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From parasite encounter to infection: multiple-scale drivers of parasite richness in a wild social primate population

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Title: From parasite encounter to infection: multiple-scale drivers of parasite richness in a wild social primate population

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Abstract

Host parasite diversity plays a fundamental role in ecological and evolutionary processes, yet the factors that drive it are still poorly understood. A variety of processes, operating across a range of spatial scales, are likely to influence both the probability of parasite encounter and subsequent infection. Here, we explored eight possible determinants of parasite richness, comprising rainfall and temperature at the population level, ranging behavior and home range productivity at the group level, and age, sex, body condition, and social rank at the individual level. We used a unique dataset describing gastrointestinal parasites in a terrestrial subtropical vertebrate (chacma baboons, *Papio ursinus*), comprising 662 faecal samples from 86 individuals representing all age-sex classes across two groups over two dry seasons in a desert population. Three mixed models were used to identify the most important factor at each of the three spatial scales (population, group, individual); these were then standardised and combined in a single, global, mixed model. Individual age had the strongest influence on parasite richness, in a convex relationship. Parasite richness was also higher in females and animals in poor condition, albeit at a lower order of magnitude than age. Finally, with a further halving of effect size, parasite richness was positively correlated to day range and temperature. These findings indicate that a range of factors influence host parasite richness through both encounter and infection probabilities, but that individual-level processes may be more important than those at the group or population level.

Understanding the forces driving the spread of infectious diseases in wild animal populations is becoming increasingly important. From a theoretical perspective, parasites and pathogens are thought to play a primary role in driving population dynamics and evolutionary processes (Anderson and May 1978; Tompkins 2001). In population dynamics, wildlife diseases can lead to rapid declines in threatened species (Smith et al. 2009) and pose a growing threat as a source of human zoonoses (Jones et al. 2008). In evolutionary processes, infectious diseases have long been proposed as a significant pressure in the shaping of mating and social systems (Freeland 1976), partly because frequent contact rates between mates and social partners might greatly facilitate the transmission of pathogens.

Since most animals are infected by several parasite species, and even individually benign infections can have a cumulative pathogenic impact (McCallum 1994; McCallum and Dobson 1995), an understanding of the factors that determine the number of parasites an individual carries (i.e. host parasite richness) may be crucial to elucidating patterns of host vulnerability and the wider impacts of parasitism on host ecology and evolution (Bordes and Morand 2009). Indeed, host parasite richness has been linked to a diverse range of micro- and macro-ecological and evolutionary processes, such as adult mortality rates (Simkova et al. 2006), the population-level maintenance of polymorphisms in immune genes such as the major histocompatibility complex (mammals: Goüy de Bellocq et al. 2008; Simkova et al. 2006), and species diversification (e.g. primates: Nunn et al. 2004). Parasite richness is also becoming an increasingly important metric for understanding the impacts of anthropogenic disturbance on threatened taxa (e.g. primates: Chapman et al. 2005b; Gillespie et al. 2005; Valdespino et al. 2010).

Despite its importance, we know surprisingly little about the determinants of host parasite richness. Indeed, theoretical progress in this area is constrained by the dearth of empirical research - and this is particularly true for field data - and a lack of information necessary for modeling (Tompkins et al. 2010). Within species, a variety of forces can potentially interact with host susceptibilities to shape parasite transmission across a range of ecological scales, from populations to individuals (Tompkins et al. 2010). At the population level, seasonal environmental factors, such as increasing rainfall and temperature, are expected to increase parasite richness (Nunn and Altizer 2006), along with intrinsic factors such as population size and density, number of groups (for social species), and degree of population fragmentation (Chapman et al. 2005b; Morand and Poulin 1998; Nunn and Altizer 2006). At the group level (in socially structured populations), the group size, area and productivity of the home range, and daily travel distance might all affect parasite richness (Nunn and Altizer 2006; Vitone et al. 2004) (but see also Bordes et al. 2009; Snaith et al. 2008). Finally, at the individual level, a wide range of traits might influence parasite richness including body mass, age, social rank, reproductive state, hormone levels, immune status, and genetic constitution (for reviews, see : Nunn and Altizer 2006; Tompkins et al. 2010). However, identifying independent, contemporaneous, effects of such myriad factors across spatial scales, and assessing their relative importance, remains a substantial challenge – especially when the complexity of factors involved necessitates an integrative approach, using concurrent monitoring of individuals and their environment through a longitudinal, rather than cross-sectional, design (Tompkins et al. 2010).

[Please insert Table 1 here]

Here we investigate the relative importance of a range of factors that might influence host parasite richness. We structure our analysis to recognise the multiple spatial scales over which these factors operate (i.e. the population, group, and individual), and specify whether their mode of action is most likely to affect parasite richness through the probability of encounter with parasites or the susceptibility to infection following encounter (sensu Nunn & Altizer, 2006). Our analysis focuses on patterns of gastrointestinal parasite richness in a wild social primate population of chacma baboons (*Papio ursinus*). While individually-based parasite studies in wild primates are uncommon (Nunn and Altizer 2006), they are of particular interest for at least three reasons. First, wild primates are perhaps the most serious wild source of cross-species disease transmission to humans, with sometimes catastrophic consequences for public health (e.g. ebola: Leroy et al. 2004). Second, primates are a taxon of high conservation concern, with disease posing a serious threat in some populations (Chapman et al. 2005a). Finally, studying a social species will contribute to our understanding of the dynamics of parasite transmission in group-living organisms that may be especially vulnerable to infectious diseases (Altizer et al. 2003).

In Table 1, we detail the eight hypotheses tested. At the population level, our hypotheses predicted that parasite richness would increase with wet (H1) or hot (H2) conditions. At the group level, we predicted that parasite richness would be higher in more productive home ranges (H3), or in association with more extensive ranging behavior (H4). At the individual level, we predicted that parasite richness would be influenced by age (H5), sex (H6), physical condition (H7), and social rank (H8). Finally, we investigated the relative magnitude of the effects of all those factors that influence parasite richness, across spatial scales, in a single global model.

