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COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Host density drives macroparasite abundance across populations of a critically endangered megaherbivore

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Abstract What determines the abundance of parasites is a central question within epidemiology. Epidemiological models predict that density-dependent transmission has a principal influence on parasite abundance. However, this mechanism is seldom tested in macroparasites, perhaps because multiple, comparable populations of the same host-parasite relationship are rare. We test the influence of a range of factors on parasite abundance across 18 populations of black rhinoceros (*Diceros bicornis*) in South Africa. Here we show that host density strongly predicts parasite abundance at the population level for both directly and indirectly transmitted parasites. All other models were not supported. The surprising influence of a single key factor, host density, within a complex ecological system demonstrates the validity of simple epidemiological models. Establishing this previously assumed relationship between host density and parasite abundance has major implications for disease control and parasite ecology. For instance, it is central to the idea of population density thresholds for parasitism, below which a parasite would become extinct. Density-dependent transmission is also essential for calculations of the basic reproductive number, and the hypothesis that parasites may regulate host population size.

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Introduction

Epidemiological theory for parasite and disease abundance relies on the assumption of density-dependent transmission (Anderson and May 1991). High host density is assumed to increase parasite abundance because parasites more easily find a host to invade. Although predicted by numerous epidemiological models (Anderson and May 1979, 1991; May and Anderson 1979; Arneberg et al. 1998) and previously shown for microparasites (Lloyd-Smith et al. 2005), density-dependent transmission has rarely been documented for macroparasites of wildlife. This may be because macroparasite transmission is often more complicated than microparasite transmission due to external free-living life stages, which obscure the mechanism and have led to a number of alternative competing theories (Hudson and Dobson 1995). Also, for indirectly transmitted parasites, the mechanism is further complicated by the interaction between primary and secondary host density (Stien et al. 2010).

Density-dependent transmission is difficult to test because multiple, isolated, suitably variable, yet comparable populations of the same host-parasite interaction are rarely found. Such real-world experimental field data are needed to further develop epidemiological theory (Diamond 1986; Anderson and May 1991; Lloyd-Smith et al. 2005).

Arneberg et al. (1998) showed a positive relationship between the average abundance of parasites in different host species and host species density. However, the demonstration of an inter-specific association is not proof of a

population-level ecological mechanism. Variability in host and parasite density through time for single host populations has been used to test the mechanism. A number of studies have shown a general positive relationship (Hudson et al. 1992; Albon et al. 2002; Jansen et al. 2012); however, negative relationships have also been reported (Haukisalmi and Henttonen 1990). It seems difficult to attribute cause where only single populations are used, but multiple influences are considered (Haukisalmi and Henttonen 1990; Cattadori et al. 2005). Here we test the influence of host density on parasite abundance by comparing multiple populations of the same host–parasite interaction.

Numerous other mechanisms may act on parasite abundance. For instance, environmental variables may impact the development rate or survival of external free-living parasite stages (Mouritsen and Poulin 2002), or for indirectly transmitted parasites, egg survival (Atkinson et al. 2013). Hence, we also test for the influence of a variety of environmental factors on parasite abundance as predicted by the literature. Likewise, the use of fire, as a form of intermediate disturbance, is likely to have a profound effect on the survival of eggs, free-living stages, and the abundance of intermediate hosts (Fuentes et al. 2007). Also, the size of a founder population may impact on the genetic diversity of either host or parasite population, potentially affecting the host–parasite interaction. The influence of fire regime and founder population size is also tested here.

Black rhinoceros (*Diceros bicornis*) are host to numerous parasites including a wide variety of both directly and indirectly transmitted gastrointestinal helminths (Penzhorn et al. 1994). Black rhino populations in South Africa are managed as an artificial meta-population. Between 1960 and 2005, in eastern South Africa, 442 rhino were reintroduced to reserves to speed species recovery. Remarkably, 17 out of the 18 populations of black rhinoceros in this study originated from only two, genetically very similar (Anderson-Lederer et al. 2012), source populations. Many are still expanding, providing a range of rhino densities that are not determined by their environment. We are able, therefore, to use these populations as different treatments in a fortuitous country-wide field or pseudoexperiment (Diamond 1986; Kerr et al. 2007). By comparing the abundance of both directly and indirectly transmitted parasites between these different populations, we can test for the influence of a range of environmental and ecological factors.

