



# Effects of precipitation on parasite burden along a natural climatic gradient in southern Africa – implications for possible shifts in infestation patterns due to global changes

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As a consequence of environmental change, it is expected that shifts in temperature and precipitation patterns will influence parasite communities and their hosts with unpredictable impact. Parasites play a vital role in ecosystems but there is only limited quantitative data which describe the effects of environmental parameters under natural conditions. We investigated the influence of rainfall, relative humidity and temperature on the prevalence, abundance and infection intensity of nematodes in southern Africa by studying the gastro-intestinal helminth community of the striped mouse *Rhabdomys pumilio*. Along a precipitation gradient from the Cape of South Africa to northern Namibia we trapped 470 mice over a geographical distance of about 1400 km. Faecal egg counts of 439 sampled individuals and dissections of 161 gastro-intestinal tracts revealed 15 different helminth species. The most abundant nematode species harboured in 62.6% of all infected mice were the oxyurid *Syphacia obvelata* followed jointly by two species (*Heligmonina spira* and *Neoheiligmonella capensis*) of the subfamily Nippostrongylinae (43.7%). We found a significant positive correlation between mean annual precipitation (rainfall and relative humidity) and nematode infestation rates of animals and a negative correlation with temperature. In addition, we found associations between precipitation and different qualitative measurements of parasite burden (mean nematode species richness, mean number of nematode worms and infection intensity per individual host). The similarity in nematode species composition decreased with distance between all study sites. Our study indicates for the first time an association between climatic variables and parasite prevalence and abundance along a continuous natural climatic gradient in a small mammal. These results might be incorporated in the development of models which can predict possible threats for the balance of ecosystems and shifts in infestation patterns due to global changes.

As a result of climate change it is expected that the mean temperatures of Earth's surface will rise by 1.4°C to 5.8°C while the mean worldwide precipitation will increase by 7% during this century (Houghton et al. 2001, Weltzin et al. 2003). Especially in arid and semi-arid environments, shifts in precipitation regimes leading to more extreme rainfall events may have an even greater impact on ecosystem dynamics than the expected increases in CO<sub>2</sub> levels and temperature (Weltzin et al. 2003). An analysis of historical precipitation data for southern Africa revealed an increase in the intensity of extreme rainfall events between 1931–1960 and 1961–1990 of more than 70% (Mason et al. 1999). Regionally, in some instances, a decrease in the number of rain days per month were associated with an increase in mean annual precipitation. It is expected that the frequency rise of heavy rain days will lead to climate scenarios that are more dynamic and variable than those of the present day (Meadows 2006). As a result of climate change we can expect

range shifts for plants and animals accompanied by species extinction of habitat specialists especially in the drier western part of South Africa (Myers et al. 2000, Erasmus et al. 2002) but also shifts in the distribution and abundance of habitat generalists which act frequently as parasite vectors (Altizer et al. 2003).

Environmental conditions play an important regulating role in the distribution, transmission and developmental success of parasites and pathogens. Meteorological parameters can influence both the parasite species richness as well as the intensity of infection in the host species (Mas-Coma et al. 2008). Temperature is known to be able to increase parasite development rates (Kutz et al. 2005, Hudson et al. 2006) while humidity and rainfall can have dramatic effects on parasite pressure (Appleton and Gouws 1996, Moyer et al. 2002). This is due to the fact that the free-living stages of e.g. helminths (cestodes, nematodes and trematodes) are directly exposed to the environmental conditions in their respective

microhabitats and rely on their own stored energy reserves until they encounter a susceptible host which is able to offer an adequate resource (Pietrock and Marcogliese 2003, Brooks et al. 2006). For instance in oxyurid nematodes (pinworms), females produce eggs which are released in the host's faeces and must survive in the external environment long enough to be ingested by a new host, thereby requiring a specific optimum of moisture to develop and survive (Grice and Prociv 1993). Given the importance of environmental factors in host-parasite interactions and parasite life-history it is anticipated that the geographical range of most parasites is likely to shift in response to host movement and a change in climate (Sutherst 2001).

The striped mouse *Rhabdomys pumilio* occurs in central and east Africa and is locally abundant and regionally wide-spread in southern Africa (De Graaff 1981). This omnivorous rodent species has adapted well to habitat transformation from pristine natural to agriculture habitats and is often found in close proximity to human dwellings. *Rhabdomys pumilio* has previously been used as model for investigations on potential threats of parasites transmitted by rodents to livestock, wildlife and humans (Shepherd et al. 1986, Matthee et al. 2007). Former descriptive parasite studies have recorded an extensive parasite diversity for this host that include 16 species of mites, 41 fleas, 1 louse, 11 ticks, 9 cestodes, 6 nematodes and unidentified trematodes (Ortlepp 1939, Collins 1972, De Graaff 1981, Matthee et al. 2007). Gastro-intestinal nematodes are a major cause of disease and death in humans, domestic animals and wildlife (Stear et al. 1997) and belong to the most prevalent groups of parasites (Hugot et al. 2001). However, only very little quantitative data are available on the helminth assemblage in reservoirs such as small mammals and how it varies between different geographic localities (Behnke et al. 2001). Moreover, to date no empirical study has been conducted to determine the relationship between climatic variables and the helminth assemblage in small mammals in southern Africa. This is potentially important information for future inferences on the effect of shifts in rainfall patterns on parasite loads of wildlife, livestock and possibly humans.