MATERIALS AND METHODS

Study system

Our study was carried out on wild chacma baboons on the edge of the Namib Desert, in central Namibia, at Tsaobis Leopard Park (22^{o}23'S 15^{o}45'W). Tsaobis is characterized by mountains and rocky foothills that descend to rolling gravel and alluvial plains. Vegetation is sparse, comprising grasses and herbs, shrubs and dwarf trees, although patches of aquifer-dependent woodland grow along the ephemeral Swakop River bordering Tsaobis to the north. The landscape is arid and strongly seasonal: annual rainfall is low (mean ± SD: 123 ± 77mm, n=68 years) and falls only during the austral summer, primarily between December and April. The altitudinal range is 683–1445m. Shade temperatures can approach zero on winter nights, but exceed 40^{o}C on summer days.

Data were collected during two field seasons (June to December 2005, May to October 2006) on two social groups. These comprised, in October 2006, 9 adult or subadult males, 16 adult females, and 32 juveniles for the larger group (Troop J) and 7 adult or subadult males, 9 females and 16 juveniles for the smaller group (Troop L). All subjects were fully habituated and individually identifiable.

Faecal sampling and analysis

A total of 662 faecal samples were collected immediately after defecation from 86 individuals. The faeces were homogenized and a portion (mean ± SEM: 0.73 ± 4.10^{-3}g) was weighed and stored in 4 ml of 10% buffered formalin solution immediately after collection, at room temperature. A mean of 8.1 samples per individual (SD=6.40, median=7, range: 1-37), and 53.4 samples per month (SD=27.8, median=61, range: 17-104), were collected through the study period. Faecal analysis was carried out using the modified formol-ether sedimentation technique (Allen and Ridley 1970), using merthiolate-formalin as a stain. Parasitic eggs, larvae, trophs, and cysts were recorded by species or morphotype, with measurements made to the nearest 0.1 mm using an ocular micrometer fitted to a compound microscope (further details on parasite indentification see Appleton et al. 1991; Appleton et al. 1986) Due to difficulties in identifying rounded-up trophozoites or pre-cystic stages within small-sized amoebae, *Entamoeba hartmanni*, *Endolimax nana*, and *Dientamoeba fragilis* were pooled together into a morphotype designated as “small amoebae” (Fiennes 1972). Similarly, *Entamoeba chattoni, Entamoeba histolytica, Entamoeba dispar* and *Iodamoeba buetchlii* were pooled as “medium amoebae”. Host parasite richness was estimated for each faecal sample by the number of different species/morphotypes recorded. We assumed that when species/morphotypes were present we were able to detect them, but some false negatives may have occurred if a species was harder to detect when its intensity of infection or reproductive output were lower.

Population-level environmental conditions (H1-H2)

Rainfall was monitored on a daily basis. Similarly, maximal temperatures (Tmax) in the shade were recorded on a daily basis and were available for 179 days (78 % of the study period). Tmax varied across the study period (maximal mean ± SD = 31.9 ± 4.8, range = [20-41]), with maximal values during summer (December) and minimal values in winter (July) in both years. Minimal and maximal daily temperatures were strongly correlated (Pearson’s correlations: rho= 0.71, n= 283, $P < 2 .10^{-16}$), so only Tmax was used here.

Group-level range productivity and ranging behavior (H3-H4)

Group location waypoints were taken at half-hour intervals over at least 100 full-day follows for each group conducted between May and November, thus covering periods of both high and low plant productivity in the late austral summer and winter. Minimum convex polygons (Heupel et al. 2004), were constructed around these waypoints in ArcMap Version 9.3 using HawthsTools extension package (http://www.spatialecology.com/htools/) to provide a simple estimation of the home range boundaries over the study period. Within the home ranges, plant production was estimated using the Normalized Difference Vegetation Index

(NDVI: Pettorelli et al. 2011): a satellite-based vegetation index based on the information collected by the Satellite Pour l'Observation de la Terre-Vegetation (SPOT VGT). NDVI is derived from the red to the near-infrared reflectance ratio [NDVI = (NIR-RED)/(NIR+RED)], where NIR and RED are the amounts of near-infrared and red light, respectively, reflected by the vegetation and captured by the satellite sensor (Jensen 2006). We use a spatial resolution of 1×1 km available at 10-day intervals in each troop's home range (J and L). The home range boundaries were also used to determine the monthly home range size for each group (J: mean± SD= 12.3± 6.5 km^2, range = [5-27], L: 26.8 ± 13.5 km^2, [8-49]), while the waypoint locations were also converted into paths to measure daily travel distance for 208 days (92% of the study period) (J: mean ± SD = 5.9 ± 0.8, range = [5.2-8.0], L: 5.9 ± 1.5, [2.6-7.3]). In the analyses, we use the mean daily travel distance per month.

Individual traits (H5-H8)

We investigated the influence of age, sex, body condition, and dominance rank on parasite richness. Age and condition were determined through individual inspection during troop captures: in J troop, 42 individuals (of 52) were captured in July 2005 and 55 (of 57) in October 2006, in L troop 32 individuals (of 32) were captured in October 2006. Briefly, troops were captured using individual cages baited with corn cobs and set-up at dusk. The baboons were captured at dawn, anaesthetised using tiletamine-zolazepam, and all processed within a day to be released together the following morning when fully awake. Age was estimated through dentition: tooth eruption schedules for wild baboons were used to assign age up to the eruption of the molars, while age beyond this point was estimated on the basis of molar wear (Huchard et al. 2009a). Body size was estimated by crown-rump length, measured during capture. Physical condition was measured through morphometric data. Because there is no consensus on the best way to index condition (Green 2001; Lukaski 1987), we used three different measures: (1) body mass, (2) mean skinfold thickness (MST), averaged across the triceps, abdominal, and subscapular regions, and (3) mid upper-arm fat (MUAF), a combination of the triceps skinfold thickness and the mid upper-arm circumference:

$$MUAF = \frac{SC}{2} - \frac{\pi S^2}{4}$$

where S = triceps skinfold thickness and C = upper-arm circumference (Gibson 2005). In order to summarize these three measures into one general index, we conducted a principal component analysis (PCA). This analysis included all data from all individuals across 2005 and 2006 for which the three indices were available (49 out of 51 individuals). The contribution of each measure to the first component (estimated through PCA square cosinus) was 0.71, 0.75 and 0.91 for MUAF, MST and body mass, respectively. The first principal component of the PCA accounted for 81 % of the total condition variation, and was then used as the body condition variable in our analyses. The mean time difference between our assessment of parasite richness (i.e. a given faecal sample) and the closest estimate of age/condition (at capture) was 73.4 ± 46.9 days.

