Spatiotemporal variation in drivers of parasitism in a wild wood mouse population

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Spatiotemporal variation in drivers of parasitism in a wild wood mouse population

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Abstract

1. Host–parasite interactions in nature are driven by a range of factors across several ecological scales, so observed relationships are often context-dependent. Importantly, if these factors vary across space and time, practical sampling limitations can limit or bias inferences, and the relative importance of different drivers can be hard to discern.
2. Here we ask to what degree environmental, host and within-host influences on parasitism are shaped by spatiotemporal variation. We used a replicated, longitudinal dataset of >1,500 observations for nearly 1000 individual wood mice, *Apodemus sylvaticus*, encompassing 6 years of sampling across five different woodland sites, and investigated drivers of infection intensity with a highly prevalent gastrointestinal nematode, *Heligmosomoides polygyrus*.
3. We used a Bayesian modelling approach to further quantify if and how each factor varied in space and time. Finally, we examined the extent to which a lack of spatial or temporal replication (i.e. within single years or single sites) would affect which drivers predict *H. polygyrus* infection.
4. Season, host body condition, and sex were the three most important determinants of infection intensity; however, the strength and even direction of these effects varied in time, but not in space. Models fit to single years and site replicates in many cases showed weak and variable detection of effects of the factors investigated, highlighting the benefits of long-term sampling for separating meaningful ecological variation from sampling variation.
5. These results highlight the importance of accounting for spatiotemporal variation in determining what drives disease dynamics and the need to incorporate replication in both time and space when designing sampling regimes. Furthermore, we suggest that embracing, rather than simply controlling for, spatiotemporal variation can reveal meaningful variation for understanding the factors impacting parasitism (e.g. season and host charateristics) which can improve predictions of how wildlife health will respond to change.

KEYWORDS
Bayesian modelling, gastrointestinal helminths, host–parasite interactions, parasitism, sampling regime, spatiotemporal variation

1 | INTRODUCTION

Host–parasite dynamics in the wild are highly context-dependent, and are driven by a wide range of factors across ecological scales. These drivers range from large-scale factors such as seasonal fluctuations in environmental conditions (Altizer et al., 2013; Dowell, 2001; Nelson & Demas, 1996) or geographical variation (Davies & Pedersen, 2008; Tompkins et al., 2011) to host-level factors such as sex (Zuk & McKean, 1996), age (Plowright et al., 2017) or nutritional status (Calder & Jackson, 2000; Sheldon & Verhulst, 1996), and even include within-host effects such as interspecific interactions between co-infecting parasites or pathogens (Cox, 2001; Fenton & Pedersen, 2005). Importantly, these factors often vary across space and time, so their importance in driving parasitism likewise varies according to the sampling regime. Many ecological studies of infectious diseases are limited in their spatiotemporal replication and sampling breadth; hence, our ability to determine the key drivers of infection and their consistency across space and time is often limited.

Disease ecologists often seek to understand generalisable drivers of parasite dynamics, yet results are unfortunately often equivocal across studies, systems and temporal or spatial replicates. For example, host body condition, a widely used metric, often considered a proxy for fitness, is typically hypothesised to be negatively correlated with parasite infection (e.g. Debeffe et al., 2016; Irvine et al., 2006; Millán et al., 2004). However, a recent meta-analysis of >500 body condition versus parasite infection relationships demonstrated high heterogeneity in both strength and direction, with a high proportion (~50%) of non-significant relationships (Sánchez et al., 2018). In some cases, robust sampling regimes and statistical analysis have been applied to anticipate and control for this variability. For example, a highly replicated study of ectoparasite burden and pathogenicity in dace *Leuciscus leuciscus*, collected over 3 years and from eight sites, demonstrated that the effects of host and environmental factors were strong but inconsistent across years (Cardon et al., 2011). Even experimental approaches using parasite removal as a means of quantifying the relationships between host and parasite are vulnerable to impacts of spatiotemporal variation (Pedersen & Fenton, 2015). This is highlighted by a 10-year study of red grouse *Lagopus lagopus*, in which both host survival and reproduction (clutch size and hatching success) were greater in animals with experimentally reduced helminth burdens after drug treatment, but the magnitude of these effects varied across years, and were not statistically significant in all years sampled (Hudson et al., 1992). Additionally, Fenton et al., (2014) showed that the most reliable methods for examining drivers of parasite intensity (in this case co-infection with other parasites) involved longitudinal sampling of the same individuals while cross-sectional approaches were less reliable. These studies make a strong case for using both well-replicated sampling and carefully structured statistical approaches to disentangle context-dependent drivers of parasitism.

The regularity of finding context-dependent results presents an important problem when understanding the dynamics of host–parasite interactions in the wild: specifically, what is the consistency and repeatability of the observed trends across different replicates of the same system, and how can researchers be sure that their replication is sufficient? Generalisability for predictions is of great interest in ecology, but often complicated by reproducibility hurdles, and spatiotemporal variation is a likely culprit impacting variation in results (Becker et al., 2020; Fidler et al., 2017; Fraser et al., 2018; Ihle et al., 2017). By quantifying how the drivers of parasitism vary over space and time for the same host–parasite system, we can address three fundamental questions: (a) what are the key (reproducible) factors that drive parasite infection intensity; (b) how much of the variation in effect sizes is biologically meaningful, rather than representing sampling biases and (c) how can we optimise sampling regimes to improve our ability to detect important biological variation in drivers within a system? Few ecological studies have systematically addressed these questions to date, due in part to practical sampling limitations: that is, it is difficult to sample large numbers of hosts, across a wide geographical range, and over a long period of time. Consequently, it is unclear how often wild host–parasite studies make biased inferences due to limited sampling.

European wood mice, *Apodemus sylvaticus*, are widely distributed rodents that represent an ideal system for robust spatiotemporal replication of host–parasite infection studies. They are commonly infected with a well-studied gastrointestinal nematode, *Heligmosomoides polygyrus* (Gregory, 1992). Like other gastrointestinal helminths, *H. polygyrus* establishes chronic infections within their hosts, shedding eggs into the environment via faeces, where onward transmission to other host occurs after the eggs develop into infective L3 larvae (~7 days; Johnston et al., 2015). As such, *H. polygyrus* infection will be determined by the environment (Abu-Madi et al., 2000; Brown et al., 1994; Eira et al., 2006; Gregory, 1992; Langley & Fairley, 1982; Montgomery & Montgomery, 1988), host factors (Ferrari et al., 2004; Gregory et al., 1990) and within-host parasite interactions (Behnke et al., 2005; Knowles et al., 2013). Building on this knowledge, we use a temporally (6 years) and spatially (five woodland sites) replicated wood mouse dataset to investigate the drivers of *H. polygyrus* infection intensity and their consistency across time and space. With Bayesian modelling methods, we first use the complete dataset to identify the overall drivers of infection and then fit interactions to investigate whether these drivers varied meaningfully over space and time. Next, we use single-site or single-year subsets of the data to investigate whether the same results are found in more limited sampling regimes. Our approach represents a rare opportunity to quantify the drivers of parasitism and their reproducibility at multiple scales, with implications for a wide range of disease ecology studies and the design of sampling regimes.