Materials and methods

Fresh faecal samples ($n = 160$, mean samples per population = 8.9, range = 3–18; Fig. 2) from 18 black rhino populations spanning a variety of climatic zones (Table 1) in

Table 1 Descriptive statistics from the environmental parameters used in candidate models

	Mean	SE	Min.	Max.
Max. temperature[a] (°C)	26.8	0.12	22.6	29.7
Summer mean max. temperature[b] (°C)	28.8	0.14	23.8	32.4
January min. temperature[b] (°C)	19.1	0.12	15.4	22.2
Min. temperature[a] (°C)	13.8	0.14	10.1	17.0
Humidity[a] (%)	76.9	0.28	68.6	86.4
Rainfall (mean monthly)[a] (mm)	45.9	0.81	31.0	79.6
Summer rainfall[b] (mm)	441.5	9.3	223.8	837.2

Max. Maximum, *Min.* minimum

[a] Mean value 2000–2011

[b] During season of collection, summer: October–March

eastern South Africa were collected. The populations studied were all fenced and intensively monitored, hence rhino density could be accurately estimated. Population size ranged between nine and 200 individuals, within reserves that ranged from 3668 ha to 90,000 ha in size. Populations varied greatly in age. All populations had been created at least 3 years prior to data collection, with a mean age of 16.5 years (range 3–46 years) excluding the two source reserves. The majority of the study populations were established from only two source populations from South Africa (which were also included in the study), the solitary exception was created using a Namibian source population.

To mitigate the effects of season all samples were collected during the wetter summer season (October–April). The date of sample collection was originally included in the competing set of models and found to have no effect on parasite abundance. Fresh faeces were located along roads and game trails in the early morning (dawn-10 a.m.). To reduce the possibility of pseudoreplication a stratified random sampling regime, modified to ensure a minimum of 1 km between sample sites, was used. Also, local knowledge of rhino home ranges was used to reject samples that were likely to have come from the same individual.

Faecal samples were stored in anaerobic conditions in a cool box before immediate (ca. 2–4 h) analysis, or refrigerated at 4 °C for no more than 48 h before analysis. Faecal egg counts were performed using a modified McMaster technique, using Sheather's sugar solution (Zajac and Conboy 2006). The quality of samples was ensured by the identification of mature or immature embryonated eggs. Samples deemed too old based on egg maturation and field observation of faeces were rejected (Stringer et al. 2014). Eggs were identified using Zajac and Conboy (2006). Representative photos of all egg types found in a population were taken to confirm identification across populations. Two parasite groups were studied—strongyle-type nematodes (species of strongyle cannot be distinguished by egg

Table 2 Information-theoretic table of candidate models explaining strongyle parasite abundance as a function of host rhinoceros density (rhino ha^{-2})

Model/hypothesis	Source	K	AIC$_c$	ΔAIC$_c$	ω
Host density[a]	Arneberg et al. (1998)	3	2696.305	0.00	1.000
Max. temperature[b]	Mouritsen and Poulin (2002)	3	2716.509	20.20	0.000
January min. temperature[c]	Hudson et al. (1992)	3	2717.377	21.07	0.000
Summer mean max. temperature[c]	Haukisalmi and Henttonen (1990)	3	2717.540	21.24	0.000
Min. temperature[b]	Mouritsen and Poulin (2002)	3	2718.423	22.12	0.000
Humidity[b]	Mouritsen and Poulin (2002)	3	2720.264	23.96	0.000
Fire regime	Fuentes et al. (2007)	3	2721.427	25.12	0.000
Population age		3	2721.172	25.87	0.000
Rainfall[b]	Mouritsen and Poulin (2002)	3	2722.378	26.07	0.000
Founder population size	Paterson et al. (1998)	3	2724.379	28.07	0.000
Summer rainfall[c]	Haukisalmi and Henttonen (1990)	3	2727.266	30.96	0.000
Base model[d]		2	2730.649	34.34	0.000