In this study, *R. pumilio* was used as a model to describe the effects of meteorological parameters on the species diversity and infection intensity of the complete gastro-intestinal helminth assemblage in a broad niche host species. We predict that the prevalence of helminth parasites in *R. pumilio* will be dependant on climatic variables such as rainfall, relative humidity and temperature – leading to higher burdens in a wetter climate. Additionally we predict that the helminth composition will vary across sampling localities due to their geographic distances to each other (distance decay hypothesis, Poulin and Morand 1999). To test these predictions we (a) characterised the helminth assemblage of a broad niche omnivorous rodent species along a natural precipitation gradient (80–1114 mm) in southern African covering an overall distance of ca 1400 km, (b) recorded the relationships between meteorological variables (rainfall, relative humidity, temperature) and prevalence, abundance and infection intensity of nematode species and (c) determined if there is geographic structuring in the nematode species diversity. Finally, we discuss possible effects of shifts in infestation patterns due to climatic changes in southern Africa.

## Material and methods

### Study sites and sample collection

We investigated seven different sites along a precipitation gradient in southern Africa (Fig. 1). Mean annual relative humidity and temperature data of the sites have been recorded between 2004 and 2006 (Table 1). The gradient reaches from the Cape Floristic Region in the south of South Africa up to the north of Namibia and the mean annual rainfall ranges from > 80mm (Fish River Canyon, FR) to 1114 mm (Jonkershoek, JH) (Fig. 1). Sampling at each locality took place twice, first during the summer season (November 2004 – March 2005) and second during the winter season (June – August 2006). Animals were caught in standardised grid systems using 120 (first capture season) and 200 (second capture season) Sherman traps, each 15 m apart from one another which have been baited with a peanut butter – oats mixture. Trapped animals ( $n = 470$  without recaptures; 20 120 trapping nights) were marked with ear tags, weighed, morphometrically measured and released at their respective trapping sites. During the second capture session 161 individuals were euthanised with Fluothane. In order to exclude age effects on parasite load only adult animals weighing  $\geq 32$  g (Apps 2000) were considered for further investigations. The gastro-intestinal tracts (stomach, small intestine and caecum) of euthanised animals were dissected out and stored for later investigation in marked containers containing an adequate volume of 70% ethanol. Additionally stool

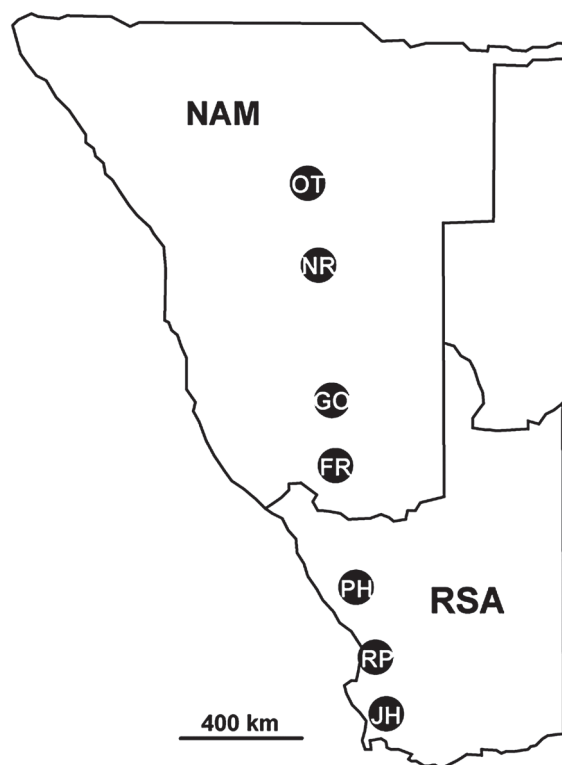


Figure 1. Map of the sampling sites for *Rhabdomys pumilio* in southern Africa. From south to north: Jonkershoek (JH), Rocherpan (RP), Paulshoek (PH), Fish River Canyon (FR), Gellap Ost (GO), Narais (NR), Otjiamongombe (OT).

Table 1. Locality names, geographic coordinates, mean annual rainfall, mean annual relative humidity and mean annual temperature; RSA = Republic of South Africa, NAM = Namibia. \*Weather data of BIOTA South observatories RP, PH, FR, GO, NR, OT by courtesy of Ute Schmiedel (Inst. of General Botany, Univ. of Hamburg) and Klaus Berger (Inst. of Soil Science, Univ. of Hamburg) and of JH by courtesy of ALTO Estate, Stellenbosch and Cape Nature Dept of the Western Cape, South Africa.

Name of study sites	Country	Coordinates	Mean annual rainfall*	Mean annual relative humidity	Mean annual temperature
Jonkershoek (JH)	RSA	33°57'50"S/18°55'32"E	1114 mm	66%	18.1°C
Rocherpan (RP)	RSA	32°36'03"S/18°18'20"E	776 mm	64%	16.8°C
Paulshoek (PH)	RSA	30°23'43"S/18°17'32"E	137 mm	58%	16.5°C
Fish River Canyon (FR)	NAM	27°41'07"S/17°48'05"E	80 mm	42%	20.6°C
Gellap Ost (GO)	NAM	26°24'04"S/18°00'17"E	146 mm	36%	22.3°C
Narais (NR)	NAM	23°07'46"S/16°53'47"E	275 mm	40%	18.3°C
Otjiamongombe (OT)	NAM	21°35'48"S/16°56'41"E	366 mm	49%	19.2°C

samples were taken from the trap of 439 individuals and fixed in 70% ethanol for faecal egg count (FEC) analyses. Traps were cleaned before re-use. Host density was estimated by trapping success (number of trapping nights multiplied by number of traps, divided by the number of trapped animals).

## Parasite screening

The gastro-intestinal tracts of 161 *R. pumilio* individuals were carefully screened for parasites. Each of the three parts of the gastro-intestinal tract was examined separately under the microscope for helminth parasites (cestodes, nematodes and trematodes). The mucosa was carefully examined, scraped and washed to remove any adhering worms. We recorded the abundance and took morphometric measurements through a calibrated eyepiece graticule for each helminth species. Species were identified using published species descriptions (a list can be supplied by the authors), scanning electron microscopy and in personal communication with leading experts (Acknowledgements) in the affiliated field. Voucher specimens are stored at the Leibniz Institute for Zoo and Wildlife Research / Berlin (ref. no: RG2.GF.NEM.).