2 | MATERIALS AND METHODS

2.1 | Data collection

We live-trapped several wild wood mouse populations located near Liverpool, UK regularly between May and December for six consecutive years (2009–2014). We sampled 16 trapping grids ranging in size from 2,500 to 10,000 m^2, spread across five different woodland sites with 2–3 sites trapped per year (Tables S1 and S2; Figure S1). Sites ranged from approximately 2 to 60 km apart. On each grid, trapping stations were placed every 10 m, with two live traps (H.B. Sherman 2 × 2.5 × 6.5 in. folding traps, Tallahassee, FL, USA) at each station baited with grains and bedding material. We sampled each grid every 4 weeks from 2009 to 2011 and every 3 weeks between 2012 and 2014; with each grid trapped 3–4 nights per week. Traps were set in the late afternoon and checked the following morning. At first capture, we tagged each wood mouse with a subcutaneous passive integrated transponder (PIT tag, AVID), and at every capture, we recorded morphometric data (age, sex, weight, body length, reproductive condition; details below) and collected a faecal sample for parasitology. Faecal samples were collected from the pre-sterilised traps, weighed and stored in 10% buffered formalin at 4°C until parasite identification.

We quantified gastrointestinal parasites (including *H. polygyrus* and coccidial protozoans [*Eimeria* spp.]) via faecal egg/oocyst counts (FEC/FOC) using salt flotation to obtain the number of eggs or oocysts (for *Eimeria* spp.) per gram faeces (EPG/OPG; Knowles et al., 2013). EPG is highly positively correlated to adult worm burdens for *H. polygyrus* in wood mice (Sweeny, Clerc, et al., 2021). Briefly, saturated salt solution was added to formalin-preserved faecal samples so that eggs/oocysts floated to the top of the solution. The eggs were collected on a coverslip, and then we counted both eggs and oocysts at 10× magnification, and identified them to species level at 40× magnification. We identified *Eimeria* to species according to unsporulated oocyst morphology (Nowell & Higgs, 1989).

2.2 | Statistical analysis

Data for this analysis are accessible via the Dryad Digital Repository https://doi.org/10.5061/dryad.0cfxpnw1q (Sweeny, Albery, et al., 2021).

2.2.1 | Defining model variables and dataset

We investigated how host, environmental and within-host- (parasite co-infection) factors drive *H. polygyrus* infection intensity (EPG from infected animals only). In 4 of the 6 years of sampling, we conducted experiments in which randomly selected mice were anthelmintic-treated (or given a water control) to remove/reduce gastrointestinal nematodes, such as *H. polygyrus* (see Knowles et al., 2013). Because anthelmintic treatment should affect *H. polygyrus* infection intensity, we restricted our analyses to only those individual mice which had not been treated. We have previously tested for, but never detected, any knock-on effects of reduced transmission or infection on untreated animals in the presence of treated animals on the same grid. The final dataset included 1,609 captures of 926 individuals (max captures per individual = 28, median captures per individual = 4; Figure S3). Sample sizes from all years and woodland sites are shown in Table S2. Although each site was not trapped in each year due to logistical reasons, every site was trapped for multiple years within the dataset, allowing investigation of both temporal and spatial scales.

We selected the following factors as fixed effects in all models: (a) Environmental factors: season (categorical, three levels: spring, summer, autumn) and (b) Host characteristics: sex (categorical, two levels: male/ female); scaled mass in grams as a measure of body condition (continuous; Peig & Green, 2009); reproductive status (categorical, two levels: active [males—descended or scrotal testes, females—lactating or gestating]; inactive [males—abdominal testes, females—perforate or non-perforate vagina]). Negative interactions between *Eimeria hungaryensis* and *H. polygyrus* have been demonstrated in this host species (Knowles et al., 2013), thus to investigate whether other gastrointestinal (GI) parasite interactions impact *H. polygyrus* infection intensity, we also included (c) Within-host factors: the presence/absence of two most common GI parasites: the coccidian *E. hungaryensis* and a Hymenolepid cestode (both categorical, two levels: present/absent).

2.2.2 | Model structure

Statistical analysis was carried out in R version 3.6.1, in the Bayesian linear modelling package MCMCGLMM (Hadfield, 2010) unless otherwise noted. MCMC methods produce a distribution of estimates for a given effect size and the proportional overlap of these estimates can be used to give a measure of significance for the difference between effects (p_{MCMC}) as well as an estimate of the mean and 95% credible intervals of the difference, without the use of post-hoc tests (Albery, Kenyon, et al., 2018; Palmer et al., 2018). Generalised linear mixed-effects models (GLMMs) were run using *H. polygyrus* EPG rounded to the nearest integer to allow for fitting with Poisson error families to account for overdispersion in the data. All models were run with individual ID as a random effect for 260,000 iterations, with a 200-iteration thinning interval and a 60,000-iteration burnin period, for a total of 1,000 stored iterations.

To investigate the ecological drivers of *H. polygyrus* infection intensity in wild wood mice and the impact of spatiotemporal variation in the detection of these factors, we constructed three sets of models which are described in detail below. Briefly, each model investigated the same aim—to determine what ecological factors drive *H. polygyrus* infection intensity—with subtle, but important differences. Specifically (a) the first model used the full dataset and included both site and year as fixed effects, (b) the second model set also used the full dataset but included interactions of site and year with each of the factors investigated and lastly (c) the third model used subsets

of the dataset (i.e. a single site or year). Details for this approach are outlined below.

First ('Model Set 1'), we used the full dataset to investigate the what factors drive *H. polygyrus* intensity across the entire 6-year, five-woodland site study using a base model, with site and year included as fixed effects in addition to the season, host and parasite community factors listed above. For each factor (fixed effect), we examined the proportional overlaps among the estimated posterior distributions for each site and year to determine the spatiotemporal variation of mean *H. polygyrus* intensity.

Next ('Model Set 2'), we added two-way interaction terms between year or site and the other fixed effect factors into the Set 1 model to investigate whether such interactions revealed spatiotemporal interactions in the environmental, host and within-host drivers of *H. polygyrus* infection intensity. A visual depiction of this approach is shown in Figure S2, where we hypothesise that unless the relationship between a factor of interest and parasite intensity is identical across space and time (Figure S2a), estimating the variation in either the magnitude and direction of this relationship (Figure S2b,c) will provide additional insight into parasitism in wild populations. We carried out a model addition approach using integrated nested laplace approximation (INLA; Rue et al., 2009) to determine a final set of interactions which improve model fit. We use INLA for this stage as it is computationally more efficient for the large scale of candidate models required and because assessment of model fit by deviance information criterion (DIC) is not suitable for non-Gaussian models in MCMCglmm, but is a common and robust approach in INLA (Albery et al., 2019; Rue et al., 2009). Starting with the base model from Model Set 1 including all fixed effects, we added interaction terms (e.g. season:year) one at a time. Each round, the interaction which lowered the DIC of the model the most (improving model fit, independent of order) was kept, and the process was repeated with the remaining interaction terms. This was repeated until the model was optimised, and could not be improved in fit with the addition of any further interaction terms (decrease DIC by >2). All INLA models used a negative binomial distribution to approximate the overdispersed Poisson error family of MCMCglmm. Because MCMCglmm facilitates row-by-row comparison of posterior distributions for interaction-level comparisons used in this analysis, we ran the final model formula in MCMCglmm and confirmed results were consistent with those from INLA model output. We then examined the posterior distributions of the effect estimates for interactions derived the final, optimal model, which gave an estimate for pairwise distribution overlaps for each year or site, demonstrating which years and sites differed in terms of their effect sizes for each fixed effect (e.g. the estimate of the effect of season was greater in 2010 than in 2011).

Last ('Model Set 3'), we investigated whether the degree to which limited sampling replicates allow detection of variation in environment, host and within-host effects on infection intensity. We ran a series of models for either each site ($N = 5$; with all years combined) or each year ($N = 6$; with all sites combined). We compare these results to Model Set 2 to infer if and how long-term sampling accounting for spatiotemporal variation can provide additional insights to inference of broader dynamics in natural host–parasite systems.