Models are in descending order from most to least supported based on Akaike second-order information criteria (AIC$_c$). The set of candidate models differs between parasite groups as they use different transmission methods. For other abbreviations, see Table 1

K Number of parameters in a model

[a] The confidence set of models, i.e. >95 % of Akaike weights (ω)

[b] Mean value 2000–2011s

[c] During season of collection

[d] The base model, which included only the random effect for population

morphology alone) and *Anoplocephala* sp. In South Africa, seven species of strongyle have been identified that infect black rhino, while only one cestode has been identified, *Anoplocephala gigantea*. All of these are thought to be host specific to black rhino (Penzhorn et al. 1994; Stringer 2015). Strongyle nematodes are directly transmitted parasites—eggs develop into free-living stages which crawl onto vegetation and are subsequently eaten. *A. gigantea* is an indirectly transmitted tapeworm—eggs are eaten by an oribatid mite (Oribatida), which are subsequently thought to crawl onto vegetation before being accidentally eaten (Zajac and Conboy 2006).

To measure parasite abundance ideally autopsies would be performed on fresh carcasses. As we were working with a long-lived and critically endangered host species this was not possible. Faecal egg counts have previously been shown in other odd-toed ungulates and with similar parasite groups to be a broadly reliable indicator of parasite abundance (Nielsen et al. 2010; Stringer et al. 2014). For instance, Kjaer et al. (2007) found a positive correlation of 0.71 between worm burden and faecal egg count for the tapeworm *Anoplocephala perfoliata* in domestic horses (*Equus ferus caballus*). Interestingly, the high abundance of eggs within faecal samples found in black rhino may increase the accuracy of faecal egg counts (Denwood et al. 2012).

Here we use the term 'abundance' as described by Bush et al. (1997), in that we calculated an estimated intensity of infection within each host, but also included non-infected hosts in our analysis. Hence, our results may reflect both the prevalence and the intensity of infection within a population.

An information-theoretic approach was used to explain parasite abundance by comparing candidate models. The competing candidate set of models (hypotheses) was developed by consulting the literature (Tables 2, 3). Sample size for some populations was very small. Hence we used mixed models to test the relationship of candidate models to parasite abundance, and either generalised linear mixed models (GLMM) or linear mixed models (LMM) were used (see "Results"). Population could then be specified as a random effect, allowing us to utilise all samples collected, rather than reducing each population to a single mean value. Furthermore, a second-order Akaike information criterion (AIC$_c$) was used to compare competing models, which takes into account sample size. For GLMMs, a negative binomial distribution with a log link was used. In all models the parameters were the same except for the fixed effect. K relates to the number of parameters in each model (i.e. $K = 3 =$ fixed effect + random effect + intercept).

Models with the lowest AIC$_c$ were deemed to have the strongest support. Model selection was based on the top performing models that represented 95 % of Akaike weights (ω). A base model containing only the random effect was included in the competing set of models to investigate how much information in the data was not

Table 3 Information-theoretic table of candidate models explaining *Anoplocephala gigantea* abundance as a function of host rhinoceros density (rhino ha^{-2})

Model/hypothesis	Source	K	AIC$_c$	ΔAIC$_c$	ω
Host density[a]	Arneberg et al. (1998)	3	507.486	0.00	0.930
Mean max. summer temperature[a, b]	Haukisalmi and Henttonen (1990)	3	514.123	6.64	0.034
Max. temperature[c]	Atkinson et al. (2013)	3	515.084	7.60	0.021
Min. temperature[c]	Atkinson et al. (2013)	3	517.383	9.90	0.007
Base model[d]		2	517.427	9.94	0.006
Humidity[c]	Atkinson et al. (2013)	3	519.885	12.40	0.002
Fire regime	Fuentes et al. (2007)	3	522.491	15.01	0.001
Rainfall	Atkinson et al. (2013)	3	523.000	15.51	0.000
Population age		3	526.305	18.82	0.000
Founder population size	Paterson et al. (1998)	3	527.218	19.73	0.000
Summer rainfall[b]	Haukisalmi and Henttonen (1990)	3	528.601	21.12	0.000