Faecal egg counts were conducted on all 439 individuals using a modification of the widely used and recommended McMaster technique (Sloss et al. 1994). Faecal samples were screened for helminth eggs by counting two chambers of the McMaster slide using a light optical microscope. Contrary to previous studies which applied the conventional saturated sodium chloride solution with a specific weight of 1.2 g ml<sup>-1</sup>, we used potassium iodide with a specific density of 1.5 g ml<sup>-1</sup> (Meyer-Lucht and Sommer 2005) to enhance the detectability of eggs with high specific weights, such as some nematode and mainly trematode eggs. This method has been used in a number of recent studies (Axtner and Sommer 2007, Schwensow et al. 2007). Subsamples of eggs have been measured for identification purpose.

## Data analyses and statistics

The prevalence (percentage of infected individuals, based on FECs and gastro-intestinal tract screening) and species richness per locality were analysed for helminths in general and for nematodes only. Due to the low prevalence of cestode species and absence of trematodes detailed investigations of individual parasite burden were restricted to nematode species only. We calculated the mean species richness (mean number of nematode worm species per individual host,

based on recovered worms), the mean abundance (mean number of nematode worms per individual host, based on recovered worms) and the infection intensity (nematode eggs per gram faeces per individual host, based on faecal egg counts). For the later two variables, worm numbers and FEC values were log transformed, respectively, to improve normality.

We used fitted generalized linear models (GLMs) and included climatic data as predictors to explain the response variables prevalence, mean species richness, mean abundance and infection intensity. Because of the collinearity between rainfall, humidity and temperature (revealed by Spearman rank correlation), we investigated the effect of each climatic variable in separate independent weighted regression models (model 1: rainfall, model 2: humidity and model 3: temperature). In each model, the year has also been included as a predictor to account for the two capture seasons. For the prevalence we applied logistic regression models with a binomial error distribution and logit link function. For species richness, nematode abundance and infection intensity data which were included in the model as mean values per site, we used a Gaussian error structure. The significance of the different variables was assessed with an F-test after a backward stepwise procedure whereas  $r^2$  is the proportion of deviance explained by each independent variable. It was calculated as null deviance – residual deviance/null deviance. The  $R^2$  represents the proportion of dependent variable variance accounted for by the regression model. It was calculated as 1 – residual deviance/null deviance.

To ensure against overparameterisation a possible effect of population density was investigated in a separate model. To assess whether prevalence and infection intensity is influenced by population density we included population density per capture season as predictor and trapping sites as a random factor in a generalized linear mixed model (fitted using penalized quasi-likelihood) which allows for overdispersion as the random factor will add extra sources of variation to the binomial and mean value variances.

The Jaccard similarity index was used to compare the similarity in the nematode species assemblage between all different geographical localities to each other (Poulin 2003). The index is calculated using the number of nematode species (based on FECs and dissections) shared by two host populations divided by the total number of nematode species found in the combined two host populations. It ranges from zero (no species in common between two host

populations) to one (the two host populations have exactly the same nematode species) (Poulin 2003). To obtain the exact linear distance between two sites we used the GPS coordinates to calculate the kilometres using the online ABE unit conversion calculator (Filip 1997). All statistical tests (Spearman rank correlation, linear regression and student's t-test) were performed using the programmes R (ver. 2.8.1, R Development Core Team 2008) and SPSS 11.5. Calculations are two-tailed and based on a 5% significance level. To account for multiple comparisons we used Bonferroni adjusted p-values as indicated for sequential adjustment.

## Results

### Gastro-intestinal helminth parasites of *R. pumilio*

A comparison of the parasites that were recorded in the gastro-intestinal tract and faecal material revealed that all of the highly abundant egg morphotypes could be linked to the adult worms found in the gastro-intestinal tract, allowing us to combine both data sets (Table 2). All, but two egg morphotypes could be clearly differentiated from each other. The exceptions were the eggs from the two nematodes *Heligmonina spira* and *Neohelgmonella capensis* which are very similar in shape and size. Both belong to the subfamily Nippostrongylinae and were grouped together for the FECs but kept separate for the total worm counts.

Based on FEC data a total 15 helminth species (nematodes and cestodes) were recorded from *R. pumilio* (Table 2). No trematodes worms were observed. *Rhabdomys* individuals harboured between 0–4 intestinal helminth species (18.0% carried one, 14.9% two, 8.7% three and 2.5% harboured four helminth species). A large percentage (55.9%) of dissected individuals was not infected and we found eggs in 43.0% of all screened faeces.

An oxyurid nematode *Syphacia obvelata* was the most prevalent and abundant nematode and helminth species (infestation rate: 62.6%) and was the only species that was recorded at all seven localities along the rainfall gradient. More than 40% of all infected mice were parasitized by two closely related nematode species *H. spira* and *N. capensis* (Nippostrongylinae). All other nematode species were found more infrequent. Two cestode species *Oochoristica* sp. A and *Oochoristica* sp. B occurred in low abundances of less than 5% each (Table 2). No individual was infected with cestode worms only.

### Effects of temperature and precipitation on parasite burden

Our tests for collinearity within meteorological variables showed significant positive correlations between rainfall and humidity (Spearman:  $r_s = 107.886$ ,  $p = 0.031$ ) and between humidity and temperature (Spearman:  $r_s = 490.577$ ,  $p = 0.009$ ).