3 | RESULTS

3.1 | Model Set 1: Ecological drivers of parasitism with fixed spatiotemporal effects

Using all data combined for years and sites found that environmental (season) and within-host factors (Hymenolepid cestode co-infection) were overall the most important predictors of *H. polygyrus* infection intensity (Figure 1). Intensity was significantly lower in both summer and autumn compared to the spring (Figure 1, p_{MCMC}:Summer < 0.001, p_{MCMC}:Autumn < 0.001) and Hymenolepid presence was associated with higher *H. polygyrus* infection intensity (Figure 1, $p_{MCMC} = 0.018$). No host characteristics were found to significantly impact intensity of infection in this model. In addition, we found significant spatiotemporal variation in mean *H. polygyrus* intensities across the five woodland sites and 6 years (Figure 2). Across sites, Haddon Wood had significantly higher infection intensities compared to all other woodlands (Figure 2A,C) and there was also significant between-year differences across several pairs of years (Figure 2A,C). Notably, *H. polygyrus* infection intensity was higher in 2010 than in any other year, and intensities in 2012–2014 were lower than 2009–2011 (Figure 2B,D). Wood mouse populations also experienced temporal variation in demographic characteristics, where population size and age structure fluctuated between years (Figure S4).

3.2 | Model Set 2: Spatiotemporal variation in ecological drivers of parasitism

Including spatiotemporal interactions with ecological factors revealed substantial temporal, but not spatial variation in the estimates

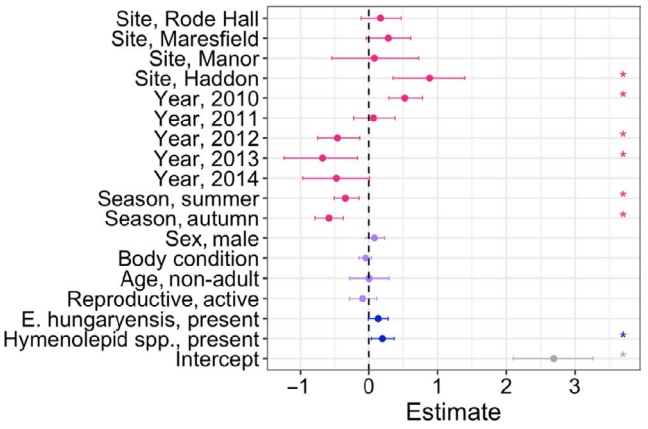

FIGURE 1 Model Set 1 output for the full dataset from all years and sites collected using longitudinal sampling, where site and year were considered fixed effects. Points and ranges represent model estimates and 95% credibility estimates for each model. Colour indicates the ecological scale for each factor (pink: environment; purple: host; blue: within-host). Asterisks indicate the significance of variables with a $p_{MCMC} < 0.05$ threshold. The Intercept represents the following baseline categories: Site, Gordale; Year, 2009; Season, Spring; Sex, Female; Age, Adult, Reproductive status, inactive

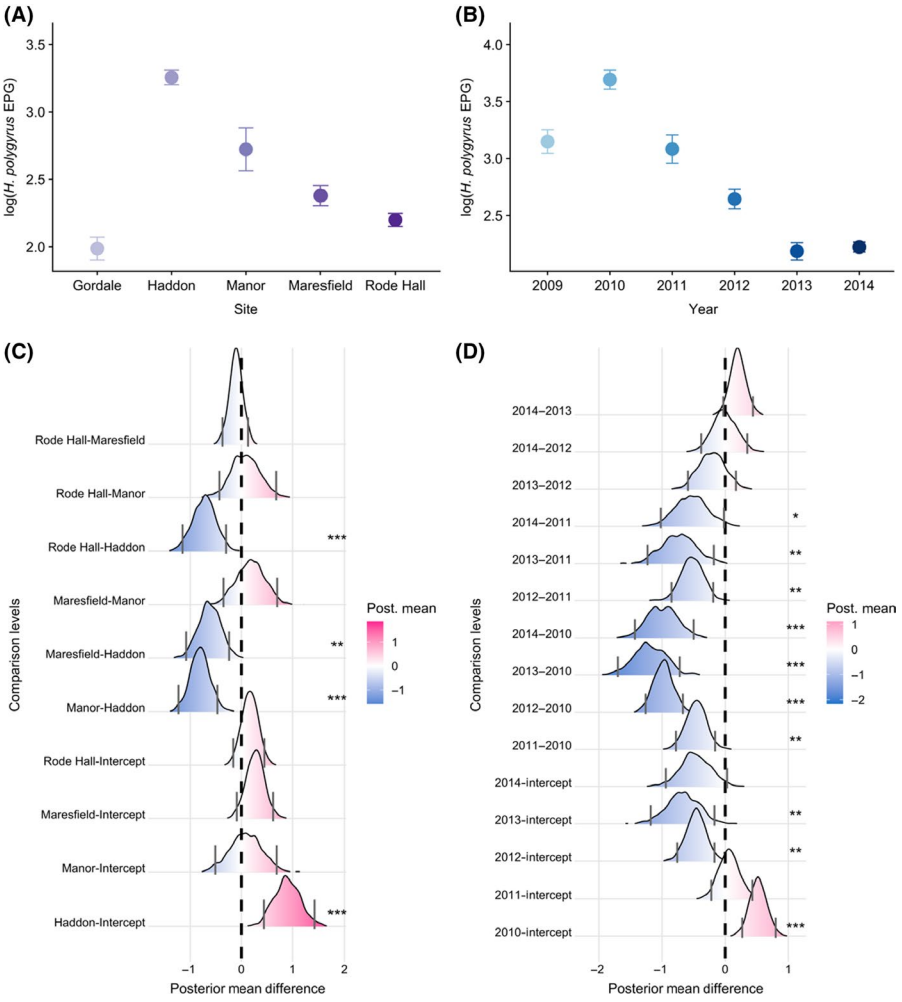

FIGURE 2 Spatiotemporal variation in mean *Heligmosomoides polygyrus* intensity from Model Set 1. Top row: raw data for the spatiotemporal main effects. Points represent mean intensity (±*SE*) for (A) site and (B) year. Bottom row: ridge plots represent pairwise comparisons for the base model output for main effects of site (C) and year (D). Density ridges represent distributions drawn from the differences between the posterior means of the indicated comparison levels [a–b] for each stored iteration. Differences between effects can be interpreted by comparison of the density ridges to zero; vertical grey lines for each ridge indicate the 95% credibility intervals for these distributions. Blue shading denotes that the mean of effect estimates for [a] is lower than that of [b] for a given factor. Pink shading denotes that mean of effect estimates from [a] is higher than that of [b]. If credibility intervals do not cross zero, this is considered a significant difference in effects between [a–b]. Significant differences between effects are indicated by ***, ** and * for $p_{MCMC} < 0.001$, $p_{MCMC} < 0.01$ and $p_{MCMC} < 0.05$ respectively. 'Intercept' represents the baseline year 2009 and site Gordale

for many of the factors (Figure 3). Specifically, three factor-by-year interactions significantly improved model fit: season (ΔDIC = −58.92), body condition (ΔDIC = −14.61) and sex (ΔDIC = −5.42; Table S3). Pairwise comparisons for the interactions which remained in the optimal model revealed significant changes across years for all three interactions (Figure 3). Change in *H. polygyrus* infection intensity from Spring to both Summer and Autumn generally represented a decrease (Figure 3B); however, comparison across years by proportional posterior overlaps still showed significant variation in both the magnitude and direction of effects (Figure 3A). For example, the change in intensity between Spring and Summer was greatest in 2011 and 2012 (Figure 3A,B) and in 2009 and 2010 the mean increased from Spring to Autumn (Figure 3A,B). We found a high degree of variation for the effect of body condition-by-year; the slope between better body condition (higher scaled mass) and intensities of infection was positive in 2009, negative in 2012, and exhibited a weak relationship in other years, resulting in seven significant pairwise differences across all years (Figure 3A,D). Proportional overlap for sex-by-year interaction effects also indicated significant variation in the relationship between sex and parasite intensity, where there was a notable change in direction of bias (female-to-male bias) between 2009 and 2010 and later years and significant variation in the magnitude of male bias in later years (Figure 3A,C).

