Abiotic and biotic determinants of tick burdens in the eastern rock sengi (*Elephantulus myurus*)

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Abstract

Ticks are important vectors of pathogens of medical and veterinary importance worldwide. Despite their economic importance our current knowledge about the factors affecting tick prevalence and abundance in tropical and subtropical regions is rather limited. Both abiotic (e.g. temperature) as well as biotic variables (e.g. host sex) have been identified as key determinants of distributions. Eastern rock sengis or elephant shrews (*Elephantulus myurus*, Thomas & Schwann) are widely distributed throughout Africa and can harbour a large number of tick species and substantial tick burdens. In the current study we evaluated the contribution of climate and host factors on tick burdens of sengis. Throughout the year sengis carried high abundances of immature stages of a single tick species, *Rhipicephalus* sp. near *warburtoni*. There was no evidence that host parameters affected tick burdens. However, larval abundance decreased with increasing ambient temperatures and both larvae and nymphs were negatively affected by rainfall two months prior to the sampling month. In addition, nymphal burdens decreased with increasing minimum temperatures. Our results suggest that climate factors are the largest constraint for the immature stages of *R.* sp. near *warburtoni* and that eastern rock sengis could play a crucial role in the dynamics of tick-borne diseases due to the large tick burdens they can sustain.

Keywords: Macroscelidea, *Rhipicephalus*, tick burden, tick-borne disease

Introduction

Ticks are the most important arthropod vector of pathogenic microorganisms of medical and veterinary importance and transmit a range of pathogens including viruses, rickettsiae, spirochaetes and protozoa (Jongejan & Uilenberg 2004). In the northern hemisphere ticks of the genus *Ixodes* play a key role in emerging zoonotic diseases that affect human health and transmit species of *Borrelia*, *Babesia* and *Anaplasma* as well as the virus responsible for tick borne encephalitis (e.g. Labuda & Nuttall 2004, Bowman & Nuttall 2008). Accordingly, there are a multitude of studies examining factors that affect the prevalence and abundance of medically important ticks in this hemisphere including the effects of climate and the role of small mammals as hosts for the immature stages of ticks (e.g. Brunner & Ostfeld 2008, Harrison et al. 2010, Kiffner et al. 2011).

Unlike in the northern hemisphere, in tropical and subtropical regions tick-borne diseases, paralysis and toxicosis pose considerable economical threats due to their impact on livestock in these regions (Perry et al. 2002, Minjauw & McLeod 2003, Jongejan & Uilenberg 2004). Although exact estimates of the economic loss due to ticks remain difficult to obtain, there is a general consensus that these are substantially exacerbated because of the strong dependence of local livelihoods on ruminant farming (Mukhebi et al. 1999, Minjauw & McLeod 2003, Kivara 2006). In the Afrotropical region alone at least 175 ixodid tick species belonging to nine genera are endemic and species of the genera *Amblyomma*, *Hyalomma*, *Ixodes* and *Rhipicephalus* are of economic importance because of their impact on domestic livestock husbandry (Spickett & Heyne 1988, Walker et al. 2000, Norval & Horak 2004). The immature stages of at least 30 species of these four genera and eight species belonging to other genera make use practically exclusively of small mammals as hosts. A number of studies have been devoted to recording the small mammal hosts of economically important ticks (Horak et al. 1993, Fourie et al. 1992, 2002, 2005; Petney et al. 2004; Matthee et al. 2007), however, there is still a need for research examining factors that affect the prevalence

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and abundance of ticks on these hosts. Such studies are needed as a basis for improvements in management policies of the threats they pose.

Throughout their life-cycle, ticks spend the majority of time off their hosts. During this time they are faced with the risk of desiccation and high temperatures as well as low humidity that can pose severe constraints to their activity and survival (Needham & Teel 1991, Sonenshine 1993, Benoit & Denlinger 2010). These constraints can shape seasonal patterns of tick prevalence and abundance (Randolph 1997, Brunner & Ostfeld 2008). Seasonal fluctuations in tick loads, however, can also be a result of host factors. The resistance of hosts may be compromised during periods of limited nutrient availability such as during winter (Nelson et al. 2002; Altizer et al. 2006, Martin et al. 2008) leading to increases in parasite burdens during this period.

