Fucikova, E., Drent, P. J., Smits, N. & van Oers, K.** 2009. Handling stress as a measurement of personality in great tit nestlings (*Parus major*). *Ethology*, **115**, 366–374.

**Gerlach, N. M. & Ketterson, E. D.** 2013. Experimental elevation of testosterone lowers fitness in female dark-eyed juncos. *Hormones and Behavior*, **63**, 782–790.

**Grear, D. A., Perkins, S. E. & Hudson, P. J.** 2009. Does elevated testosterone result in increased exposure and transmission of parasites? *Ecology Letters*, **12**, 528–37.

**Grutter, A. S. & Pankhurst, N. W.** 2000. The effects of capture, handling, confinement and ectoparasite load on plasma levels of cortisol, glucose and lactate in the coral reef fish *Hemigymnus melapterus*. *Journal of Fish Biology*, **57**, 391–401.

**Guinn Sellers, J., Mehl, M. R. & Josephs, R. A.** 2007. Hormones and personality: testosterone as a marker of individual differences. *Journal of Research in Personality*, **41**, 126–138.

**Harrison, A., Bastos, A. D. S., Medger, K. & Bennett, N. C.** 2013. Ticks and tick-borne diseases eastern rock sengis as reservoir hosts of *Anaplasma bovis* in South Africa. *Ticks and Tick-borne Diseases*, **4**, 503–505.

**Hopkins, M.** 1948. The host-associations of the lice of mammals. *Proceedings of the Zoological Society of London*, **119**, 387 – 604.

**Kitaysky, A. S., Wingfield, J. C. & Piatt, J. F.** 1999. Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. *Functional Ecology*, **13**, 577–584.

**Kurvers, R. H. J. M., Eijkelenkamp, B., Van Oers, K., van Lith, B., van Wieren, S. E., Ydenberg, R. C. & Prins, H. H. T.** 2009. Personality differences explain leadership in barnacle geese. *Animal Behaviour*, **78**, 447–453.

**Lutermann, H., Medger, K. & Horak, I. G.** 2011. Abiotic and biotic determinants of tick burdens in the eastern rock sengi (*Elephantulus myurus*). *Medical and Veterinary Entomology*, **26**, 1–9.

**Lutermann, H., Bodenstein, C. & Bennett, N. C.** 2012. Natural parasite infection affects the tolerance but not the response to a simulated secondary parasite infection. *PloS ONE*, **7**, e52077.

**Mashburn, K., Öst, M., Seltmann, M. W., Atkinson, S., Jaatinen, K. & Hollmén, T.** 2012. Stress responsiveness, age and body condition interactively affect flight initiation distance in breeding female eiders. *Animal Behaviour*, **84**, 889–896.

**Metcalfe, N. B., Valdimarsson, S. K. & Morgan, I. J.** 2003. The relative roles of domestication, rearing environment, prior residence and body size in deciding territorial contests between hatchery and wild juvenile salmon. *Journal of Applied Ecology*, **40**, 535–544.

**Montiglio, P., Garant, D., Pelletier, F. & Réale, D.** 2012. Personality differences are related to long term stress reactivity in a population of wild eastern chipmunks, *Tamias striatus*. *Animal Behaviour*, **84**, 1071–1079.

**Moore, M. C.** 1984. Changes in territorial defense produced by changes in circulating levels of testosterone: a possible hormonal basis for mate-guarding behavior in white-crowned sparrows. *Behaviour*, **88**, 215–226.

**Morand, S., Krasnov, B. R. & Poulin, R.** 2006. *Micromammals and Macroparasites From Evolutionary Ecology to Management.* Japan: Springer.

**Neal, D. M. O., Reichard, D. G., Pavilis, K. & Ketterson, E. D.** 2008. Experimentally-elevated testosterone, female parental care, and reproductive success in a songbird, the Dark-eyed Junco (*Junco hyemalis*). *Hormones and Behavior*, **54**, 571–578.