3.3 | Model Set 3: Ecological drivers of parasitism from limited spatial and temporal sampling regimes

We found that in models fit to data from single year or site replicates within the full longitudinal dataset, the estimates of drivers of parasite infection varied considerably, in qualitatively similar fashions to models using the full dataset and interactions (Figure 4). Across year-specific models, season was the most consistent effect in both direction and detection, with Summer and Autumn having generally lower intensities (Figure 4A). However, as in Model Set 2, these within-year models showed that the host characteristics were less consistent than environmental factors in their relationships with parasite intensity (Figure 4A). Effect of sex was not consistent in direction across years, where males had higher intensity of infection compared to females in only 1 year. Likewise, body condition had a significant association with *H. polygyrus* infection in 2 years, but this relationship was negative in 2014 and positive in 2009 (Figure 4A). The presence of both co-infecting GI parasites was associated with higher *H. polygyrus* infection intensity in just 1 (Hymenolepid spp.) or 2 (*E. hungaryensis*) years each (Figure 4A).

In the five site-specific models, we found again that the seasonal effects were the most consistent and frequently detected

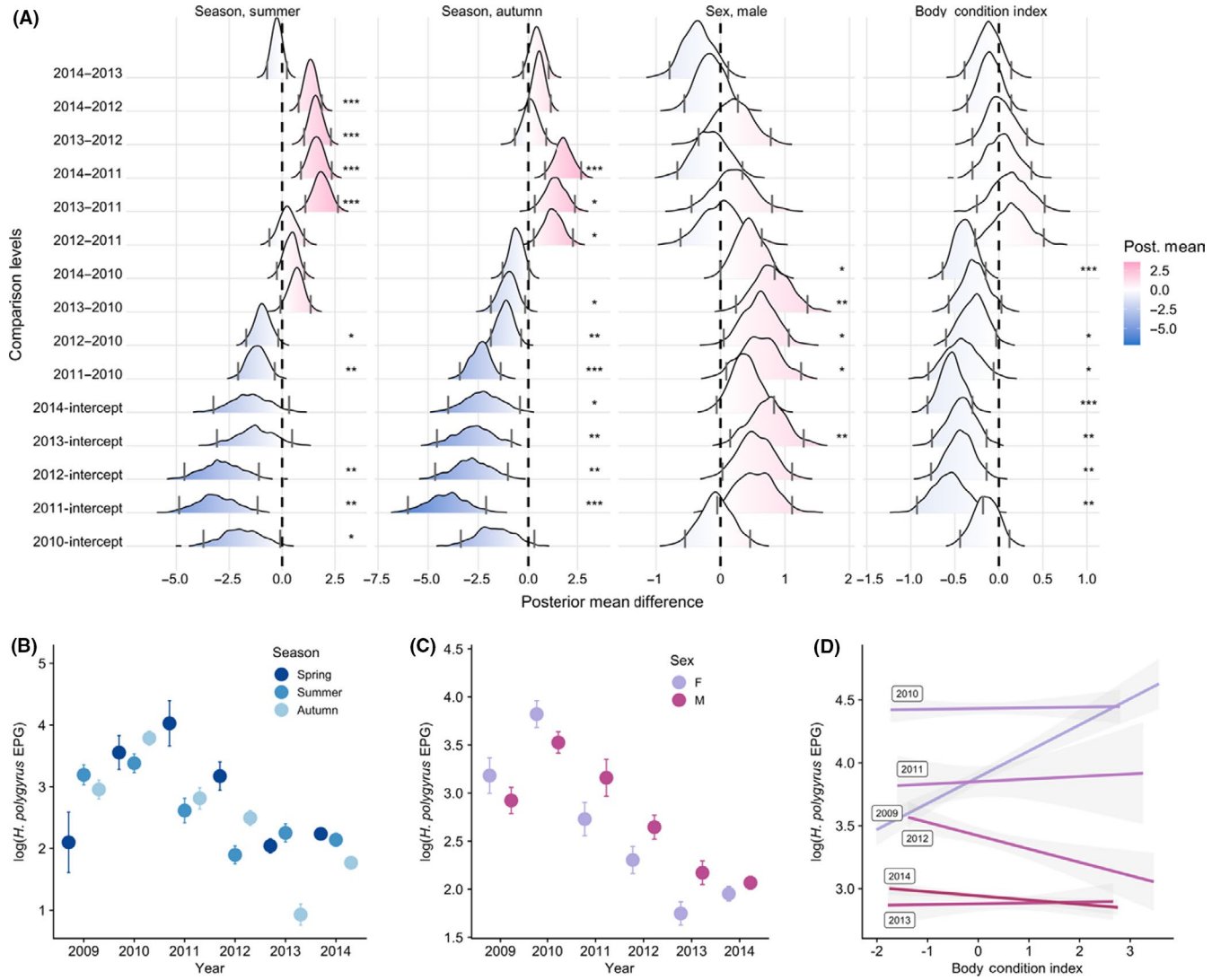

FIGURE 3 Top panel (A): Differences across estimated effects (with 95% credible intervals) for Model Set 2 including the interactions with site/year which improved full model fit for the longitudinal dataset. Density ridges represent distributions drawn from the differences between the posterior means of the indicated comparison levels [a–b] for each stored iteration. Differences between effects can be interpreted by comparison of the density ridges to zero; grey lines for each ridge indicate the 95% credibility intervals for these distributions. Blue shading denotes that the slope of effect for [a] is lower than that of [b] for a given interaction. Pink shading denotes that slope of effect from [a] is higher than that of [b]. If credibility intervals do not cross zero, this is considered a significant difference in effect slope of [a–b]. Significant differences between effects are indicates by ***, ** and * for $p_{MCMC} < 0.001$, $p_{MCMC} < 0.01$ and $p_{MCMC} < 0.05$, respectively. 'Intercept' represents the baseline year of the model (2009) in all panels. Bottom Panel: Raw data, interactions selected for final longitudinal models (B) Season:year, (C) Sex:year and (D) Body condition:year. (B)–(C) represents mean ± *SE* of log *Heligmosomoides polygyrus* intensity per category, (D) represents regression with *SE* ribbons for log *H. polygyrus* intensity versus body condition index

(Figure 4C). Meanwhile, the direction of the effect of body condition varied in the 2/5 site models in which it was detected. Similarly, we found a significant male bias in only 2/5 sites. Lastly, we found positive associations between the presence of *E. hungaryensis* and *H. polygyrus* intensity for only one woodland site (Figure 4).

4 | DISCUSSION

Using an extensively replicated dataset, we demonstrate that the drivers of parasitism can vary across space and time in a wild mammal population, and that the observed relationships depend on the sampling effort employed to detect them. Specifically, we give evidence for consistent overarching effects of seasonality, context-dependent effects of sex and body condition and varying presence of within-host co-infection associations as important factors impacting *H. polygyrus* infection (Figure 5). These results suggest that ecological drivers of parasitism are not likely to be static, highlight the importance of examining the spatiotemporal context when estimating drivers of parasitism and suggest caution when generalising from analyses that are limited in their spatial or temporal replication.