Sex was determined by visual inspection. To establish dominance ranks, agonistic and approach/avoid interactions (following Smuts 1985) were collected using *ad libitum* and focal observations across the study period (for details see: Huchard et al. 2009b). In order to control for differences in troop size, an animal's absolute rank is divided by the total number of individuals in the group – thus alpha animals have the smallest rank. Ranks were estimated for sexually mature individuals (females reach sexual maturity around 4 years of age and males around 5 years of age: e.g. Altmann and Alberts 2003).

In summary, the data available for each individual variable were as follows: 86 individuals (662 samples) for sex, 76 individuals (613 samples) for age, 73 individuals (456 samples) for body condition, and 44 individuals (298 samples) for dominance rank.

Statistical analyses

To test the influence of socio-ecological factors on individual parasite richness, we ran five sets of Linear Mixed Models (LMMs) with parasite richness as the response variable. Although our response variable was discrete, we used LMMs rather than Generalized Linear Mixed Models (GLMMs) due to the need to incorporate temporal autocorrelation in the analysis (see below) which is so far only possible using LMMs fitted with a Gaussian distriution (Pinheiro and Bates 2000). The residuals of all models were constant and normally distributed as checked by Q-Q plots and Shapiro-Wilk normality tests ($P > 0.05$ in all models). However, we also ran our models using GLMMs with a Poisson distribution (but without the autocorrelation term) and obtained the same results. All models tested include "baboon identity" nested in "troop membership" as random effects, to account for the non-independence of multiple data collected from the same individual within a troop. Because estimations of parasite richness can increase (in a non-linear way) with faecal sample weight (Walther et al. 1995), we also controlled in each model for a potential effect of sample weight by introducing it as a fixed factor at the third polynomial degree. This degree was selected using an information theoretic approach: briefly, for each of the five models presented below, we initially compared the Akaike Information Criterion (AIC) scores of three alternative models with faecal sample weight fitted at the first, second and third order, and found that the latter consistently performed best (i.e. presented an AIC score at least two points lower than the alternative models). This third order relationship was further confirmed graphically by an asymptotic curve linking parasite richness to faecal sample weight. As a final statistical control, we also included the year of sample collection as a fixed effect. However, this was not found to be significant in any model examined and was therefore excluded in the final set of analyses, for simplicity.

The first set of analyses occurred in three successive stages, exploring the effects of the different variables at each considered scale (population, group, individual). The first model was designed to investigate the effect of a population-level factor on host parasite richness, specifically the effects of the maximum daily temperature (Tmax) averaged over the seven-day period during which the individual was sampled (Hypothesis H2; the effects of rainfall, Hypothesis H1, were tested independently due to the limited number of rainfall events: see below). We further explored if Tmax collected before the time of faecal collection predicted parasite richness better than contemporary measures by using an additional subset of lagged models for Tmax. These models included maximum daily temperature averaged across the seven-day period occurring one, two, three, four or five weeks before the sampling date, compared by AIC and the Tmax p-value. The model including Tmax averaged four weeks before sampling performed best (see Supporting Information Table S1), and was therefore used in further analyses (the global model).

The second model was designed to investigate the group-level effects of home range productivity (H3) and ranging behavior (H4.a,b) on host parasite richness. Therefore, it included home range NDVI, home range area, and daily travel distances as fixed effects. As for Tmax, we also tested the NDVI measure lagged for 10, 20 and 30 days before sampling (as NDVI data were available for 10 days intervals), but found that contemporary NDVI performed best (see Supporting Information Table S2).

The third model was designed to investigate the first three of our four individual-level effects, namely age (H5), sex (H6), and body condition (H7), on host parasite richness. These variables were all included as fixed effects in the same model. Age was introduced at the third polynomial degree to account for a potential non-linear effect, which was suggested by graphical exploration of the raw data and by a model AIC score 2 points lower than the alternative models (i.e. with first or second polynomial degrees). Crown-rump length was additionally introduced in the model, to control for body size when investigating condition effects (Jakob et al. 1996). To investigate the effects of our fourth individual-level factor on host parasite richness, namely social rank (H8), we ran the individual-level model again for the subset of animals for whom social ranks were available (N = 44 adults), adding social rank as a fixed effect. We also included a sex*rank interaction term to account for profound sex differences in the acquisition of rank in this species (stable and heritable ranks among females; fluctuating ranks determined by fighting ability among males).

Following our analyses of the factors determining host parasite richness at each of the three spatial scales, we ran a final model to integrate our findings and to explore the relative importance of each of these factors across scales. This global model included all the variables that were found to be significant in the single-scale models, and was run using the full sample (juveniles and adults). In order to compare the effect sizes of each variable in this global model, all variables were standardized to have a mean of zero and a standard deviation of one. In each model, we controlled for the temporal dependence of observations (i.e. temporal autocorrelation) by including a temporal correlation structure of the residuals. We compared the AIC of models having an autoregressive structure of order 1 to 7 (i.e. 1 to 7 lags of dependence between observations). In all the model sets described above, the final model with order 5 obtained the lowest AIC and was therefore selected. This was implemented using the correlation structure corARMA (Pinheiro and Bates 2000) in the nlme package of R 2.8.0 (R Development Core Team, 2003). The significance of fixed effects was evaluated using F-tests according to the principle of marginality, testing each fixed effect coefficient when all other fixed effects are present in the model. Statistical significance is reported for full models (i.e. inferences were drawn with all predictors present) throughout (Mundry and Nunn 2009; Whittingham et al. 2006). The significance of random effects was tested by performing likelihood ratio tests (following a $\chi 2$ distribution) comparing two models differing only in the presence of this effect. In all models, the random effect "troop identity" did not significantly affect individual parasite richness (Likelihood Ratio Test, $P > 0.05$) whereas "baboon identity" always had a significant effect (Likelihood Ratio Test, $P < 0.001$).

RESULTS

A total of 11 species or morphotypes of intestinal parasites including five nematodes, one acanthocephalan and nine protozoan, were found in the faeces of *P. ursinus* at Tsaobis (Table 2). One type of nematode egg, that occurred in 6% of individuals, could not be identified further (named Egg 1 hereafter). Based on species/morphotype, the median individual parasite richness was 3.00 (range= 0-8, mean ± SD= 3.2 ± 1.3).