Models are in descending order from most to least supported based on AIC$_c$. The set of candidate models differs between parasite groups as they use different transmission methods. For abbreviations, see Tables 1 and 2

[a] The confidence set of models, i.e. >95 % of ω

[b] During season of collection

[c] Mean value 2000–2011

[d] The base model, which included only the random-effect for population

being explained by competing models. To avoid overfitting (Zuur et al. 2009), within each model *K* was kept to a minimum by initially including only one fixed effect per model (excluding the base model which had no fixed effects). A suite of models with two fixed effects was then produced that contained the top performing predictor variable plus each of the other parameters in turn. As full models could not be used the information-theoretic approach could not be utilised fully in this study. However, we view this study as providing a useful framework which can be improved upon, either with further populations of black rhino, or with species that are not as rare as black rhino.

SPSS (IBM 2011) was used for all statistical calculations. Fire regime was estimated based on reserve records. Environmental variables were obtained by the South African Weather Service station closest to the reserve (mean distance 27.6 km) monthly, and varied extensively between reserves (Table 1).

Results

The directly transmitted strongyle-type nematodes were found in all populations except one, at a mean population abundance of 1918 eggs g^{-1} (e.p.g.) (range 44–4075 e.p.g., SD = 1438). The indirectly transmitted cestode, *A. gigantea*, was found in all populations at a mean population abundance of 228 e.p.g. (range 33–546 e.p.g., SD = 149).

Model fit when analysing the data utilising a GLMM with a negative binomial distribution and a log link for the strongyle parasite group was poor. Further investigation revealed that the data did not follow a negative binomial distribution; skewness was low (0.5), with the mean egg count (2280 e.p.g.) close to the median (2150 e.p.g.). Also, kurtosis was very low (−0.5) indicating a wide flat peak to the data, which was likely to be the reason why the data were considered non-normal based on the Kolmogorov–Smirnov test (statistic = 0.98, p = 0.001). This distribution is likely a result of combining data from multiple populations. While each individual population has an aggregated parasite distribution, when combined, different levels of the distribution peak for each population will create multiple peaks. This ultimately results in a single wide flat peak, which when viewed in a p–p plot does not seem to differ meaningfully from normality. This does not occur for *A. gigantea*, as egg counts for the different populations were much less variable. The competing set of models taken from single-factor model tables did not differ between using a GLMM and a LMM on untransformed data for the strongyle group. Hence, results from the LMM are presented and plotted (Fig. 1). While using a GLMM, no two-factor model improved on the top model. However, when using a LMM all two-factor models containing the top model improved on the original model, while all three-factor models including the top two models improved on all two-factors models. This is a clear sign of overparameterization, hence only one-factor models for the strongyle group are presented.