Independent GLM's revealed significant relationships between the climatic variables and nematode infestation rates as well as all quantitative measurements of parasite burden within *R. pumilio* (Table 3). These relationships are mainly driven by precipitation as variances show higher proportions (rainfall: between 66.52% and 90.40%; relative humidity: between 46.77 and 86.26%) in comparison to temperature (between 0.27% and 33.16%). Trap season only showed substantial influence for the *Syphacia* burden. The explanatory variances ( $R^2$ ) of the models lie between 14.58% and 93.72%.

We found significant positive correlation between precipitation and prevalence of all nematodes (based on FECs and recovered worms) along the gradient (Table 3a). The nematode prevalence was highest (98%) at the site with the highest annual rainfall (Jonkershoek) and lowest at Fish River Canyon (23%) which also shows the lowest annual rainfall (Fig 2a). The prevalence of the most abundant

Table 2. Helminth species recorded from faecal samples (FEC) and the gastro-intestinal tract (GIT), infestation rates (%) of all infected *Rhabdomys pumilio* individuals, nematode species richness as well as average trapping success (in % based on trapping nights) at the different study sites (locality codes as in Table 1). n = number of mice; X = occurrence, blank = absence.

Helminths species	n =	FEC 439	GIT 161	Infestation [%] 439	JH 42	RP 49	PH 64	FR 40	GO 83	NR 120	OT 41
<i>Syphacia obvelata</i>		X	X	62.6	X	X	X	X	X	X	X
Nippostrongylinae		X	X	43.7	X	X	X		X		
<i>Heligmonina spira</i>				-	X	X	X		X		
<i>Neohelgmonella capensis</i>				-	X	X	X				
<i>Trichuris muris</i>		X	X	11.1	X	X	X				
<i>Aspicularis tetraptera</i>		X	X	8.9				X	X		X
<i>Subulura elongata</i>			X	3.2						X	X
<i>Trichostrongylus probulurus</i>		X	X	1.6	X	X					
<i>Streptopharagus sudanensis</i>		X	X	0.5							X
Nematode A		X		7.4	X			X	X	X	
Nematode B		X		1.6						X	
Nematode C		X		1.1					X		
Nematode D		X		1.1						X	
Nematode E		X		1.1						X	
<i>Oochoristica</i> sp. A		X	X	4.7				X	X	X	X
<i>Oochoristica</i> sp. B		X	X	4.2	X		X			X	X
Nematode species richness					6	5	4	3	5	6	4
Trapping success (%)					2.2	2.9	1.5	3.8	1.8	3.5	2.3



nematode species *S. obvelata* and the Nippostrongyliinae (*H. spira* and *N. capensis*) followed widely the same pattern and were also significantly positive associated with rainfall and relative humidity (Table 3b–c), whereas climatic variables showed even stronger correlations to the prevalence of Nippostrongyliinae compared to *S. obvelata*. Temperature was throughout negatively correlated to prevalence. Also, trap season had significant influence on the prevalence of

*S. obvelata*. Here the overall mean prevalence was higher during the second trapping period ( $38 \pm 26\%$ ) compared to the first one ( $21 \pm 14\%$ ) while the Nippostrongyliinae did not reveal large seasonal differences.

The mean species richness (Fig. 2b) and the mean abundance (Fig. 2c) of nematodes recovered from the gastro-intestinal tract per site showed significant positive correlation with rainfall (Table 3d–e). Mean species richness was highest

Table 3. Results of regression analyses from independent fitted generalized linear models (see Material and methods for details) for the relationships among climatic variables (rainfall, humidity, temperature), capture season (year) and (a) prevalence<sub>all nematodes</sub>, (b) prevalence<sub>*S. obvelata*</sub>, (c) prevalence<sub>Nippostrongyliinae</sub> (infection statuses based on FECs and gastro-intestinal tract data;  $n = 439$ ) (d) mean species richness (mean number of nematode worm species per individual host; based on recovered worms,  $n = 161$ ), (e) mean abundance (mean number of nematode worms per individual host; based on recovered worms,  $n = 161$ ), (f) infection intensity (nematode eggs per gram faeces per individual host, based on faecal egg counts;  $n = 439$ ). In (d) and (e) year could not be included in testing for the mean species richness and mean abundance (model 4) because here only data from the second capture season was available. Further humidity could not be included due to collinearity with temperature and rainfall.  $\beta \pm SE$  = coefficient  $\pm$  standard error;  $r^2$  = proportion of variance explained by each independent variable;  $R^2$  = explanatory variable. Significant p-values (Bonferroni adjusted,  $p < 0.017$ ) for F-tests are indicated in bold.