**Negro, S. S., Caudron, A. K., Dubois, M., Delahaut, P. & Gemmell, N. J.** 2010. Correlation between male social status, testosterone levels, and parasitism in a dimorphic polygynous mammal. *PloS ONE*, **5**, e12507.

**Oppliger, A., Giorgi, M. S., Conelli, A. & Nembrini, M.** 2004. Effect of testosterone on immunocompetence, parasite load, and metabolism in the common wall lizard (*Podarcis muralis*). *Canadian Journal of Zoology*, **82**, 1713–1719.

**Patterson, L. D. & Schulte-Hostedde, A. I.** 2011. Behavioural correlates of parasitism and reproductive success in male eastern chipmunks, *Tamias striatus*. *Animal Behaviour*, **81**, 1129–1137.

**Pruitt, J. N., Burghardt, G. M. & Riechert, S. E.** 2012. Non-conceptive sexual behavior in spiders: a form of play associated with body condition, personality type, and male intrasexual selection. *Ethology*, **118**, 33–40.

**Randolph, S. E.** 2004. Tick ecology: processes and patterns behind the epidemiological risk posed by ixodid ticks as vectors. *Parasitology*, **129**, 37–65.

**Ribble, D. O. & Perrin, M. R.** 2005. Social organization of the eastern rock elephant-shrew (*Elephantulus myurus*): the evidence for mate guarding. *Nature*, **135**, 167–173.

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

**Salvador, A., Veiga, J. P., Martín, J. & López, P.** 1997. Testosterone supplementation in subordinate, small male lizards: consequences for aggressiveness, color development, and parasite load. *Behavioral Ecology*, **8**, 135–139.

**Schurch, R. & Heg, D.** 2010. Life history and behavioral type in the highly social cichlid *Neolamprologus pulcher*. *Behavioral Ecology*, **21**, 588–598.

**Seivwright, L. J., Redpath, S. M., Mougeot, F., Leckie, F. & Hudson, P. J.** 2005. Interactions between intrinsic and extrinsic mechanisms in a cyclic species: testosterone increases parasite infection in red grouse. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 2299–2304.

**Seltmann, M. W., Öst, M., Jaatinen, K., Atkinson, S., Mashburn, K. & Hollmén, T.** 2012. Stress responsiveness, age and body condition interactively affect flight initiation distance in breeding female eiders. *Animal Behaviour*, **84**, 889–896.

**Sih, A., Cote, J., Evans, M., Fogarty, S. & Pruitt, J.** 2012. Ecological implications of behavioural syndromes. *Ecology letters*, **15**, 278–89.

**Smith, B. R. & Blumstein, D. T.** 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, **19**, 448–455.

**Stamps, J. A., Briffa, M. & Biro, P. A.** 2012. Unpredictable animals: individual differences in intraindividual variability (IIV). *Animal Behaviour*, **83**, 1325–1334.

**Stoinski, T. S., Beck, B. B., Bloomsmith, M. A. & Maple, T. L.** 2003. A behavioral comparison of captive-born, reintroduced golden lion tamarins and their wild-born offspring. *Behaviour*, **140**, 137–160.

**Svartberg, K. & Forkman, B.** 2002. Personality traits in the domestic dog (*Canis familiaris*). *Applied Animal Behaviour Science*, **79**, 133–155.

**Tremmel, M. & Müller, C.** 2012. Insect personality depends on environmental conditions. *Behavioral Ecology*, **24**, 386–392.

**While, G. M., Isaksson, C., McEvoy, J., Sinn, D. L., Komdeur, J., Wapstra, E. & Groothuis, T. G. G.** 2010. Repeatable intra-individual variation in plasma testosterone concentration and its sex-specific link to aggression in a social lizard. *Hormones and Behavior*, **58**, 208–213.

**Wilson, D. S., Coleman, K., Clark, A. B. & Biederman, L.** 1993. Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology*, **107**, 250–260.

**Wilson, D. S., Clark, A., Coleman, K. & Dearstyne, T.** 1994. Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, **9**, 442–446.


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