Using multi-model selection and inference to explain parasite abundance, host density models performed best for
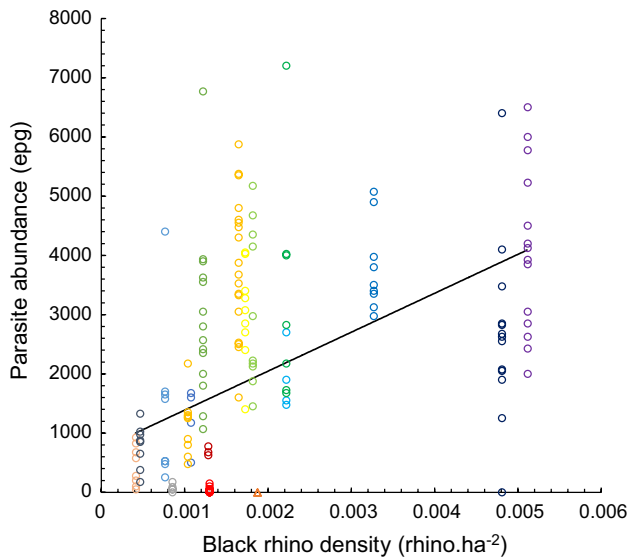
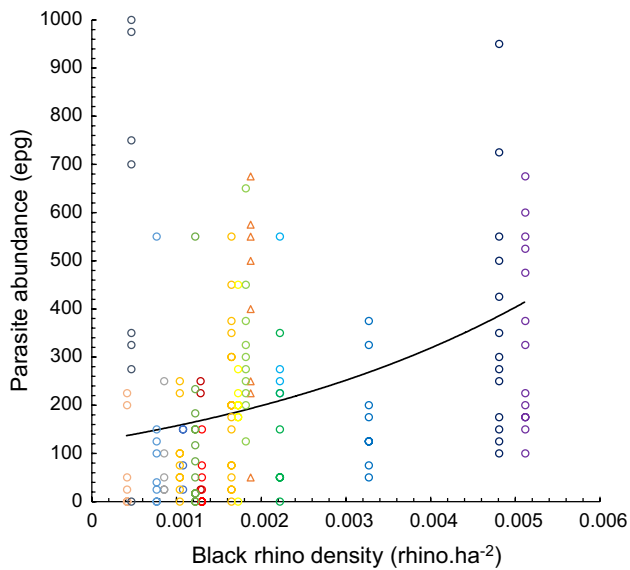**Fig. 1** Scatter plot showing strongyle abundance in host populations against the density of black rhino (rhino ha^{-2}) in that population. *Open circles* represent individual samples ($n = 160$), and the *colour* of the circle (available in the online version only) can be used to differentiate between different populations. The *triangle* represents all samples that came from the single population that was sourced from a Namibian source population. The *trend line* represents the fitted line using parameters from our results (linear mixed models)

Fig. 2 Scatter plot showing *Anoplocephala gigantea* abundance in host populations against the density of black rhino (rhino ha^{-2}) in that population. *Open circles* represent individual samples ($n = 160$), and the *colour* of the circle (available in the online version only) can be used to differentiate between different populations. *Triangles* represent individual samples that came from the single population that was sourced from a Namibian source population. Two data points are not included in this graphic for ease of display [2516 eggs g^{-1} (e.p.g.) × 0.0012 rhino ha^{-2}, 1875 e.p.g. × 0.0051 rhino ha^{-2}]. The *trend line* represents the fitted line using parameters from our results (generalised linear mixed models)

the directly transmitted, strongyle parasite group (Table 2; Fig. 1; coefficient 657,404.5, SE 212,871, intercept 730.5, SE 485.9). Host density contributed 100 % of ω, while all other models were implausible, receiving no support. For the indirectly transmitted *A. gigantea* the host density model performed best, contributing 93 % of ω (Table 3; Fig. 2; coefficient 235.4, SE 117.0, intercept 4.8, SE 0.3). Parasite abundance was again not explained by most environmental parameters, although mean maximum summer temperature was included in the confidence set of models ($\sum \omega > 0.95$) (Zuur et al. 2009).

Each predictor was added to host density to see if models with two fixed effects could improve on the host density model for *A. gigantea*. A model containing host density and mean maximum summer temperature was the only model to improve on the original host density model ($\Delta AIC_c = -0.35$, maximum temperature coefficient -0.06, SE 0.09, host density coefficient 188.1, SE 142.4, intercept 7.1, SE 3.0). However, auto-correlation between the two fixed effects in the model means that estimates of these parameters are not reliable, and the model table comparing the single fixed effects (Table 3) should be utilised.