(a) Prevalence <sub>all nematodes</sub>		$\beta \pm SE$	$r^2$	p	$R^2$
Model 1:	Year	$0.420 \pm 0.233$	2.48%	0.071	87.59%
	Rainfall	$0.004 \pm 0.000$	86.37%	<b>&lt; 0.001*</b>	
Model 2:	Year	$0.025 \pm 0.226$	0.01%	0.911	64.99%
	Humidity	$0.087 \pm 0.01$	63.77%	<b>&lt; 0.001*</b>	
Model 3:	Year	$0.198 \pm 0.205$	0.71%	0.335	14.58%
	Temperature	$-0.214 \pm 0.052$	13.58%	<b>&lt; 0.001*</b>	
(b) Prevalence <sub><i>S. obvelata</i></sub>		$\beta \pm SE$	$r^2$	p	$R^2$
Model 1:	Year	$1.278 \pm 0.277$	28.01%	<b>&lt; 0.001*</b>	88.36%
	Rainfall	$0.003 \pm 0.000$	66.52%	<b>&lt; 0.001*</b>	
Model 2:	Year	$0.987 \pm 0.261$	17.80%	<b>&lt; 0.001*</b>	68.61%
	Humidity	$0.065 \pm 0.011$	46.77%	<b>&lt; 0.001*</b>	
Model 3:	Year	$1.011 \pm 0.252$	20.33%	<b>&lt; 0.001*</b>	35.91%
	Temperature	$-0.209 \pm 0.062$	14.07%	<b>&lt; 0.001*</b>	
(c) Prevalence <sub>Nippostrongyliinae</sub>		$\beta \pm SE$	$r^2$	p	$R^2$
Model 1:	Year	$-0.606 \pm 0.390$	1.11%	0.120	75.90%
	Rainfall	$0.004 \pm 0.000$	71.46%	<b>&lt; 0.001*</b>	
Model 2:	Year	$-0.480 \pm 0.394$	0.70%	0.233	91.81%
	Humidity	$0.293 \pm 0.046$	86.26%	<b>&lt; 0.001*</b>	
Model 3:	Year	$-1.197 \pm 0.318$	6.80%	<b>&lt; 0.001*</b>	38.71%
	Temperature	$-0.605 \pm 0.092$	33.16%	<b>&lt; 0.001*</b>	
(d) Mean species richness		$\beta \pm SE$	$r^2$	p	$R^2$
Model 4:	Rainfall	$0.002 \pm 0.000$	72.43%	<b>0.002</b>	93.72%
	Temperature	$-0.023 \pm 0.056$	0.27%	0.701	
(e) Mean abundance		$\beta \pm SE$	$r^2$	p	$R^2$
Model 4:	Rainfall	$0.002 \pm 0.000$	67.21%	<b>0.003</b>	93.67%
	Temperature	$-0.037 \pm 0.046$	1.00%	0.467	
(f) Infection intensity		$\beta \pm SE$	$r^2$	p	$R^2$
Model 1:	Year	$-0.093 \pm 0.236$	1.96%	0.703	92.16%
	Rainfall	$0.003 \pm 0.000$	90.40%	<b>&lt; 0.001*</b>	
Model 2:	Year	$-0.157 \pm 0.493$	0.39%	0.757	65.70%
	Humidity	$0.085 \pm 0.021$	63.94%	<b>0.003*</b>	
Model 3:	Year	$-0.236 \pm 0.776$	0.27%	0.768	15.19%
	Temperature	$-0.229 \pm 0.192$	13.43%	0.263	