Other host factors such as host sex may further contribute to variations in tick loads. Indeed sex-biases in parasite loads are common in vertebrates and males frequently harbour larger numbers of parasites than females (Moore and Wilson 2002; Morand et al. 2004; Krasnov et al. 2005). This male-biased parasitism has been alternatively attributed to morphological, behavioural as well as physiological mechanisms. Males of many vertebrate species tend to be larger (Moore & Wilson 2002) and if this equates to a larger or more rewarding resource from a parasites perspective males may be able to sustain greater parasite numbers. Alternatively, the sexes may differ in behavioural traits such as space use and if males roam over larger areas in search of mates, the increased exposure can lead to greater tick burdens (e.g. Morand et al. 2004; Krasnov et al. 2005; Scantlebury et al. 2010). Furthermore, it has been shown that the hormone testosterone can impair the immunological response to ticks and greater numbers of ticks successfully attach and engorge on males (Hughes and Randolph 2001).

In the southern African region sengis also known as elephant shrews of the order Macroscelidea are a group of small mammals that are likely to play a role in the dynamics of

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medically and economically important tick species. This ancient order comprises 17 species and is endemic to Africa (Smit et al. 2008) suggesting a long shared evolutionary history between Macroscelidea and African tick species. Indeed, sengis can harbour the immature stages of a large variety of tick species (Fourie et al. 1995, 2005, Horak et al. 2011) and have been recorded as hosts for a number of species of veterinary importance (Walker et al. 2000, Fourie et al. 2005). These include *Ixodes rubicundus* Neumann, *Rhipicephalus warburtoni* (as an undescribed *Rhipicephalus* species, Walker et al. 2000) of which the adults can cause paralysis in small ruminants (Spickett & Heyne 1988, Fourie et al. 1988) as well as *Rhipicentor nuttali* Neumann that causes paralysis in dogs (Norval & Colborne 1985). Moreover, sengis occur sympatrically with a number of similar sized small mammal species, however, their tick burdens can be several magnitudes larger than those of sympatric rodent hosts (Fourie et al. 1992, Harrison et al. in press, H. Lutermann et al., unpublished data). This suggests that they could play an important role in the tick life-cycle and transmission of tick-borne diseases.

The entire order Macroscelidea is considered monogamous with a lack of sexual dimorphism and extensively overlapping home ranges among pairs (Rathbun 1979, FitzGibbon 1997, Rathbun and Rathbun 2006, Schubert et al. 2009). In the current study we focused on eastern rock sengis (*Elephantulus myurus* Thomas & Schwann). This species has a large distributional range stretching from Mozambique north of the Zambezi River throughout the southern and eastern parts of Zimbabwe, eastern Botswana, wide parts of north-east South Africa as well as western Swaziland (Skinner & Chimimba 2005). Like other sengi species pairs share a common home range (Ribble & Perrin 2005). No less than 12 tick species have been reported for *E. myurus* (Fourie et al. 1995, 2005) and laboratory data suggest the lack of a noticeable resistance of *E. myurus* to repeated infestations by ticks (Du Toit et al. 1994). This may render *E. myurus* a particularly competent host for ticks. The aim of the current

study was to assess seasonal patterns of tick burdens of an *E. myurus* population and evaluate the role that climate and host factors, respectively, play in generating the observed patterns.

Materials and Methods

The study was conducted at Goro Game Reserve (22°58'S, 29°25'E) in the Limpopo Province, South Africa. Sengis were collected under permit number: CPM-333-00002 issued by the Department of Environmental Affairs, Limpopo Province South Africa. Animals were trapped with Sherman live traps baited with oats, peanut butter and sardines and set overnight on rocky outcrops. Sengis were caught on a monthly basis from September 2007 to August 2008 as part of a study of their reproductive biology that aimed to collect ten individuals (five of each sex) per month (Medger 2011). For each individual the body mass was recorded to the nearest 0.1g on the day of capture using a digital balance (Scout Pro SPU123, Ohaus Corporation, USA). Animals were maintained in standard rodent cages with wood shavings as bedding. They were fed a diet of Pronutro (high protein cereal, Pioneer Foods Ltd, South Africa), canned dog food (Promeal Ltd, South Africa), meal worms as well as grated apples and carrots with water freely available.