Discussion

For directly transmitted parasites, we conclude that host density is the only predictor in this study that influences population-level parasite abundance. This is despite numerous other hypotheses predicting that environmental factors, such as temperature, rainfall, and humidity, will influence larval survival and hence are of importance to parasite abundance (Haukisalmi and Henttonen 1990; Paterson et al. 1998; Mouritsen and Poulin 2002; Fuentes et al. 2007; Atkinson et al. 2013). The relationship between primary host density and parasite abundance for indirectly transmitted parasites is thought to be more complex due to the influence of secondary host density (Stien et al. 2010). Despite this we show a clear relationship between primary host density and parasite abundance for the indirectly transmitted *A. gigantea* (Fig. 2). Secondary host density does not mask the relationship between primary host density and parasite abundance for *A. gigantea* and its black rhino host, perhaps because of the ubiquity of the secondary host across the landscape and between different populations of black rhino (Van Nieuwenhuizen et al. 1994).

The host density model was marginally improved for *A. gigantea* by also including mean maximum summer temperature. This weak negative relationship between summer maximum temperature and parasite abundance has been found previously in other mammal–cestode relationships, and is likely due to egg desiccation reducing abundance in hotter areas (Haukisalmi and Henttonen 1990).

Strongyle nematode eggs were found in all populations, except the single population that originated from a Namibian source population. The Namibian population's habitat and rainfall are very different from those of all directly studied populations, and it also has an extraordinarily low black rhino density (i.e. 0.00013 rhino ha^{-2}). Hence, it is possible that strongyles became extinct or never existed in the source population, or were not translocated with the host when reintroduced to the South African reserve.

There may be other mechanisms, rather than density-dependent transmission, that cause host density to drive parasite abundance. An individual's parasite abundance has been linked to their age. If a population is founded with younger individuals, then, as that population ages and grows denser, the age-structure within the population may change. However, in this study the age of a population had no impact on parasite abundance.

There was little or no support for models including only the random effect compared to mixed-effect models—indicating that the fixed effects in the supported models had substantial value in explaining variation in the response variable (parasite burden). The leading mixed-effect models might still be improved in the future by the addition of other fixed effects not tested here. These mechanisms may include host susceptibility, where inbred hosts may be more susceptible to parasite invasion, and within-host parasite community interactions, where competition and facilitation between parasite species may limit or increase parasite abundance (Pedersen and Fenton 2007). For instance, it has been shown that host susceptibility may affect variation in parasite abundance between individuals (Paterson et al. 1998; Poulin 2007).

Black rhino are a critically endangered and elusive species which meant that samples were not readily available, and sample size for some populations was very low. However, black rhino may be an excellent model organism for testing these hypotheses, due to their solitary nature (Altizer et al. 2003), the slow rate of any natural changes in population size, and the host species specificity of the parasites studied. We also used modern statistical techniques that meant populations did not have to be reduced to a single statistical average (mixed models). Furthermore, by utilising the fortuitous experiment created by the translocation and reintroduction of black rhino in South Africa we were able to compare multiple populations of the same host-parasite interaction, a novel method for investigating epidemiological hypotheses. Hence, despite the restrictions of small sample size, and using faecal egg counts rather than directly measuring abundance, we were still able to show that host density is a singularly powerful predictor of macroparasite abundance for a directly transmitted parasite, and a highly influential predictor within an indirectly transmitted parasite.

Our demonstration of a previously assumed mechanism for parasite abundance gives real-world evidential support to epidemiological theory. This may have a wide range of implications for parasite control (Gortázar et al. 2006), disease prevention (Anderson and May 1991), and conservation (Woodroffe 1999). The assumption of density-dependent transmission is often used for determining the basic reproductive number (Anderson and May 1991)— the expected number of secondary cases arising from one infected individual, and hence underpins much of current epidemiology. It also underpins some key questions in parasitology, such as whether sub-clinical parasitism can regulate host population size (Hudson et al. 1992). The dominance of host density in explaining population-level parasite abundance also supports the expectation of a population density threshold (Lloyd-Smith et al. 2005), below which a parasite will become extinct. This paper, then, gives support to many current parasite- and disease-control programs that work to reduce the density of susceptible individuals. As susceptible host density is a determinant of parasite abundance, reducing susceptible host density by rising vaccination rates should increase the likelihood of local parasite extirpation.

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