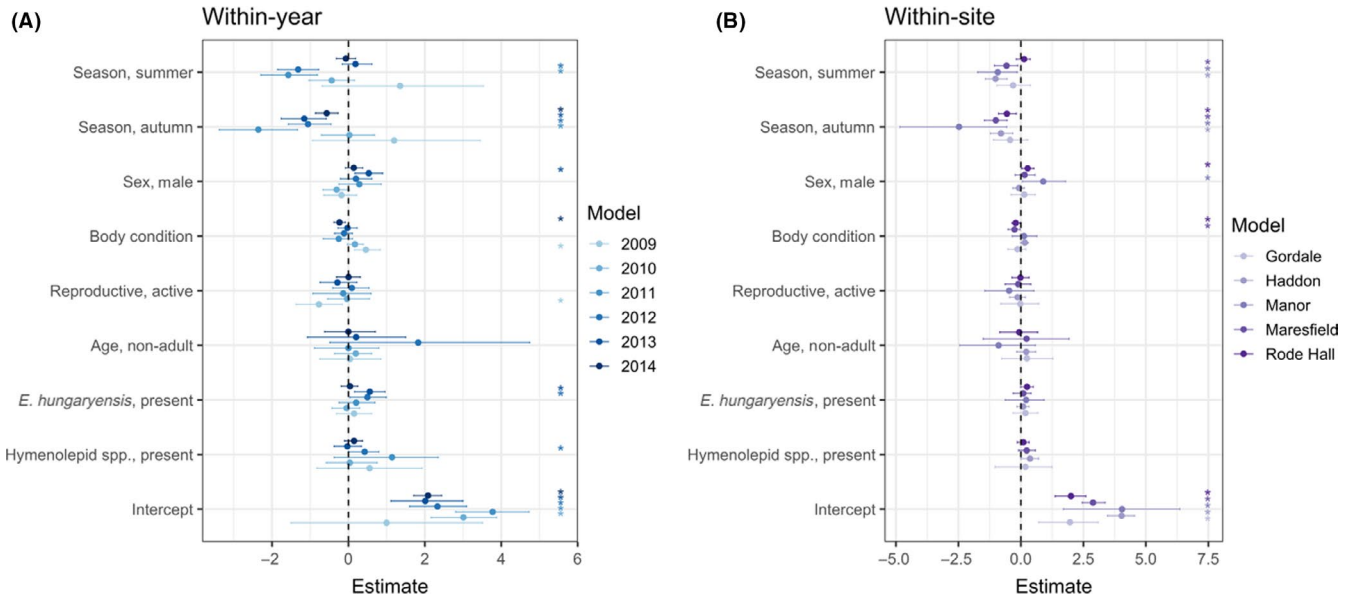

FIGURE 4 Effect size estimates from Model Set 3, investigating the effect environment, host and parasite community-level predictors of *Heligmosomoides polygyrus* intensity within (A) year and (B) site replicates. Points and ranges represent model estimates and 95% credibility estimates for each model. Asterisks indicate significance at a threshold of $p_{MCMC} < 0.05$. Intercepts for categorical covariates are as follows: Season, Spring; Sex, Female; Reproductive status, Inactive; Age, Adult; *E. hungaryensis* & Hymenolepid spp., absent

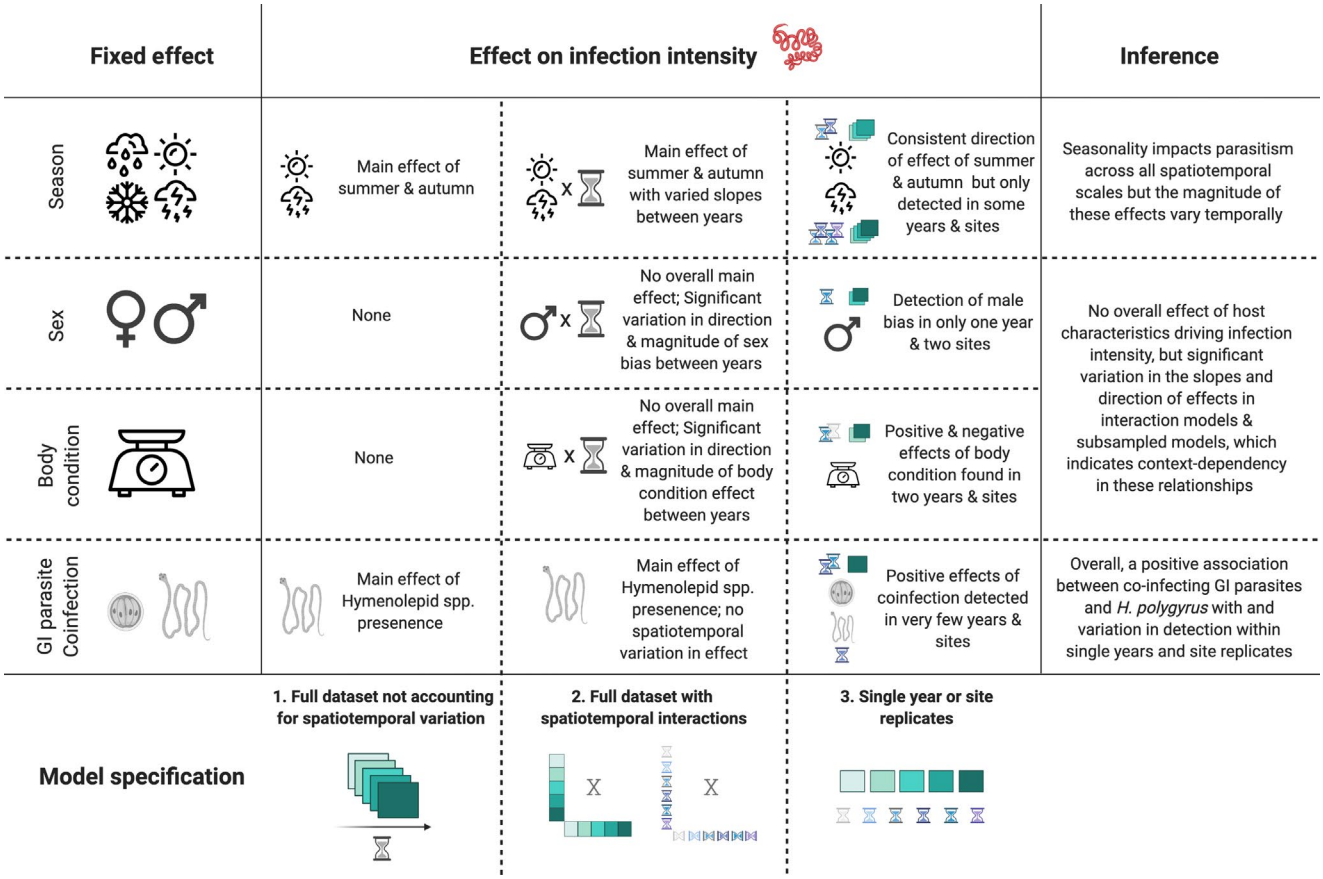

FIGURE 5 Comparison of the ecological factors driving *Heligmosomoides polygyrus* infection intensity across the three models sets

Despite large sample sizes, our full model simply accounting for year and site as main effects (Model Set 1) revealed weak overarching evidence for host effects on impacting parasitism, with much stronger support for environmental effects as key drivers. Aside from weak positive correlations between co-infecting GI parasites (Hymenolepid) presence and *H. polygyrus* infection intensity, no

host-level characteristics were significant predictors across all years and sites. This somewhat contradicts results from several smaller scale studies of *H. polygyrus* in *Apodemus* spp. populations, many of which document significant host-level drivers such as male-bias in both transmission (Ferrari et al., 2004) and burden (Gregory et al., 1990; Langley & Fairley, 1982). Similarly, effects of age (Behnke et al., 1999; Clerc et al., 2019), reproduction (Albery, Watt, et al., 2018), body condition (Warburton et al., 2016) and interactions between co-infecting parasites (Behnke et al., 2005; Clerc et al., 2018) are well documented as important drivers of infection across a range of mammal-helminth systems. Instead, the strongest and most consistent drivers here were the environmental factors of year, site and season, which aligns with evidence for the influence of these factors from extensive previous research in multiple *A. sylvaticus* populations (Abu-Madi et al., 1998, 2000; Behnke et al., 1999; Bordes et al., 2012; Eira et al., 2006; Gregory, 1992; Gregory et al., 1992; Montgomery & Montgomery, 1990). Taken together, these findings imply that environmental drivers across space and time can dwarf the effects of individual host-level factors such that scale is a key consideration for host factor-level analyses. To investigate this possibility, we asked: does allowing spatiotemporal variation in the drivers of *H. polygyrus* intensity across sites and years provide a more biologically driven picture of infection dynamics than estimating global main effects?