[Please insert Table 2 here]

Population-level environmental determinants of parasite richness (H1-H2)

Host parasite richness decreased across the dry season (Fig. 1). However, a peak was observed in November 2005 (median= 4.0; mean ± SD= 3.8 ± 1.3), 10 days after the first and only rain recorded in the study period (16mm, 29/10/05). During November, average individual values of parasite richness were significantly higher than in October 2005 (median= 3.0, mean ± SD= 2.9 ± 1.1, Mann-Whitney test: W= 1345.5, n= 86 individuals, $P = 0.002$), supporting our hypothesis that parasite richness increases after rainfall (H1). This difference was driven by protozoans (analyses excluding protozoans: W= 3435, n=86, $P = 0.25$).

The best temperature predictor was Tmax averaged across the fourth week preceding the sampling date (Table 3, Table S1), suggesting a lagged response of parasite richness. Thus, host parasite richness was higher following hot weather four weeks earlier (Fig. 2).

Group-level ranging determinants of parasite richness (H3-H4)

Host parasite richness increased when groups travelled further, as predicted by hypothesis H4.b. In contrast, there was no effect of home range NDVI (H3, for either contemporary or lagged measures, Table S2) or home range area (H4.a) (Table 3).

Individual-level trait determinants of parasite richness (H5-H8)

Across all individuals, host age, sex, and body condition (together with body size, included as a control variable for condition) influenced host parasite richness (Table 3). Host parasite richness initially increases with age (supporting H5.a), but then peaks around sexual maturity, following which it declines (supporting H5.b) (Fig. 3). The sex effect indicated that parasite richness was higher in females than in males (contrary to H6), while the condition effect suggested that animals in better condition exhibited lower parasite richness (in support of H7.b) (Table 3, Fig. 4). Among adults only, we found no evidence that dominance rank affected parasite richness (failing to support H8), while the effects of age and sex were no longer significant ($P > 0.05$ in each case). The age effect remained non-significant when age was included at the first or second order (instead of the third) in this last model (after sexual maturity, the relationship between age and parasite richness appears roughly linear, Fig. 3). However, adults in better condition still exhibited lower parasite richness than those in poor condition ($F = 4.43$, $P = 0.03$).

[Please insert Table 3 here]

Integrated global model for multiple-scale effects on parasite richness

The integrated model corroborated the single-scale models (Table 4). A comparison of the effect sizes indicates that age had by far the strongest influence on parasite richness (effect size = 3.92 ± 1.46) followed by sample weight (effect size = 2.75 ± 1.03). Sex and body condition (together with body size) had comparable effect sizes, which were almost an order of magnitude smaller than the age effect (effect size mean ± SD = -0.47 ± 0.19 and -0.43 ± 0.13 respectively). Finally, travel distance and lagged Tmax had the smallest effects (effect size = 0.21 ± 0.06 and 0.22 ± 1.07 respectively).

[Please insert Table 4 here]

DISCUSSION

Identifying the determinants of multiple parasite infections in wild animals is crucial for both fundamental and applied, conservation-based, reasons, since they may represent important drivers of both evolutionary change and population dynamics. However, there are surprisingly few studies of the drivers of parasite richness in wild populations (Tompkins et al. 2010), and most of these have worked at a single spatial scale. In this study, we found that gut parasite richness in a wild primate population increases with higher rainfall and maximum daily temperature at the population level, and with longer daily travel distances at the group level, as well as showing more complex covariation with age, sex, and body condition at the individual level. These findings, and how they compare to previous studies on parasite richness in wild populations, are summarised in Table 5. Finally, integrating our analyses across the three scales of population, group, and individual, suggests that host age is the primary predictor of parasite richness.

[Please insert Table 5 here]

At the population level, we observed significant effects of rainfall and maximum daily temperature on host parasite richness, indicating an important influence of climatic conditions on parasite encounter rates. The increase in water-borne protozoan parasites associated with rainfall represents a preliminary result since it is based on only a single rainfall event. Nevertheless, it provides circumstantial evidence that precipitation can increase parasite richness on a short timescale (H1). Parasite richness also increased following a period of hot weather but with a four-week lag (H2). The mechanisms linking temperature to gastro-intestinal parasite prevalence have been extensively studied, with several species of helminths requiring a minimum temperature for development (Boag 1985), having shorter generation times at relatively high temperatures, and/or producing more intermediate stages in their life cycle when temperature increases (Pietrock and Marcogliese 2003). Protozoan taxa are similarly affected, commonly displaying higher reproductive rates at higher temperatures (Rodriguez-Zaragoza 1994). The lagged response most likely reflects the cumulative time required by the free-living stages of parasites to react to environmental variation and for the host to be exposed to, and contaminated by, the growing populations of infectious parasitic forms.

At the group level, we found that longer daily travel distances (H4.b) but not larger home ranges (H4.a) were associated with higher host parasite richness. This supports the idea that more intensive movement patterns within a relatively stable home range, rather than variation in the home range area itself, are associated with increased parasite exposure and subsequent infection with parasites that accumulate in the environment and mature in the host to produce ova (Nunn and Altizer 2006). The lack of association between home range NDVI and parasite richness (H3) further suggests that group-level changes in parasite encounter rates primarily result from the group's behavioral response to environmental variation rather than fluctuations in the density of infectious parasite stages, i.e. the baboons encounter more parasites because their groups are travelling further, not because there are more parasites to encounter per unit distance travelled.

At the individual level, we found co-variation between parasite richness and age, sex and body condition. Previous research on the age-parasite richness relationship (H5) has produced inconsistent results when assuming a linear pattern (Table 5). Our finding of a non-linear relationship, positive before sexual maturity but negative afterwards, might help to explain these inconsistencies – and reflect a combined effect of both encounter and infection probabilities. In the first case, the positive part of the curve might reflect cumulative exposure to parasites if the probability of encountering new parasite species is constant over time (Nunn and Altizer 2006). This would suggest a relatively slow rate of acquisition of new infections by young animals in this population. In the second case, the negative part of the curve, exhibiting a weaker slope, might reflect an improved adaptive immune response following repeated exposures to parasites (Hudson and Dobson 1997) and/or better survivorship of those individuals possessing stronger immune defenses against multiple infections. This hypothesis is supported by a recent study in this same population, where MHC heterozygotes (class II *Mhc*-DRB region) appeared to show higher survivorship (Huchard et al. 2010). Heterozygosity at MHC class II loci has already been found to mediate individual parasite richness in natural populations (Goüy de Bellocq et al. 2008; Oliver et al. 2009). Multiple infections might thus constitute the selective pressure increasing the mortality rate of individuals with low MHC diversity, if they display limited ability to fight multiple parasites, as previously found in fish hosts (Simkova et al. 2006). Notably, a recent comparative primate study found that parasitic nematode richness associated positively with the nonsynonymous nucleotide substitution rate at the functional part of the MHC molecule, but not with MHC allelic diversity (Garamszegi and Nunn 2011). It is also possible that the weaker relationship linking age to parasite richness after sexual maturity might at least partially reflect the stabilization of individual parasite communities when they have reached a given threshold, mediated through competitive interactions among multiple co-infecting parasites (decreasing the probability of subsequent infection by additional parasite species) (Graham 2008).