Animals were euthanized with an overdose of halothane. All procedures were approved by the animal ethics committee of the University of Pretoria (EC028-07). The body length of each individual was measured (mm) from the neck to the base of the tail once the entire body had been searched for ticks. These were removed using tweezers and stored in 70% ethanol until identification. They were identified, counted and their developmental stage recorded as larvae, nymph or adult under a stereo-microscope (Walker et al. 2000).

Throughout the study period we measured the ambient temperature (°C) with a digital data logger (iButton, Maxim Integrated Products, Dallas Semiconductor, USA). The iButton was programmed to record ambient temperature at 2 h intervals with a resolution of 0.01°C. Temperature measurements were taken at the centre of the study area near the ground and the

iButton was shaded to protect it from solar radiation. We calculated mean monthly minimum (T_{min}) and maximum (T_{max}) temperatures by averaging the daily T_{min} and T_{max} over a month. In addition, the total monthly rainfall (mm) was obtained from the Goro Game Reserve.

Statistical analyses

The prevalence of ticks was 100% and we assessed variation in larval and nymphal tick abundances by employing a generalised linear model (GLM) with a negative binomial distribution and a log-link function with month and host sex as independent variables. Due to sample size limitations, we did not include the interaction between month and sex. Body length was added as covariate in the model. We used body length rather than body mass to exclude the confounding effects of pregnancies on body mass. Furthermore, body length was significantly correlated with body mass in non-pregnant individuals (R_S=0.374, n=96, p<0.0001). To evaluate the effects of the climate variables on tick abundance, we repeated the above analyses but instead of the variable month, the mean monthly T_{min}, T_{max} and total monthly rainfall were included as covariates in the model. Since off-host climate can affect tick survival and questing behaviour, we furthermore included rainfall data for up to three months prior to a sampling month. As temperature was only measured from the start of the sampling period, effects of prior ambient temperatures on tick abundance could not be considered in our analysis. Model selection was conducted based on the Akaike information criterion (AIC) and non-significant variables sequentially dropped from the model (Burnham & Anderson 2002). Only the minimal model is reported here and results are presented as means ± SE.

Results

Tick identification and burdens

Apart from one specimen (*Haemaphysalis elliptica*), all ticks collected belonged to a species we have chosen to designate *Rhipicephalus* sp. near *warburtoni*. We have based this identification on a comparison of adult ticks, moulted from engorged nymphs collected from the sengis, and also identical adult ticks collected from the vegetation in the Goro Game Reserve, with the adults of *Rhipicephalus warburtoni* Walker and Horak (Walker et al. 2000). Preliminary phylogenetic analysis has confirmed this relationship and places this tick within the *Rhipicephalus pravus* group of six species proposed by Walker et al. (2000). Comparison of the immature stages, collected from the sengis, with those of the six species in this group, eliminated all but those of *R. warburtoni s. str*. A total of 20664 larvae and 1670 nymphs of *R.* sp. near *warburtoni* was collected from 113 sengis (58 females, 55 males).

Climate

Mean monthly temperatures ranged from 11.8°C in July to 28.2°C in February (Figure 1). The highest T_{max} measured during the study period was 37.1°C (September) while the lowest T_{min} was 7.5°C (July). Rainfall only occurred during the months from September to April with a peak of 146 mm in December (Figure 1).

Determinants of tick abundance

Throughout the year, individual sengis harboured an average of 187.3±16.6 larvae and 14.9±1.1 nymphs of *R.* sp. near *warburtoni*. The abundance of tick larvae varied significantly with month and larval burdens were lowest during September, January and February (Table 1, Figure 2a). Larval abundance did not differ significantly between the sexes and was not affected significantly by body length (Table 1). The abundance of nymphs varied significantly with month (Table 1). Nymphal burdens were lowest in October and significantly greater in July than any other month (Figure 2b). Nymphal burdens were neither affected by host sex or body length and both variables were dropped from the final model (Table 1).