We found strong evidence of variation in the effects of season, sex and body condition between years in our interaction models, which may be driven by multiple possible biological processes. Seasonality is ubiquitous in wildlife disease ecology but complex; seasonal fluctuations in climatic environment act on exposure via influence on survival of environmental stages of parasites while hosts also experience annual cycles that alter their susceptibility (Altizer et al., 2006; Martin et al., 2008; Nelson & Demas, 1996). Across many helminth species, abundance is often highest in the spring and declines throughout the winter (Stromberg, 1997), and results from our initial model (Model Set 1) support these seasonal patterns. Although season was the most consistent factor investigated here, variation in the overall trends suggest that seasonality of *H. polygyrus* in this system is vulnerable to dynamic population or environment characteristics. For example, seasonal bouts of reproductive effort can significantly limit energy allocation to immunity (Martin et al., 2008) and age structure of a population can shape epidemiology when susceptibility is variable across host age (Clark et al., 2017; Clerc et al., 2019; Plowright et al., 2017). It is therefore possible that annual variation in population size or age structure can alter seasonal transmission dynamics of *H. polygyrus* within wood mouse populations. Future work using higher-resolution local climate data or time series akin to those applied to longer-term systems (Coulson et al., 2001) can offer additional insight into the mechanisms underpinning the roles of both extrinsic and demographic influences on seasonality in parasitism.

Extensive investigation into the relationship of both sex and body condition with parasitism across a range of systems has suggested males and individuals of poor condition are more susceptible to parasites (Ezenwa et al., 2012; Sánchez et al., 2018; Zuk & McKean, 1996). However, cross-species meta-analyses of this proposed sex bias (Moore & Wilson, 2002) and body condition (Sánchez et al., 2018) have shown that the importance of both factors vary by host system and/or the method of sampling. Our results corroborate this observation within a single host species and imply that these relationships are dynamic over time. The impact of sex and body condition as well as seasonality on infection may be linked to reproductive traits of wild animals, with context-dependent outcomes. Positive impacts of testosterone for sexual signalling can impose restrictions for investment in immunity (Muehlenbein & Bribiescas, 2005), and reduced condition and immunity due to energy requirements of reproduction are associated with higher infection intensities (Houdijk, 2008). Costs of testosterone or poor condition due to the difficult conditions or energetic demands of reproduction are likely to be exaggerated in years of poor climatic conditions or resource availability, making these effects vulnerable to annual environmental variation. Additionally, young animals are likely to vary from sexually mature adults in their energetic demands, so age structure variations across years may shape condition and sex effects as well as seasonal variation. Although it is beyond the scope of this study to ascribe exact mechanisms, we suggest future work integrating additional measures of condition and immunity alongside parasite monitoring can aid our understanding of the drivers of these dynamic host–parasite relationships.

Finally, we asked: are single-site or single-year models capable of detecting these variable effects? By combining the findings from models fit to subsets of data from each year and site replicate (Model Set 3) with the more powerful full dataset models incorporating interaction effects (Model Set 2), we were able to show that limited sampling replication detected qualitatively similar results, but can complicate inference (Figure 5). For example, our single site/year models showed qualitatively similar variation in season, sex and body condition effects as did the full dataset interaction models, but in isolation these effects often were not significant (despite significant interactions in models using the full dataset). These results highlight that it may often be difficult to separate ecological variation versus variation in detection or sampling power. Additionally, some results (e.g. lower intensity of infection in reproductively active individuals in 2009) were not supported by results from any other single year or site model or by models using the full dataset, suggesting that caution should be taken when inferring biological relationships from limited spatial or temporal sampling scales. These comparisons highlight the value of long-term, longitudinal sampling of known individuals for separating ecological signal from noise in parasite dynamics across spatiotemporal scales.

Although our sampling regime was not suited to identifying specific environmental drivers such as climatic or resource availability, most variation occurred at the between-year rather than the between-site level, implying that temporal (and not spatial) variation is more important in determining *H. polygyrus* intensity. However, year and site combinations in this dataset were not perfectly independent, and so it is difficult to fully disentangle the impact of space from time (Table S1). It is therefore possible that some apparent temporal variation is attributable to spatial site changes, and vice versa. In addition, the woodlands included in this study were

initially chosen because they were similar deciduous woodlands, and it is therefore possible that the habitats were not diverse enough to detect biological variation in drivers of parasitism due to spatial environmental context. Given previous work showing variable effects of seasonality on helminth infections of *A. sylvaticus* across highly different habitats (i.e. sand dunes vs. lake margins) (Eira et al., 2006), further application of this approach to include sites across varied habitats and addressing more fine-scale spatial variation would be useful. We also focused exclusively on those factors that influence infection intensity. Although helminth egg count was examined here and is a common proxy for infection burden (Margolis et al., 1982), prevalence (proportion of individuals infected in a population) is also a key metric of disease for many study systems and it is worth nothing that factors that increase exposure and infection probability may differ from those that dictate infection intensity, and this should be kept in mind for interpretation of these results.

By carrying out substantial spatiotemporal sampling replication, we have provided evidence for important temporal changes in seasonality, sex and body condition effects on helminth infection dynamics in a wild wood mouse population. As well as confirming significant spatiotemporal variation in parasitism itself, our findings suggest that the drivers of infection intensity exhibit variation over time. This suggests that varied support for hypotheses regarding factors influencing parasitism may represent important biological variation rather than simply variation in detection or limited statistical power across different populations and replicates. Given practical limitations of many ecological studies, this is of broad relevance for understanding whether sampling resolution in a wild system alters estimates of effects of interest. Overall, we hope that more studies will investigate and control for spatiotemporal variation in effects influencing important aspects of host–parasite dynamics. Particularly as environmental change accelerates, understanding to what degree factors driving parasitism vary in response can help shape broader insights into epidemiology of wild populations.

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AUTHORS' CONTRIBUTIONS

Data for this study were provided by long-term study led and designed by A.B.P. & A.F.; A.R.S. conceived of the analysis with A.B.P. and A.F.; A.R.S., G.F.A. and S.V. designed the statistical approach; A.R.S. analysed the data; A.R.S. led the writing of the manuscript. All authors contributed critically to analysis discussion and manuscript drafts and approved a final version for publication.

DATA AVAILABILITY STATEMENT

Data for this analysis are accessible via the Dryad Digital Repository https://doi.org/10.5061/dryad.0cfxpnw1q (Sweeny, Albery, et al., 2021).

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REFERENCES

Abu-Madi, M. A., Behnke, J. M., Lewis, J. W., & Gilbert, F. S. (1998). Descriptive epidemiology of *Heligmosomoides polygyrus* in *Apodemus sylvaticus* from three contrasting habitats in south-east England. *Journal of Helminthology*, *72*, 93–100.

Abu-Madi, M. A., Behnke, J. M., Lewis, J. W., & Gilbert, F. S. (2000). Seasonal and site specific variation in the component community structure of intestinal helminths in *Apodemus sylvaticus* from three contrasting habitats in south-east England. *Journal of Helminthology*, *74*, 7–15.