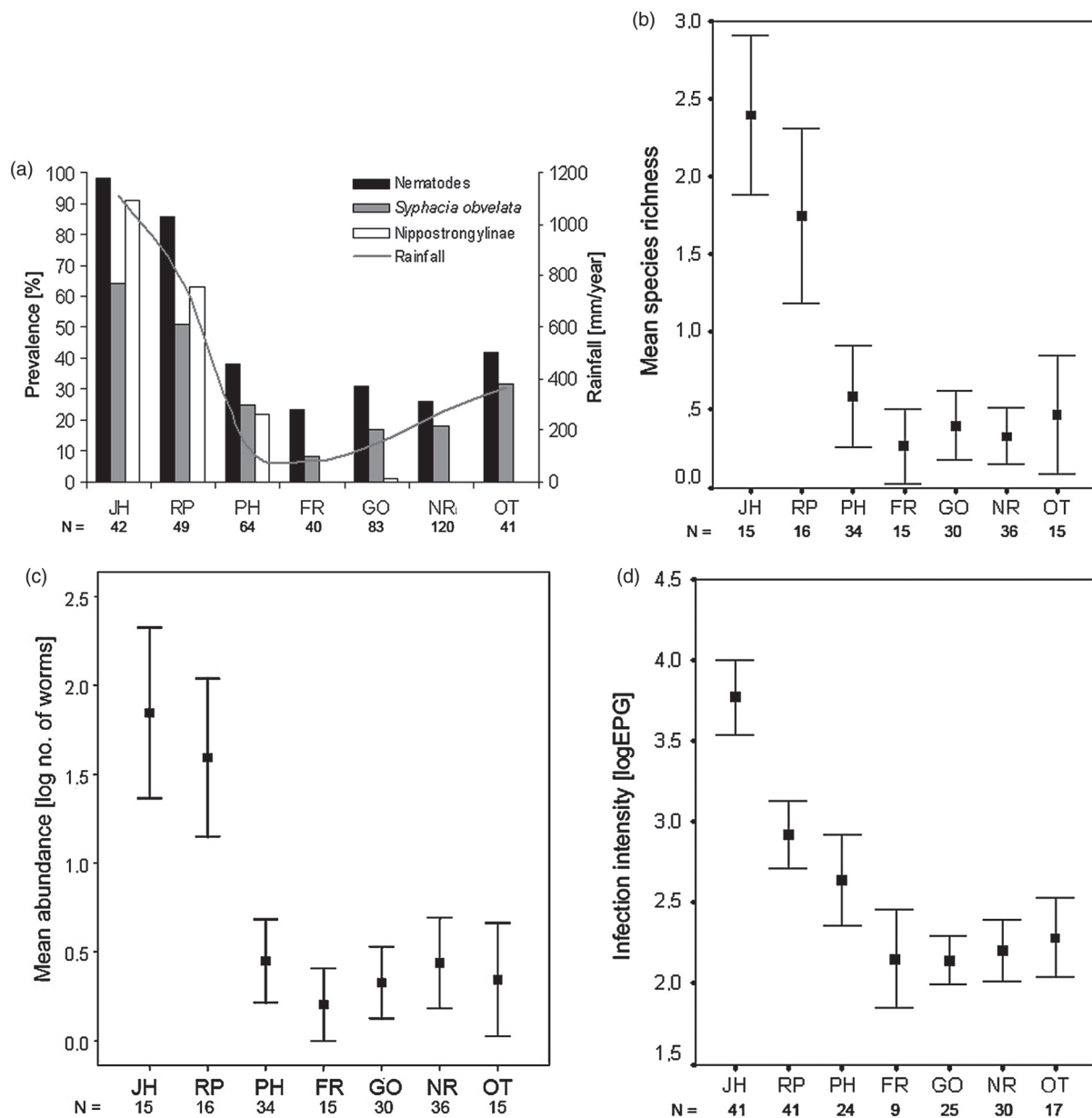


Figure 2. Associations between parasite burden and precipitation (mm rainfall per year): (a) prevalence (%) per site by nematodes in general and separately by the most prevalent nematodes *Syphacia obvelata* and *Nippostrongylus* (gastro-intestinal tract and FEC data;  $n = 439$ ); (b) mean species richness  $\pm$  SE per site observed in dissected animals (gastro-intestinal tract data;  $n = 161$ ); (c) mean abundance (log no. of worms) per site  $\pm$  SE of all dissected individuals (gastro-intestinal tract data;  $n = 161$ ); (d) infection intensity (logEPG) per site  $\pm$  SE of all infected animals (FEC data;  $n = 186$ );  $n$  = number of mice.

Table 4. Effects of the predictors population density and capture season (year) on the response variables (a) prevalence  $_{all\ nematodes}$  and (b) infection intensity [log EPG] obtained from a mixed model with trapping sites as random variables.

Linear mixed models	$\beta \pm SE$	t	p
(a) Prevalence $_{all\ nematodes}$			
Year	$0.371 \pm 0.202$	1.837	0.164
Population density	$-1.112 \pm 4.036$	-0.276	0.800
(b) Infection intensity			
Year	$-0.158 \pm 0.295$	-0.536	0.630
Population density	$-4.465 \pm 7.793$	-0.573	0.607

at Jonkershoek ( $2.4 \pm 0.3$ ) and lowest at Fish River Canyon ( $0.3 \pm 0.1$ ). The infection intensity of all infected individuals per site showed highly significant positive correlation with precipitation (Table 3f, Fig. 2d). Thereby, prevalence and infection intensity are not influenced by seasonal shifts in population density (Table 4).

### Effect of spatial distance on nematode parasites

The nematode species richness per locality was highest at Jonkershoek (JH) and Narais (NR) and the lowest at Fish River (FR) Canyon (Table 2). Our spatial distance analysis confirmed a significant negative correlation between the

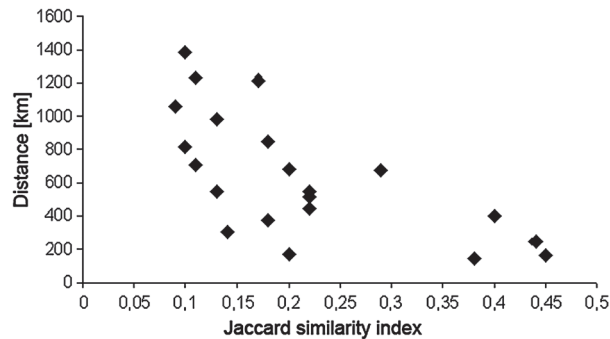


Figure 3. Jaccard similarity index for all pairwise comparisons of nematode communities in *Rhabdomys pumilio* in relation to distance (km) between study sites.

similarity in the nematode species assemblage (Jaccard similarity index) and the distance in kilometers between the different localities to each other that were sampled (Spearman,  $r_s = -0.748$ ,  $p < 0.001$ ) (Fig. 3).

## Discussion

In this study we used the striped mouse, *R. pumilio*, as a model organism to examine the effects of climatic variables on the helminth assemblage and the abundance and infection intensity of nematode parasites in a broad niche host species. This is the first empirical study conducted along a natural precipitation gradient that showed significant correlations between annual rainfall and humidity and parasite burden over a large geographic range in small mammals in southern Africa. Natural shifts in parasite burden along a climatic gradient which has been established over a longer time period might be a first step to discuss possible threats for the balance of ecosystems and shifts in infestation patterns due to global changes.

### Gastro-intestinal helminth parasites of *R. pumilio*

*Rhabdomys pumilio* harbours a diverse helminth assemblage consisting of nematodes and cestodes with both geographically diverse and restricted species. Less than half of the host population was infected with helminths and most of the infected mice harboured a single nematode species. A negative binomial frequency distribution is characteristic for parasite infections within a host population and has been recorded previously for helminth parasites in small mammal species (Morand and Guégan 2000) and also for various ectoparasite taxa present on *R. pumilio* (Matthee and Krasnov 2009 in press). *Syphacia obvelata* was the most abundant nematode species and was recorded from the caecum. This oxyurid nematode species has a world wide distribution and is common mainly in mice and rats (Chan 1951, Bazzano et al. 2002, Pisanu et al. 2002). Pinworms of the order Oxyurina (e.g. *S. obvelata*, *Aspiculuris tetraptera*) were initially regarded as non-pathogenic. However pinworm infection has been associated with rectal prolapse, mucoid enteritis, and intestinal impaction/intussusceptions and it has been shown to influence the susceptibility of mice to other intestinal nematodes (Michels et al. 2006). The life cycle is