Climate effects on tick abundance

Neither sex nor body length significantly affected larval tick burdens when climate variables were included in the model (Table 2). The abundance of larvae did not significantly vary with T_{min}. However, larval abundance decreased significantly with increasing T_{max} (Figure 3a). Larval burden did not vary significantly with either rainfall in the current month or three months prior to the sampling month and the former variable was dropped from the final model (Table 2). Furthermore rainfall during the previous month did not affect larval abundances. In contrast, the abundance of tick larvae decreased significantly with increasing rainfall two months prior to the current one (Figure 3b).

The abundance of nymphs did neither differ significantly between the sexes nor did it vary with body length (Table 2). Nymphal abundance decreased significantly with increasing T_{min} (Figure 4a). Neither T_{max} nor rainfall in the current, one or three months prior to the sampling month did significantly affect nymphal tick burdens (Table 2) and the latter was dropped from the final model. In contrast, rainfall two months prior to the sampling month did significantly affect the abundance of nymphs (Figure 4b).

Discussion

In the current study, we explored the influence of host specific as well as abiotic factors (i.e. climate) on burdens of *R.* sp. near *warburtoni* on *E. myurus*. In the light of the vast diversity of ticks described for the study species the low tick diversity in our study was unexpected. However, a number of tick species recorded for sengis only occurred at very low abundances and are probably accidental (Fourie et al. 1992, 2005). In addition, all of the previous studies have been conducted on commercial farms while the current study was carried out in a game reserve and thus may affect the diversity and abundance of questing tick species. Sengis do not build nests but habitat changes caused by the grazing activity of livestock and the great

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density of potential hosts for adult ticks may affect the number of tick species a sengi can encounter in its home range.

Our results suggest that neither host sex nor body size play a significant role in determining tick burdens. This contrasts with other studies that suggest that tick burdens may increase with body size (e.g. Harrison et al. 2010, Kiffner et al. 2011). The lack of a body size effect could also explain why host sex did not influence tick loads (Moore & Wilson 2002) as the study species is not sexually dimorphic. Alternatively, sex-biases in parasite load have been linked to physiological and behavioural differences between the sexes. In the study species however, male and female home ranges largely coincide (Ribble & Perrin 2005) and male testosterone levels are undetectable for six months of the year and peak in July at low levels (Medger 2011). Other studies similarly failed to identify particular host groups that harbour particularly large numbers of ticks (e.g. host sex, Brunner & Ostfeld 2008).

The immature stages of *R.* sp. near *warburtoni* were present year-round in significant numbers and their prevalence on sengis amounted to 100% for larvae and 98.2% for nymphs similar to *R. warburtoni sensu stricto* on the study species in the Free State Province, South Africa (Fourie et al. 1992, 2005). This contrasts markedly with the complete absence of tick stages during part of the year that is characteristic for a number of well-studied tick species in the northern hemisphere (Sonenshine 1993, Randolph 2004, Brunner & Ostfeld 2008). The seasonal absence of ticks is often linked to climate factors and for some northern hemisphere ticks, activity is limited by low temperatures (Randolph et al. 2002). The mild winters in our study area meant that even during the coldest month (July) T_{min} did not fall below 10°C and thus, low temperatures do not appear to constrain the questing activity of immature stages of *R.* sp. near *warburtoni* at the study site.

Despite the lack of an apparent lower threshold temperature, our results suggest strong seasonal effects for both larvae and nymphs of *R.* sp. near *warburtoni*, and tick burdens for both stages were markedly lower during the peak of summer (i.e. February) compared to the

winter months (May-August). Similar seasonal variation in tick burdens is well documented

for other small mammals (e.g. Randolph 2004, Brunner & Ostfeld 2008, Kiffner et al. 2011).

This has been linked to abiotic factors such as temperature and humidity that can affect

hatching success as well as the survival of immature ticks (Short et al. 1989, Needham & Teel

1991, Sonenshine 1993, Randolph 1997). Indeed, our analyses of the effects of climate

variables indicate that such a relationship may also exist for the immature stages of *R*. sp. near

warburtoni. However, the data suggests that these effects vary between the different life

stages.