Albery, G. F., Becker, D. J., Kenyon, F., Nussey, D. H., & Pemberton, J. M. (2019). The fine-scale landscape of immunity and parasitism in a wild ungulate population. *Integrative and Comparative Biology*, *16*, e2003538. https://doi.org/10.1093/icb/icz016

Albery, G. F., Kenyon, F., Morris, A., Morris, S., Nussey, D. H., & Pemberton, J. M. (2018). Seasonality of helminth infection in wild red deer varies between individuals and between parasite taxa. *Parasitology*, *85*, 1–11. https://doi.org/10.1017/S0031182018000185

Albery, G. F., Watt, K. A., Keith, R., Morris, S., Morris, A., Kenyon, F., Nussey, D. H., & Pemberton, J. M. (2018). Reproduction has different costs for immunity and parasitism in a wild mammal. *bioRxiv*, 472597.

Altizer, S., Dobson, A., Hosseini, P., Hudson, P., Pascual, M., & Rohani, P. (2006). Seasonality and the dynamics of infectious diseases. *Ecology Letters*, *9*, 467–484. https://doi.org/10.1111/j.1461-0248.2005.00879.x

Altizer, S., Ostfeld, R. S., Johnson, P. T. J., Kutz, S., & Harvell, C. D. (2013). Climate change and infectious diseases: From evidence to a predictive framework. *Science*, *341*, 514–519. https://doi.org/10.1126/science.1239401

Becker, D. J., Albery, G. F., Kessler, M. K., Lunn, T. J., Falvo, C. A., Czirják, G. Á., Martin, L. B., & Plowright, R. K. (2020). Macroimmunology: The drivers and consequences of spatial patterns in wildlife immune defence. *Journal of Animal Ecology*, *89*, 972–995. https://doi.org/10.1111/1365-2656.13166

Behnke, J. M., Gilbert, F. S., Abu-Madi, M. A., & Lewis, J. W. (2005). Do the helminth parasites of wood mice interact? *Journal of Animal Ecology*, *74*, 982–993. https://doi.org/10.1111/j.1365-2656.2005.00995.x

Behnke, J. M., Lewis, J. W., Zain, S. N. M., & Gilbert, F. S. (1999). Helminth infections in *Apodemus sylvaticus* in southern England: Interactive effects of host age, sex and year on the prevalence and abundance of infections. *Journal of Helminthology*, *73*, 31–44.

Bordes, F., Ponlet, N., de Bellocq, J. G., Ribas, A., Krasnov, B. R., & Morand, S. (2012). Is there sex-biased resistance and tolerance in Mediterranean wood mouse (*Apodemus sylvaticus*) populations facing multiple helminth infections? *Oecologia*, *170*, 123–135. https://doi.org/10.1007/s00442-012-2300-5

Brown, E. D., Macdonald, D. W., Tewand, T. E., & Todd, I. A. (1994). *Apodemus sylvaticus* infected with *Heligmosomoides polygyrus* (Nematoda) in an arable ecosystem: Epidemiology and effects of infection on the movements of male mice. *Journal of Zoology*, *234*, 623–640.

Calder, P. C., & Jackson, A. A. (2000). Undernutrition, infection and immune function. *Nutrition Research Reviews*, *13*, 3–29. https://doi.org/10.1079/095442200108728981

Cardon, M., Loot, G., Grenouillet, G., & Blanchet, S. (2011). Host characteristics and environmental factors differentially drive the burden and pathogenicity of an ectoparasite: A multilevel causal analysis. *Journal of Animal Ecology*, *80*, 657–667. https://doi.org/10.1111/j.1365-2656.2011.01804.x

Clark, J., Garbutt, J. S., McNally, L., & Little, T. J. (2017). Disease spread in age structured populations with maternal age effects. *Ecology Letters*, *20*, 445–451. https://doi.org/10.1111/ele.12745

Clerc, M., Babayan, S. A., Fenton, A., & Pedersen, A. B. (2019). Age affects antibody levels and anthelmintic treatment efficacy in a wild rodent. *International Journal for Parasitology: Parasites and Wildlife*, *8*, 240–247.

Clerc, M., Devevey, G., Fenton, A., & Pedersen, A. B. (2018). Antibodies and coinfection drive variation in nematode burdens in wild mice. *International Journal for Parasitology*, *48*, 785–792. https://doi.org/10.1016/j.ijpara.2018.04.003

Coulson, T., Catchpole, E. A., Albon, S. D., Morgan, B. J., Pemberton, J. M., Clutton Brock, T. H., Crawley, M. J., & Grenfell, B. T. (2001). Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*, *292*, 1528–1531. https://doi.org/10.1126/science.292.5521.1528

Cox, F. E. G. (2001). Concomitant infections, parasites and immune responses. *Parasitology*, *122*, S23–S38. https://doi.org/10.1017/S0031182000016 98X

Davies, T. J., & Pedersen, A. B. (2008). Phylogeny and geography predict pathogen community similarity in wild primates and humans. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1643), 1695–1701. https://doi.org/10.1098/rspb.2008.0284

Debeffe, L., McLoughlin, P. D., Medill, S. A., Stewart, K., Andres, D., Shury, T., Wagner, B., Jenkins, E., Gilleard, J. S., & Poissant, J. (2016). Negative covariance between parasite load and body condition in a population of feral horses. *Parasitology*, *143*, 983–997. https://doi.org/10.1017/S0031182016000408

Dowell, S. F. (2001). Seasonal variation in host susceptibility and cycles of certain infectious diseases. *Emerging Infectious Diseases*, *7*, 369–374. https://doi.org/10.3201/eid0703.017301

Eira, C., Torres, J., Vingada, J., & Miquel, J. (2006). Ecological aspects influencing the helminth community of the wood mouse *Apodemus sylvaticus* in Dunas de Mira, Portugal. *Acta Parasitologica*, *51*, 300–308. https://doi.org/10.2478/s11686-006-0046-0

Ezenwa, V. O., Stefan Ekernas, L., & Creel, S. (2012). Unravelling complex associations between testosterone and parasite infection in the wild. *Functional Ecology*, *26*, 123–133. https://doi.org/10.1111/j.1365-2435.2011.01919.x

Fenton, A., Knowles, S. C. L., Petchey, O. L., & Pedersen, A. B. (2014). The reliability of observational approaches for detecting interspecific parasite interactions: Comparison with experimental results. *International Journal for Parasitology*, *44*, 437–445. https://doi.org/10.1016/j.ijpara.2014.03.001

Fenton, A., & Pedersen, A. B. (2005). Community epidemiology framework for classifying disease threats. *Emerging Infectious Diseases*, *11*, 1815–1821. https://doi.org/10.3201/eid1112.050306

Ferrari, N., Cattadori, I. M., Nespereira, J., Rizzoli, A., & Hudson, P. J. (2004). The role of host sex in parasite dynamics: Field experiments on the yellow-necked mouse *Apodemus flavicollis*. *Ecology Letters*, *7*, 88–94. https://doi.org/10.1046/j.1461-0248.2003.00552.x

Fidler, F., Chee, Y. E., Wintle, B. C., Burgman, M. A., McCarthy, M. A., & Gordon, A. (2017). Metaresearch for evaluating reproducibility in ecology and evolution. *BioScience*, *28*, biw159. https://doi.org/10.1093/biosci/biw159

Fraser, H., Parker, T., Nakagawa, S., Barnett, A., & Fidler, F. (2018). Questionable research practices in ecology and evolution. *PLoS ONE*, *13*, e0200303. https://doi.org/10.1371/journal.pone.0200303

Gregory, R. D. (1992). On the interpretation of host-parasite ecology: *Heligmosomoides polygyrus* (Nematoda) in wild wood mouse (*Apodemus sylvaticus*) populations. *Journal of Zoology*, *226*, 109–121.