direct (no intermediate host required to complete life cycle) and transmission generally takes place through grooming or contaminated food (Taffs 1976). The second most abundant species *H. spira* and *N. capensis* were recovered from the small intestine and have been identified from *Rhabdomys* samples collected in Jonkershoek before (Durette-Desset and Digiani 2005). Members of Nippostrongylineae are widespread over the world in the Muridae and in Africa the subfamily is represented by Heligmonoides, Heligmoninna and Neohelgimonella (Diouf et al. 2005). However, our dissections did not reveal any other species from the subfamily and their eggs could be easily distinguished from other nematodes. Belonging to the superfamily Trichostrongyloidea, the life cycle of Nippostrongylineae include free-living larval stages although the exact life cycles of *H. spira* and *N. capensis* still remain unknown. The whipworm *Trichuris muris* (recovered from the small intestine) is a common cosmopolitan parasite and has been found in several other species of Muridae as well (Feliu et al. 2000, Brouat et al. 2007). It is transmitted by egg ingestion and the eggs remain in the soil for about one month to mature (Brouat et al. 2007). Also *Aspiculuris tetraptera* was found in the small intestine and it is a frequent parasite of laboratory mice and various wild rodents (Ibrahim et al. 1984, Bazzano et al. 2002). Nematodes of the genus *Subulura* are known parasites of birds and mammals (Yamaguti 1961, Vassiliadès 1980) and *S. elongata* (recovered from caecum) has been described from different African rodents (Baylis 1928, Quentin 1965). *Trichostrongylus probulurus* (recovered from the small intestine) is a nematode which is mainly known within ruminants (Anderson 2000) but also occurred in the Cape Hare (Eslami et al. 2000) while *Streptopharagus sudanensis* has been collected from the small intestines of Egyptian rodents (Wanas 1993).

All of the nematode species recorded in *Rhabdomys* are common parasites of rodents. However this study provides the first host species record of *S. obvelata*, *A. tetraptera*, *T. probulurus* and *S. sudanensis* in *R. pumilio* in South Africa and Namibia.

### Effect of precipitation gradient and temperature on parasite prevalence and abundance

This study confirms previous studies in that environmental variables play an important role in parasite transmission and infestation patterns (Moyer et al. 2002, Nwosu 2007). A strong positive correlation was found between mean annual precipitation (rainfall and relative humidity, respectively) and the prevalence of nematodes as well as the mean species richness, the mean abundance and the infection intensity along a natural climatic gradient in *Rhabdomys*. Our models confirm our predictions that parasite burdens will be higher in wetter climates compared to drier ones. Temperature was negatively correlated with prevalence indicating that nematodes and their free-living stages only tolerate heat in dry climates up to a certain degree. Although previous studies have shown that temperature does have an effect on egg and larval development (Hudson et al. 2006) no correlation was recorded between mean species richness, mean abundance, infection intensity and mean annual temperature in our study. A raise in temperature may lead to reduced humidity and this reduces the availability of infective eggs or larvae

(Hudson et al. 2006). One response cancels out the other so that there is no effective increase in parasites with temperature visible. Similar to our findings, precipitation plays a key role and Appleton and Gouws (1996) showed that the prevalence of the nematodes *Ascaris lubridoides* and *Necator americanus* were correlated with rainfall-derived variables and that these variables overshadowed any other temperature effects on egg development. Other studies indicated that moisture availability is an important factor for the development of the free-living stages of the nematode *Haemonchus contortus*, a common species of sheep (O'Connor et al. 2007). Although similar patterns have been found in goats (McCulloch et al. 1986) and humans (Appleton and Gouws 1996) in South Africa, this is the first study that investigated the parasite prevalence and abundance along a continuous natural climatic gradient over such a large geographic distance in small mammals.

We did not observe any density compensation, like i.e. increase in parasite abundance in relation to the decrease in parasite species richness. It thus seems like climatic variables overshadow possible inter-specific interactions between parasites. However, up to now there is no general consensus on how interactions between parasites shape the dynamics of other parasite species and their host (Cattadori et al. 2006).

Helminth parasites differ with respect to life history; some parasites are transmitted through direct contact, whereas other parasites spend part of their life as free-living stages in the environment or make use of intermediate hosts as part of their life cycle (Levine 1968). The strength of the effect of environmental conditions on the parasite will depend on the extent to which various stages of the parasite's life cycle are exposed to the external environment. For example, *T. muris* and all other known spirurids have an indirect life cycle that involves an arthropod as an intermediate host (Owen 1992). The life cycles of species within the Nippostrongylinae are direct and include free-living larval stages suggesting that environmental conditions may have a larger impact on their development compared to the life cycle of for example *S. obvelata* where the second-stage larvae are protected within the egg capsule and transmission mainly takes place through direct contact between host individuals (Chan 1951, Grice and Procvic 1993, Pisanu et al. 2002). Indeed a stronger correlation was recorded between climatic variables and the prevalence of Nippostrongylinae than compared to *S. obvelata*. This might explain why *S. obvelata* in contrast to the Nippostrongylinae occurred along the whole gradient. Nevertheless Chan (1951) and Grice and Provic (1993) showed that the eggs of *S. obvelata* are also depended on the degree of wetness. The eggs opened up too prematurely in excessively moist conditions and in relative dryness the percentage of viable eggs was decreased. Jex et al. (2007) suggest that the pinworm fauna of widely distributed hosts varies in relation to different local climatic conditions. Our results are in accord with this hypothesis and we state that precipitation is at least one crucial factor which influences the prevalence and abundance of *S. obvelata* and other gastro-intestinal nematodes within *R. pumilio*. Other variables, not investigated in this study, such as soil composition and vegetation cover may have profound impacts on the free-living stages that require suitable microclimatic conditions for development and survival (Hubert and Boag 2001, Brouat et al. 2007).

## Effect of spatial distance and host biology on nematode parasites distribution

Geographical distance influences the species composition of nematodes in *R. pumilio* with a decrease in similarity associated with an increase in distance, demonstrating thus that the pattern of distance decay of biological similarity found in other organisms is universal (Poulin 2003). For the analysis we included all nematode species and disregarded whether the occurring parasites are generalists or specialists. A recent comparative study on the nematodes across different mammalian species disproved the hypothesis that generalist nematode species should exhibit a wider range of distributions and have higher average abundance than specialists (Morand and Guégan 2000). Some nematode species like *S. elongata* and *S. sudanensis* only occurred at the most northern localities. Both of these species exhibited a narrow geographical distribution (present at one or two localities) and a low infestation rate (2.3% and 0.5%, respectively) which may be a consequence of *R. pumilio* not being the preferred host of these species and or limited annual precipitation at the neighbouring sites to the south. In contrast, *H. spira* and *N. capensis*, the second most abundant worms recorded in this study, were largely restricted to three of the southern localities. This range pattern might be a result of the combination of higher precipitation and a possible requirement of a specific vegetation structure for the free-living larval stages in this region.