Larval tick burdens on sengis decreased significantly with increasing T_{max}. Assuming

that similar to other tick species the number of immature *R*. sp. near *warburtoni* found on

hosts is positively correlated with the number of questing ticks (Brunner & Ostfeld 2008), this

could imply that a smaller number of larval ticks is questing during hotter months. The greater

risk of desiccation during hotter periods is likely to be responsible for this relationship (Short

et al. 1989, Benoit & Denlinger 2010) and may constrain questing activity of larvae in this

species. This is in accordance with patterns for a number of other South African ticks where

immature stages are entirely absent during the hot summer months while larval activity peaks

in early winter (Spickett et al. 2011). However, T_{max} did not significantly predict nymph

burdens indicating that they may suffer less from the risk of desiccation. The difference in the

effect of T_{max} on the immature stages is likely to be a result of the less favourable volume to

surface ratio of larval ticks which results in larger water losses for larvae compared to nymphs

under the same climatic conditions (Short et al. 1989, Randolph 1997).

The burden of nymphal ticks decreased significantly with increasing T_{min} while this

was not the case for larvae. This unexpected finding may be a result of temperature-dependent

modifications of host behaviour and physiology. Sengis are well known for their ability to

lower their body temperature in response to low ambient temperatures (i.e. torpor, Mzilikazi

& Lovegrove 2005) and lower body temperatures could also impair the feeding ability of

ticks. In the study species, such torpor bouts increase in frequency and depth during cold periods (Mzilikazi & Lovegrove 2004) and consequently, the feeding duration of ticks may be prolonged during this period of the year. Similarly, dramatic differences in feeding durations of individual ticks have been reported depending on whether they were feeding on a mammal or reptile hosts and this has been attributed to differences in host body temperatures (e.g. Fielden et al. 1992). That this effect was only apparent for nymphs but not larvae could be linked to the larger blood meals required by the former stage (Sonenshine 1993). Indeed, while feeding times were doubled for *Amblyomma marmoreum* Koch larvae that fed on a reptilian compared to a mammalian host they increased 7-fold for nymphs (Fielden et al. 1992). Future studies should address this possibility for the current study system.

Both immature stages of *R.* sp. near *warburtoni* were affected by rainfall. Interestingly however, this was not the case for current rainfall but with a two month time lag. This strongly suggests that this relationship is mediated by off-host factors. One of the biggest threats for survival during this period is considered the risk of desiccation and accordingly, the negative correlation between rainfall and number of immature is surprising. However, in the study area precipitation peaks coincide with high ambient temperatures and these are also conditions favourable to the proliferation of fungi. Particularly during periods of impaired mobility such as during the egg stadium or shortly after moulting fungi may represent a threat to immature stages of ticks (e.g Randolph 1997). Empirical tests are needed in the future to corroborate this hypothesis.

In conclusion, our data suggest that sengis can sustain extraordinarily large tick burdens that may be particularly favourable for pathogen transmission between host and tick as well as among co-feeding ticks. Indeed, *Anaplasma bovis* Dumler (previously *Ehrlichia bovis* Donatien & Lestoquard), an organism that can cause anorexia, fever and mortality in cattle (Sumption & Scott 2004), has recently been detected in *R.* sp. near *warburtoni* (Harrison et al. in press). Furthermore, host-specific factors such as sex and body size did not

appear to affect tick burdens. However, physiological peculiarities of the eastern rock sengi (i.e. torpor, lack of immunity) may make them particularly suitable as hosts for *R.* sp. near *warburtoni*. In addition, tick burdens were strongly affected by abiotic factors that may be linked to the risk of desiccation and fungal infection that can significantly reduce the number of questing ticks.

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Figure legends

Figure 1. Climate at Goro Game Reserve. Displayed are mean monthly minimum (T_{min}, dashed line) and maximum (T_{max}, solid line) temperatures (°C) as well as the total monthly rainfall (mm) from June 2007 to August 2008.

Figure 2. Seasonal variation in tick abundance for larvae and nymphs of *R*. sp near *warburtoni*. Displayed are means ± SE.

Figure 3. Relationship between larval abundance and a) T_{max} and b) rainfall two months prior to the sampling month.