We also found that females harbour more parasite species than males (H6). Although males are generally found to be more susceptible to parasitism than females (e.g. Klein 2004), results from primate field studies have been less consistent, with several reported cases of female-biased parasitism (e.g. Clough et al. 2010; reviewed in Nunn and Altizer 2006). In this case, there is no reason to expect female baboons to have a higher probability of encounter with parasites than males, so the most likely explanation for this difference is that females have a higher susceptibility to infection. One possibility is a social effect, given that all adult males outrank all adult females, but the lack of a sex*rank interaction does not support this. Alternative explanations may relate to the costs of reproduction in females, including the production of exaggerated sexual swellings when cycling and the nutritional stress associated with pregnancy and lactation, or to complex interactions between sex hormones and immune status. A recent field study in lemurs reported immune-enhancing effects of testosterone on parasite species richness, suggesting that differences in immune responses due to sex steroids might potentially lead to female-biased parasitism, at least in the case of host parasite richness (Clough et al. 2010).

Parasite richness was higher in poor-condition animals (H7.b) but there was no evidence that dominant animals carried more or fewer parasite taxa (H8). Our findings for the effects of physical condition corroborate the results of the one previous study to date that has also explored this relationship (Lello et al. 2005). The negative association between body condition and parasite richness suggests a role of infection rather than encounter probability, but the direction of the causal arrow remains uncertain: while poor condition might reflect a host's weak capacity to fight parasites on the one hand, it's also possible that the deleterious effects of multiple infections could lead to poor condition on the other. In the latter case, although most of the parasites reported here are not thought to be highly pathogenic, some might still impact baboon health (Ruch 1959). The amoeba *E. histolytica* can cause severe diarrheal and dysenteric diseases, and affect the liver, lungs, brain, and other areas; while others like *B. coli* can become pathogenic if the host's natural resistance is depleted by a poor diet (Ruch 1959). Whatever the causal direction, the observed association may help to explain why females in better condition in this population display a higher reproductive success (Huchard et al. 2009b). Our lack of rank effect was in contrast to theoretical expectations but consistent with most previous empirical studies in primates (Table 5), and may reflect confounding co-variation between rank and condition.

When focusing solely on adults, body condition remained the only individual trait influencing parasite richness. In comparison with the full model including juveniles, the disappearance of both age and sex effects reflects either decreased statistical power arising from a smaller sample, or a weaker influence of such traits after sexual maturity. The latter hypothesis is plausible in the case of age, since the slope of the relationship linking age to parasite richness weakens in adulthood (Fig. 3), but seems counter-intuitive in the effect of sex, which is usually reinforced among sexually mature individuals. Given that sex ratios are relatively balanced in both our full and restricted sample, the disappearance of this effect among adults might reflect a genuine pattern. Post-hoc interpretation is necessarily speculative, but could involve parental investment or maternal effects preferentially biased towards male offspring, which might translate into improved parasite resistance in early life (Hayward et al. 2010) - although the hypothesis of sex-biased maternal investment has not been strongly supported by empirical studies of non-human primates so far (Bercovitch 2002; Brown 2001).

The final global model integrating variables across scales largely confirmed the results obtained within scales (all variables previously found to be significant in their respective single-scale models remained significant in the multi-scale model), but also emphasized the importance of working at multiple ecological scales. Comparing the effect sizes of each variable in the global model suggests that the individual-level factors have a higher influence on patterns of variation in parasite richness than population- or group-level factors. In fact, age had by far the biggest effect on parasite richness, followed by sex and body condition, and finally by maximal daily temperature and daily travel distance. As such, the global model suggests that, while variation in encounter probability at both the population and group level do influence host parasite richness, the strongest effects are related to both encounter and infection probabilities at the individual level. Two areas of uncertainty in this interpretation should be highlighted. First, due to the difficulties involved in working at wider spatial scales with large social vertebrates, our sample of groups and populations is necessarily small. Similarly, we only sample one season (the dry winter season) over two years, and it is possible that in other seasons and/or years different patterns would be obtained. Extrapolation of our conclusion (that individual-level processes play the predominant role) beyond the sample and conditions investigated here should therefore be made with caution. Second, estimation of the relative importance of encounter and infection probabilities at the individual level is challenging. On the one hand, the effects of body condition (and probably sex) emphasize the importance of susceptibility to infection at the individual level. On the other, the age effect includes both encounter and susceptibility to infection, with the former having the strongest effect (since the negative relationship between age and parasite richness after maturity is relatively weak). While neither of these uncertainties can be fully resolved here, they do help to highlight those areas that might be prioritized for further research.

In conclusion, these findings demonstrate that host parasite richness in animal populations may be associated with a range of factors operating on multiple scales. In this case, parasite richness is highest in poor-condition females at the time of sexual maturity, when their social group is travelling longer daily distances, and when environmental conditions are characterized by high rainfall and temperature. This study also suggests that individual traits, acting through both encounter and infection rates, can have a higher impact on parasite richness than group- or population-level factors acting through encounter rates alone. Our results emphasise the value of integrative approaches based on the longitudinal sampling of known animals in well-documented ecological contexts, and suggests that such a design can provide unique insights into the relative importance of different factors shaping host parasite richness and its impact in wild populations.

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Table 1. Potential factors influencing host parasite richness explored in this study. Factors are grouped by the scale at which they operate (population, group, and individual). Further information is also provided on the proposed mechanism (whether each factor is more likely to influence parasite richness through the probability of parasite encounter or susceptibility to infection following encounter). The positive effect of a considered factor is noted (+), and a negative effect is noted (-).