Furthermore the structure of parasite communities can be affected by parameters of host biology such as population density (Poulin and Morand 2004). Host population density of rodents again is often influenced by rainfall, indirectly through food resources and breeding success (Shenbrot and Krasnov 2001). Schradin (2005) showed that the social organization of the striped mouse differs dramatically in correlation with the habitat it occupies. In more arid regions, the social structure of *R. pumilio* is described as a territorial group living solitary forager with communal breeding. In contrast, in regions with higher rainfall the striped mouse is regarded as solitary living. Communal breeding or large home ranges – it remains to be discussed which of the social systems is more likely to cause more infections with parasites. On one hand, an increase in social group size increases the rate of contact between individuals, and, thus can favor the transmission of contagious parasites (Loehle 1995). On the other hand, a positive correlation between parasite species richness and the size of the host geographic range is expected because hosts with larger geographic ranges would presumably encounter more parasite species. In our study the nematode species richness was generally higher at the wetter southern and northern sites compared to the drier ones in the middle of the gradient. Thus our findings go along with the second theory although host trapping success as a surrogate of population density could not reflect possible differences in social systems in dependence to precipitation. No correlation between population density and nematode prevalence or infection intensity could be found. However, precipitation as a direct or indirect factor seems to be one of the major extrinsic drivers to influence parasite burdens and compositions.



## Possible shifts in infestation patterns in southern Africa due to global changes

Current rainfall models based on analyses of historical rainfall data from South Africa hypothesis that rainfalls will be more variable and dynamic than those of the present day (Mason et al. 1999). Range shifts of animals due to changes in precipitation are widely expected and depending on the dispersal ability, ecology and tolerance levels of the individual taxa either range expansions or contractions will occur. This might also affect species acting as parasite reservoirs and vectors and might change infestation pattern of wildlife and livestock. Erasmus et al. (2002) used data sets of 179 animal species (including 19 mammals) to model the responsiveness of South African fauna to climate change and predicts a range contraction in 78% of the species with a predominant range shift from west to east of the country. Similar patterns are predicted for various vegetation types. For example, the semi-desert Succulent Karoo (one of the biodiversity hotspots, Myers et al. 2000) located in the southern part of South Africa will experience a range contraction towards the south and east of South Africa. On the other hand the current geographical range of the desert biome will increase towards the south and also possibly towards the north of the Fish River Canyon.

Our study showed a strong association between precipitation and parasite infestation within a small mammal with higher parasite burden in wetter areas. The distribution of small mammal vectors like *R. pumilio* depends on environmental factors such as vegetation cover (Jensen et al. 2003) which is again positively correlated with rainfall pattern. Therefore it can be expected that parasite pressure will decrease in dry areas but increase in wetter zones which are usually of high agricultural relevance. *Rhabdomys* for instance seems to benefit from agricultural development (Bond et al. 1980). The presence of domestic animals and domesticated livestock that are susceptible to parasites generally associated with rodent species can facilitate host switching events. This can be a potential problem as emerging infectious diseases are often associated with parasites that infect naïve host species (host species having no previous history of association with the parasite species). Only a minor increase in disease distribution may expose new host populations lacking in immunity (de La Rocque et al. 2008). The ability of many parasite taxa to colonize many different hosts is more widespread than previously thought. Host switches are not only driven by pathogen evolution in response to novel conditions, but rather by pre-existing parasite biology (evolutionary history) and chance (Brooks et al. 2006). Parasites may be able to track a resource that is distributed across many host species (ecological fitting, Janzen 1985). Host switching is an omnipresent and important impact of climate change and can involve cascading changes in ecosystem (Kutz et al. 2005, Brooks and Hoberg 2007). The increase in variability and extreme climatic events will even add to the uncertainty of how possible emerging infective diseases can be predicted in the future and may trigger unexpected pathogen range expansions.

Although our study indicates that precipitation and temperature are crucial factors in host parasite loads, it is important to gain more knowledge and quantitative data about

additional parameters effecting parasite distributions and host-parasite interactions. Especially these abilities of parasites could be critical to predict future disease spreads. Ongoing studies will include parasitological investigations of other rodents and wildlife at the respective locations and will add host intrinsic factors like the adaptive immunity. This data are pre-requisites to predict possible threats for the balance of ecosystems and possible threats by emerging infectious diseases due to global changes.

**Acknowledgements** – The study has been conducted under accordance of the Ministry of Environment and Tourism, Namibia (permit no 853/2004 and 1065/2006), the Northern Cape Nature Conservation Service, South Africa (permit no 0592/04 and 0133/06) and the Cape Nature Department of the Western Cape, South Africa (permit no. 001-202-00021 and AAA004-00029-0035). We declare that all aspects of the study comply with the current law of the country in which they were performed. We are grateful to K. Junker and J. Boomker from the Dept of Veterinary Tropical Diseases, Pretoria Univ. and R. Bray from the Natural History Museum, London for helping with the helminth identification. Further we would like to thank Y. Meyer-Lucht, M. A. McGeoch, J. U. Ganzhorn and I. Homburg for their support. S. Morand and H. McCallum provided very useful comments on an earlier version of the manuscript. The study was supported by the Hansische Universitätsstiftung, the German Academic Exchange Service (DAAD) and Stellenbosch University. SS and MS equally supervised the study.

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