Figure 4. Relationship between nymphal abundance and a) T_{max} and b) rainfall two months prior to the sampling month.
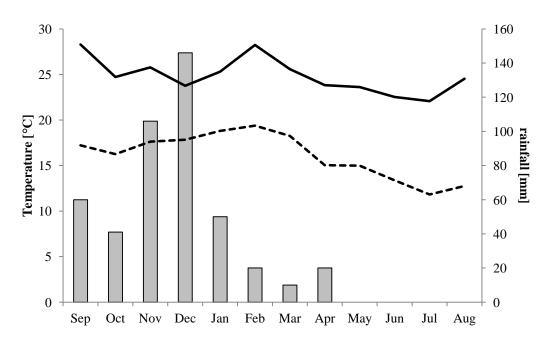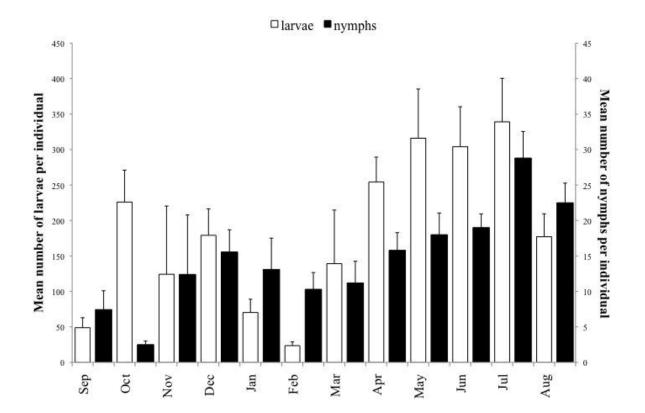
Figure 1

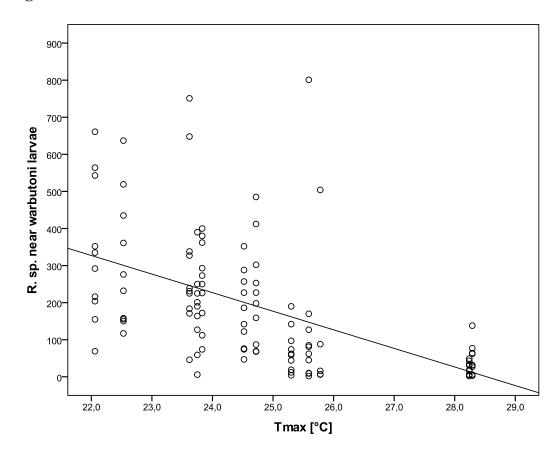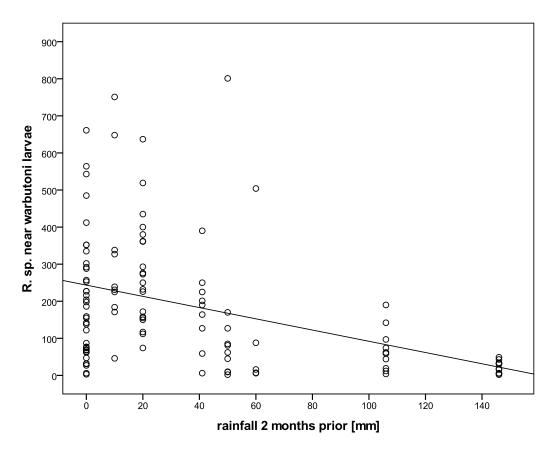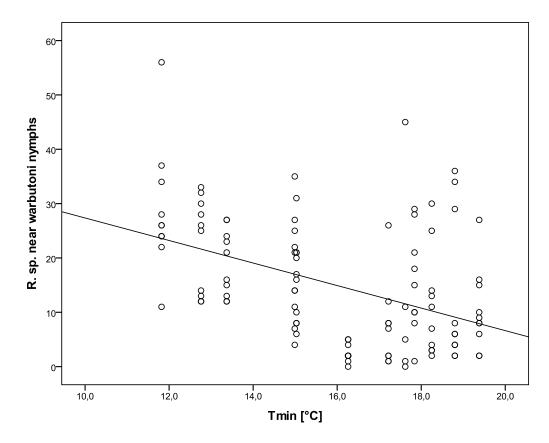**Figure 2**