Scale	**Factor**	**Hypotheses under test**	
Population	Rainfall	H1	(+) encounter probability ~ due to the accelerated development, replication or survival of parasites in wetter conditions (Nunn and Altizer, 2006).
	Temperature	H2	(+) encounter probability ~ due to the accelerated development, replication or survival of parasites in hotter conditions (Nunn and Altizer, 2006).
Group	Home range productivity	H3	(+) encounter probability ~ because vegetation can be a surrogate measure of environmental moisture and thermal conditions for parasites (Bavia et al., 2001) or can represent a breeding or sheltering site for parasites (Ceccato et al., 2005; Lindsay et al., 1991)
	Ranging behavior	H4.a	Home range size: (+) encounter probability ~ due to an increased probability of encounters with parasites in a larger home range (Nunn and Altizer, 2006).
		H4.b	Daily travel distance: (+) encounter probability ~ due to an increased probability of encounters with parasites in a more intensively used home range (Nunn and Altizer, 2006).
Individual	Age	H5.a	(+) encounter probability ~ due to an accumulation of parasites in older individuals resulting from a stable probability of encounters with new parasites over time (Nunn and Altizer, 2006)
		H5.b	(-) susceptibility to infection ~ due to a reinforced immunity in older individuals following repeated contacts with multiple parasites (Hudson and Dobson, 1997)

	Sex	H6	**(+ males)** encounter probability ~ higher parasite richness in males due to higher consumption of food and thus more opportunity to eat contaminated items (Nunn and Altizer, 2006)
			(+ males) susceptibility to infection ~ higher parasite richness in males (Zuk and McKean, 1996), due to immunosuppression typically resulting from elevated testosterone levels (Roberts et al., 2004)
	Physical condition	H7.a	**(+)** exposure probability ~ animals that eat more are in better physical condition but also have more opportunity to eat contaminated items (Nunn and Altizer, 2006)
		H7.b	**(-)** susceptibility to infection ~ due to a better ability to resist infections for animals in good physical condition (Irvine et al., 2006)
	Social rank[1]	H8.a	**(+)** encounter probability ~ higher parasite richness in dominant individuals due to higher consumption of food and thus more opportunity to eat contaminated items (Nunn and Altizer, 2006)
		H8.b	**(-)** susceptibility to infection ~ higher parasite richness in subordinate individuals due to stress compromising immunocompetence (Nunn and Altizer, 2006)

[1] Here assuming high social rank for dominant individuals, low social rank for subordinates

Table 2. Individual patterns of parasite infection (662 samples, 86 individuals), with species/morphotypes ordered by prevalence. The "Medium Amoebae" category includes *E. histolytica, E. dispar* and *I. buetchlii.* The "Small Amoebae" category includes *E. hartmanni, E. nana,* and *D. fragilis*. "Egg 1" corresponds to an unidentified nematode species. For nematodes, the median and range of intensity of infection is expressed in egg per gram. For protozoans, the intensity of infection is expressed as a score on a 5-point semi-quantitative scale (0-4). Parasite prevalence is expressed as the number of individuals infected by a given parasite species (or category in the case of medium and small amoebae) divided by the total number of individuals, and is given in percentage.

Species	**Median**	**Range**	**Prevalence (%)**	**Parasite phylum**
Streptopharagus pigmentatus	153.4	0.0-4431.5	77.5	Nematode
Entamoeba coli	1.6	0.0-3.0	77.1	Amoeboid
Balantidium coli	1.3	0.0-4.0	66.6	Ciliate
Small-sized amoebae	0.4	0.0-3.0	30.3	Amoeboid
Chilomastix mesnili	0.3	0.0-1.7	23.1	Flagellate
Medium-sized amoebae	0.5	0.0-2.0	21.9	Amoeboid
Physaloptera caucasia	0.0	0.0-464.5	14.6	Nematode
Unidentified species (Egg1)	0.0	0.0-30.7	5.8	Nematode
Ascaris sp.	0.0	0.0-81	0.02	Nematode
Subulura sp.	0.0	0.0-98	0.01	Nematode
Macracanthorhynchus hirudinaceus	0 .0	0.0-1	0.01	Acanthocephalan

Table 3. Influence of environmental factors, ranging behavior, and individual traits on individual baboon parasite richness. Each model represents a different scale: population-level factors (524 samples, 82 individuals, AIC=1685.28), group-level factors (599 samples, 86 individuals, AIC=1955.47) and individual-level factors (456 samples, 73 individuals, AIC=1437.07).

Model	Variables	Estimate	SE	F-value	df	P-value
Population level	Sample weight^3	2.06	1.17	3.16	3	0.03
	Tmax [1]	4.83	1.73	7.75	1	<0.01
Group level	Sample weight^3	2.20	1.19	3.02	3	0.03
	Home range NDVI	3.31	4.28	0.6	1	0.44
	Home range area	-0.01	0.01	1.44	1	0.23
	Travel distance	0.28	0.07	15.95	1	<0.001
Individual level	Sample weight^3	3.30	1.06	4.32	3	<0.01
	Age^3	3.45	1.58	2.85	3	0.03
	Sex [2]	-0.53	0.19	7.5	1	<0.01
	Body condition	-0.18	-0.08	5.08	1	0.02
	Body size	0.01	0.01	4.45	1	0.04

[1] Daily maximum temperature is averaged over the seven-days occurring four weeks before sample collection (see results)

[2] The reference category for sex is female.

Table 4. Multiple-scale influences on baboon parasite richness (386 samples, 72 individuals, AIC= 1170.02). All variables were standardised (mean of zero, standard deviation of one) and are ordered by their effect size.

Variables	Estimate	SE	F-value	df	*P*-value
Age^3	3.92	1.46	4.41	3	<0.01
Sample weight^3	2.75	1.03	5.79	3	<0.001
Body size	0.48	0.19	6.24	1	0.01
Sex [1]	-0.47	0.19	5.97	1	0.02
Body condition	-0.43	0.13	11.22	1	<0.001
Tmax (with four-week lag) [2]	0.22	1.07	5.79	1	<0.01
Travel distance	0.21	0.06	10.56	1	0.001

[1] The reference category for sex is female.

[2] Daily maximum temperature is averaged over the seven-days occurring four weeks before sample collection (see results)

Table 5. Evidence from previous empirical studies. Previous studies in captivity, or studies examining other parasitic measures such as prevalence or load, are not reported here. The positive effect of a considered factor is noted (+), a negative effect is noted (-), and no effect is noted by (0).

Scale	**Factor**	**Evidence from previous empirical studies**	**This study**
Population	Rainfall	**(+)** comparative studies: bacteria across human populations (Guernier et al., 2004); gamasid mites across small mammals (Krasnov et al., 2008) **(0)** field study of helminths in red foxes (Barbosa et al., 2005)	**(+)**
	Temperature	**(+)** comparative study of fungi in French forest (Vacher et al., 2008); field study of helminthes in red-legged partridge (Calvete, 2003) **(0)** comparative studies: all parasite types in humans at large geographical scale (Guernier et al., 2004); endo- and ectoparasites in fish (Rohde and Heap, 1998); field study of helminthes in red foxes (Barbosa et al., 2005)	**(+)**
Group	Home range productivity	No previous studies	**0**
	Home range size	**(0)** comparative study of gut parasites in mammals (Watve and Sukumar, 1995) **(-)** comparative study of helminths in mammals (Bordes et al., 2009)	**0**
	Daily travel distance	**(+)** comparative study of helminths in primates (Nunn and Dokey, 2006); field study of chigger infections in California meadow mice (Mohr and Stumpf, 1964)	**(+)**
Individual	Age	**(+)** Longevity: comparative studies of Protozoans across primates (Nunn et al., 2003); ectoparasites across Pericidae fish (Ranta, 1992); helminths across freshwater fish (Bell and Burt, 1991); field study of endo- and ectoparasites in coral-reef fish (Lo et al., 1998) **(0)** Longevity: comparative study of ectoparasites across cyprinid fish (Simkova et al., 2006); field studies of gut parasites: red-fronted lemurs (Clough et al., 2010); mandrills (Setchell et al., 2007); chimpanzees (Muehlenbein, 2005) **(-)** Longevity: comparative study of helminths across mammals (Morand and Harvey, 2000)	Polynomial relationship with **(+)** effect before sexual maturity and a **(-)** effect for adults
	Sex	**(+ males)** comparative study: ectoparasites in small mammals (Morand et al., 2004); field study of fleas in desert rodents (Krasnov et al., 2005) **(+ females)** field studies: fleas in rodent *Acromys russatus* (Krasnov et al., 2005); lice in neotropical birds (Clayton et al., 1992) **(0)** No bias: field study of gut parasites in red-fronted lemurs (Clough et al., 2010)	**(+ females)**
	Physical condition	**(-)** field study of helminths of the wild rabbit (Lello et al., 2005)	**(-)**
	Social rank[1]	**(+)** field study of gut parasites in chimpanzees (Muehlenbein, 2005) but analyses not shown. **(0)** field studies: gut parasites in ursine colobus (Teichroeb et al., 2009); red-fronted lemurs (Clough et al., 2010); mandrills (Setchell et al., 2007)	**0**

[1] Here assuming high social rank for dominant individuals, low social rank for subordinates

Figure legends

Fig. 1. Temporal variation of parasite richness during the study period. Monthly variation in parasite richness for the 2005 and 2006 study periods (means and standard errors) are displayed in the top panel. Monthly parasite prevalence (expressed as a fraction of total individuals) for each parasite species or morphotype for the 2005 study period are displayed on the bottom panel.

Fig. 2. Relationship between host parasite richness and daily maximum temperature (Tmax), averaged over the seven-days occurring four weeks before sample collection. The means and standard errors of Tmax for each parasite richness score are shown.

Fig. 3. Relationship between host parasite richness and age. Circles represent the mean parasite richness for an individual. The fitted line was drawn using a locally weighted polynomial regression (Cleveland, 1979) with the lowess command in R 2.8.0 (R Development Core Team, 2003).

Fig. 4. Relationship between host parasite richness and physical condition. The means and standard errors of physical condition for each parasite richness score are shown.