Figure 3a

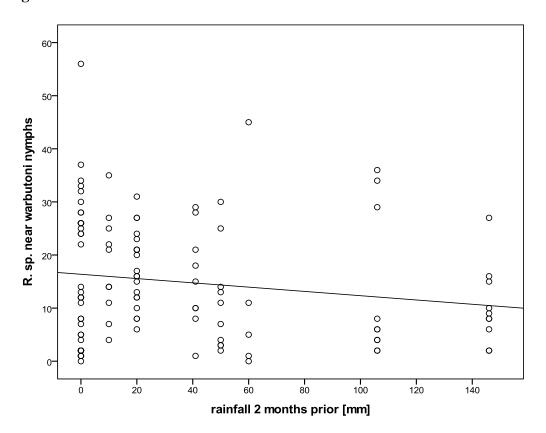Figure 3b

Figure 4a

Figure 4b

Table 1. Generalised linear models investigating the effects of host characteristics and season on larval and nymphal tick burdens of *E. myurus*. Presented are parameter coefficients ± standard error (SE) as well as the associated z- and p-values.

	larvae				nymphs			
	beta coefficient	SE	z-value	p-value	beta coefficient	SE	z-value	p-value
Intercept	5.760	1.401	4.113	0.000***	2.095	0.252	8.303	0.000***
Oct	1.716	0.390	4.403	0.000***	-1.179	0.377	-3.125	0.002**
Nov	1.117	0.478	2.338	0.019*	0.423	0.396	1.067	0.286
Dec	1. 463	0.400	3.658	0.0003**	0.650	0.337	1.926	0.054
Jan	0.454	0.395	1.150	0.250	0.478	0.332	1.441	0.150
Feb	-0.527	0.394	-1.336	0.181	0.237	0.335	0.709	0.479
Mar	1.153	0.400	2.884	0.004**	0.293	0.342	0.857	0.392
Apr	1.937	0.399	4.859	0.000***	0.665	0.330	2.018	0.044*
May	2.037	0.393	5.187	0.000***	0.795	0.328	2.422	0.015*
Jun	2.052	0.396	5.178	0.000***	0.850	0.328	2.590	0.010
Jul	2.108	0.392	5.384	0.000***	1.265	0.325	3.891	0.000***
Aug	1.473	0.393	3.751	0.0002***	1.019	0.327	3.118	0.002**
Sex	0.231	0.156	1.479	0.179	-	-	-	-
Body length	-0.032	0.021	-1.548	0.122	-	-	-	-

***: significance at the level p=0.001, **: significance at the level p=0.01, *: significance at the level p=0.05

Table 2. Generalised linear models investigating the effects of host characteristics and climate factors on larval and nymphal tick burdens of *E. myurus*. Presented are parameter coefficients ± standard error (SE) as well as the associated z- and p-values.

		beta coefficient	SE	z-value	p-value
larvae	Intercept	15.224	1.955	7.786	0.000***
	Sex	0.207	0.158	1.311	0.190
	Body length	-0.024	0.020	-1.213	0.225
	T_{min}	0.146	0.085	1.715	0.086
	T_{max}	-0.429	0.080	-5.332	0.000***
	Rainfall (-1)	-0.004	0.003	-1.409	0.159
	Rainfall (-2)	-0.008	0.003	-2.836	0.005**
nymphs	Intercept	7.627	1.769	4.312	0.000***
	Sex	0.102	0.143	0.712	0.477
	Body length	-0.002	0.018	-0.129	0.897
	T_{min}	-0.317	0.084	-3.773	0.0002***
	T_{max}	-0.018	0.065	-0.282	0.778
	Rainfall	0.005	0.003	1.788	0.076
	Rainfall (-2)	0.008	0.003	3.163	0.0016*
	Rainfall (-3)	0.004	0.002	1.639	0.101

(-1): one month prior, (-2): two months prior, (-3): three months prior, ***: significance at the level p=0.001, **: significance at the level p=0.01, *: significance at the level p=0.05