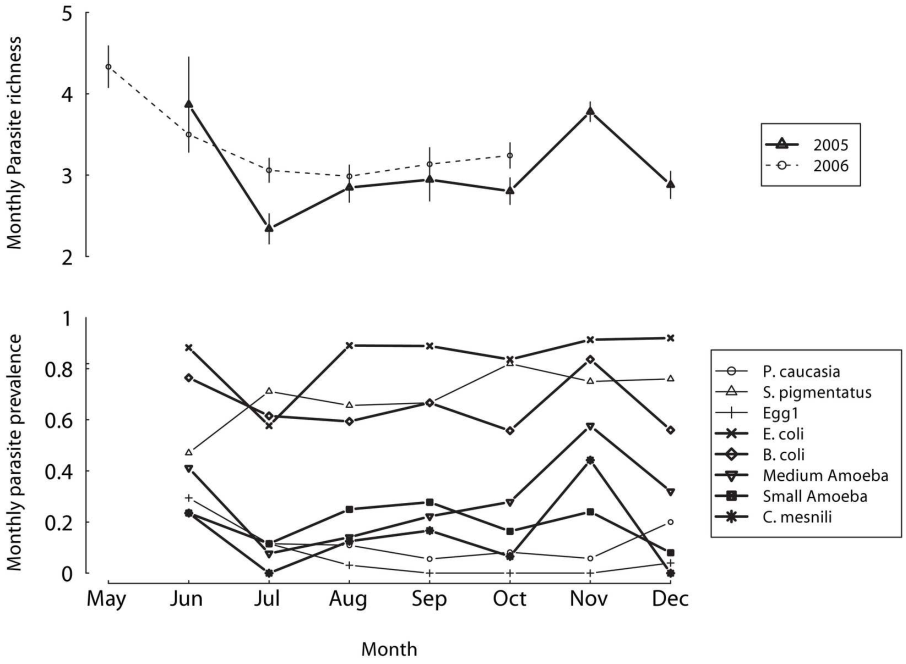

Fig1
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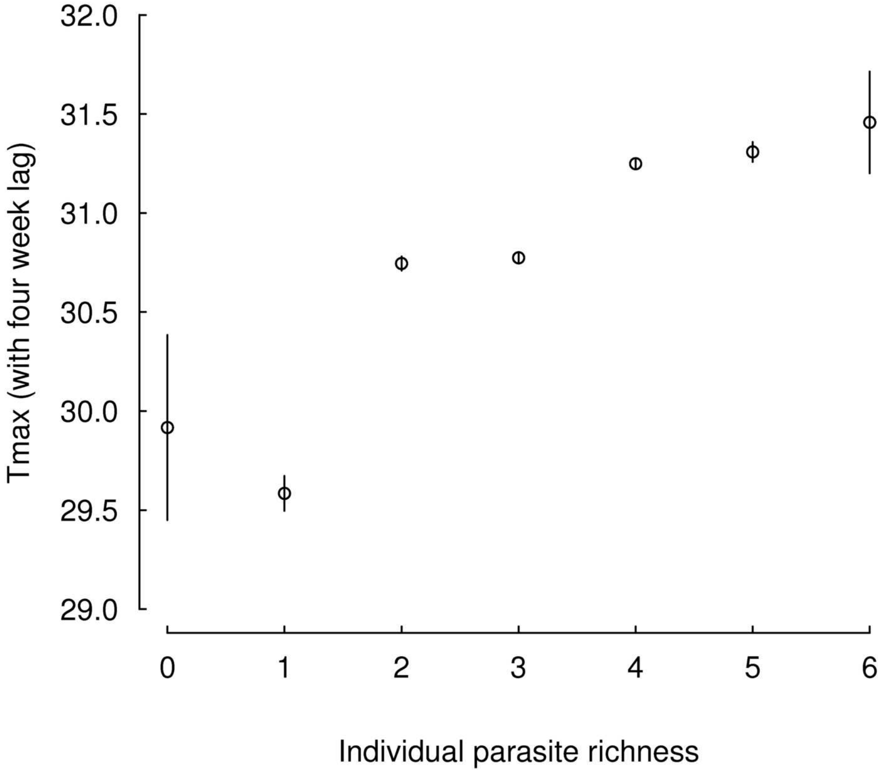

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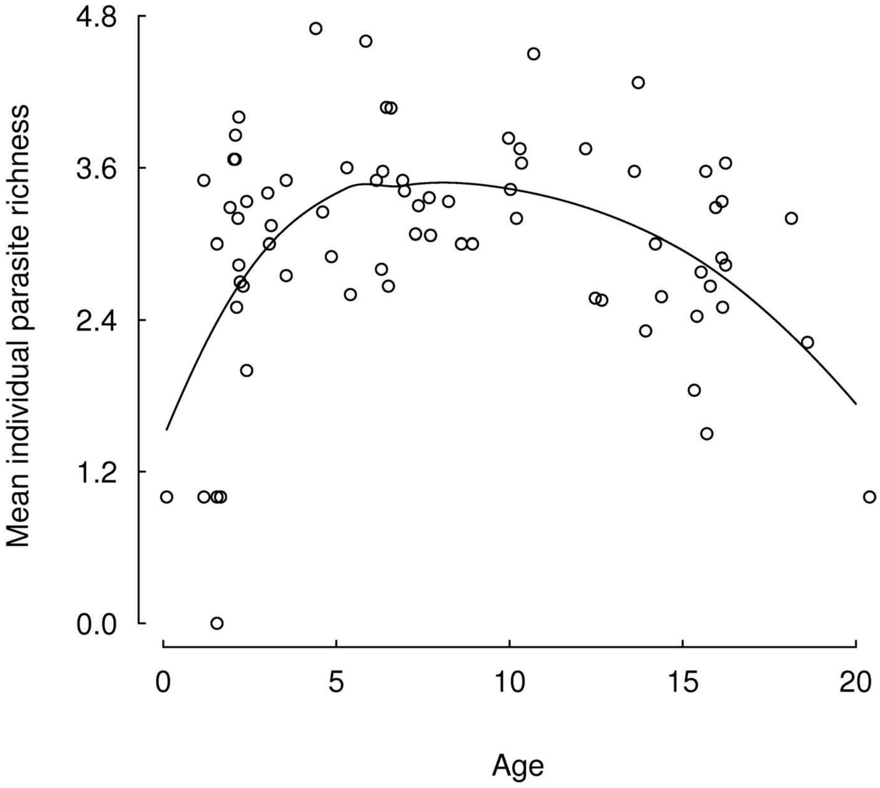

Fig3
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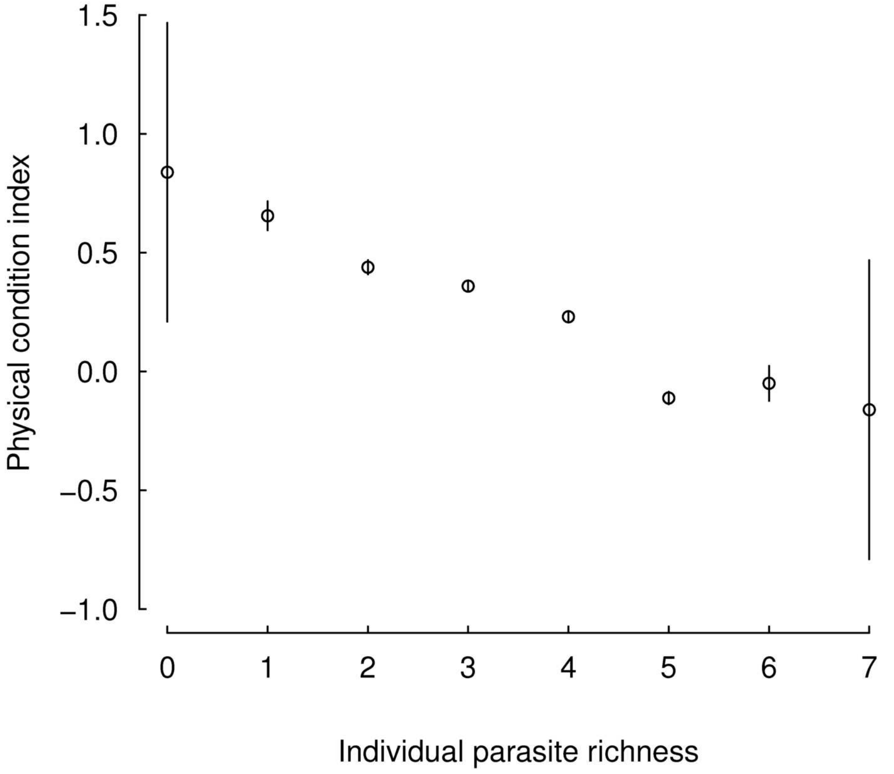

Fig4
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