Gregory, R. D., Keymer, A. E., & Clarke, J. R. (1990). Genetics, sex and exposure: The ecology of *Heligmosomoides polygyrus* (Nematoda) in the wood mouse. *The Journal of Animal Ecology*, *59*, 363. https://doi.org/10.2307/5178

Gregory, R. D., Montgomery, S. S. J., & Montgomery, W. I. (1992). Population biology of *Heligmosomoides polygyrus* (Nematoda) in the wood mouse. *The Journal of Animal Ecology*, *61*, 749. https://doi.org/10.2307/5628

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, *33*, 1–22.

Houdijk, J. G. M. (2008). Influence of periparturient nutritional demand on resistance to parasites in livestock. *Parasite Immunology*, *30*, 113–121. https://doi.org/10.1111/j.1365-3024.2008.00992.x

Hudson, P. J., Newborn, D., & Dobson, A. P. (1992). Regulation and stability of a free-living host-parasite system: *Trichostrongylus tenuis* in Red Grouse. I. Monitoring and parasite reduction experiments. *The Journal of Animal Ecology*, *61*, 477. https://doi.org/10.2307/5338

Ihle, M., Winney, I. S., Krystalli, A., & Croucher, M. (2017). Striving for transparent and credible research: Practical guidelines for behavioral ecologists. *Behavioral Ecology*, *28*, 348–354. https://doi.org/10.1093/beheco/arx003

Irvine, R. J., Corbishley, H., Pilkington, J. G., & Albon, S. D. (2006). Low-level parasitic worm burdens may reduce body condition in free-ranging red deer (*Cervus elaphus*). *Parasitology*, *133*, 465–475.

Johnston, C. J. C., Robertson, E., Harcus, Y., Grainger, J. R., Coakley, G., Smyth, D. J., McSorley, H. J., & Maizels, R. (2015). Cultivation of *Heligmosomoides polygyrus*: An immunomodulatory nematode parasite and its secreted products. *Journal of Visualized Experiments: Jove*, *98*, e52412.

Knowles, S. C. L., Fenton, A., Petchey, O. L., Jones, T. R., Barber, R., & Pedersen, A. B. (2013). Stability of within-host–parasite communities in a wild mammal system. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1762), 20130598. https://doi.org/10.1098/rspb.2013.0598

Langley, R., & Fairley, J. S. (1982). Seasonal variations in infestations of parasites in a Wood mouse *Apodemus sylvaticus* population in the West of Ireland. *Journal of Zoology*, *198*, 249–261. https://doi.org/10.1111/j.1469-7998.1982.tb02074.x

Margolis, L., Esch, G. W., Holmes, J. C., Kuris, A. M., & Schad, G. A. (1982). The use of ecological terms in parasitology (Report of an Ad Hoc Committee of the American Society of Parasitologists). *The Journal of Parasitology*, *68*, 131. https://doi.org/10.2307/3281335

Martin, L. B., Weil, Z. M., & Nelson, R. J. (2008). Seasonal changes in vertebrate immune activity: Mediation by physiological trade-offs. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *363*, 321–339. https://doi.org/10.1098/rstb.2007.2142

Millán, J., Sevilla, I., Gerrikagoitia, X., García-Pérez, A. L., & Barral, M. (2004). Helminth parasites of the Eurasian badger (*Meles meles L.*) in the Basque Country (Spain). *European Journal of Wildlife Research*, *50*, 37–40. https://doi.org/10.1007/s10344-003-0032-x

Montgomery, S. S., & Montgomery, W. I. (1988). Cyclic and non-cyclic dynamics in populations of the helminth parasites of wood mice, *Apodemus sylvaticus*. *Journal of Helminthology*, *62*, 78–90.

Montgomery, S. S. J., & Montgomery, W. I. (1990). Structure, stability and species interactions in helminth communities of wood mice,

Apodemus sylvaticus. *International Journal for Parasitology*, *20*, 225–242. https://doi.org/10.1016/0020-7519(90)90105-V

Moore, S. L., & Wilson, K. (2002). Parasites as a viability cost of sexual selection in natural populations of mammals. *Science*, *297*, 2015–2018. https://doi.org/10.1126/science.1074196

Muehlenbein, M. P., & Bribiescas, R. G. (2005). Testosterone-mediated immune functions and male life histories. *American Journal of Human Biology*, *17*, 527–558. https://doi.org/10.1002/ajhb.20419

Nelson, R. J., & Demas, G. E. (1996). Seasonal changes in immune function. *The Quarterly Review of Biology*, *71*, 511–548. https://doi.org/10.1086/419555

Nowell, F., & Higgs, S. (1989). Eimeria species infecting wood mice (genus *Apodemus*) and the transfer of two species to *Mus musculus*. *Parasitology*, *98*(Pt 3), 329–336.

Palmer, W. H., Hadfield, J. D., & Obbard, D. J. (2018). RNA-interference pathways display high rates of adaptive protein evolution in multiple invertebrates. *Genetics*, *208*, 1585–1599. https://doi.org/10.1534/genetics.117.300567

Pedersen, A. B., & Fenton, A. (2015). The role of antiparasite treatment experiments in assessing the impact of parasites on wildlife. *Trends in Parasitology*, *31*, 200–211. https://doi.org/10.1016/j.pt.2015.02.004

Peig, J., & Green, A. J. (2009). New perspectives for estimating body condition from mass/length data: The scaled mass index as an alternative method. *Oikos*, *118*, 1883–1891. https://doi.org/10.1111/j.1600-0706.2009.17643.x

Plowright, R. K., Manlove, K. R., Besser, T. E., Páez, D. J., Andrews, K. R., Matthews, P. E., Waits, L. P., Hudson, P. J., & Cassirer, E. F. (2017). Age-specific infectious period shapes dynamics of pneumonia in bighorn sheep. *Ecology Letters*, *20*, 1325–1336. https://doi.org/10.1111/ele.12829

Rue, H., Martino, S., & Chopin, N. (2009). Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, *71*, 319–392. https://doi.org/10.1111/j.1467-9868.2008.00700.x

Sánchez, C. A., Becker, D. J., Teitelbaum, C. S., Barriga, P., Brown, L. M., Majewska, A. A., Hall, R. J., & Altizer, S. (2018). On the relationship between body condition and parasite infection in wildlife: A review and meta-analysis. *Ecology Letters*, *21*, 1869–1884. https://doi.org/10.1111/ele.13160

Sheldon, B. C., & Verhulst, S. (1996). Ecological immunology: Costly parasite defences and trade-offs in evolutionary ecology. *Trends in Ecology & Evolution*, *11*, 317–321. https://doi.org/10.1016/0169-5347(96)10039-2

Stromberg, B. E. (1997). Environmental factors influencing transmission. *Veterinary Parasitology*, *72*, 247–256; discussion 257–264. https://doi.org/10.1016/S0304-4017(97)00100-3

Sweeny, A. R., Albery, G. F., Venkatesan, S. V., Fenton, A., & Pedersen, A. B. (2021). Spatiotemporal variation in drivers of parasitism in a wild wood mouse population. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.0cfxpnw1q

Sweeny, A. R., Clerc, M., Pontifes, P. A., Venkatesan, S., Babayan, S. A., & Pedersen, A. B. (2021). Supplemented nutrition decreases helminth burden and increases drug efficacy in a natural host–helminth system. *Proceedings of the Royal Society of London B. Biological Sciences*, *288*, 20202722–10.

Tompkins, D. M., Dunn, A. M., Smith, M. J., & Telfer, S. (2011). Wildlife diseases: From individuals to ecosystems. *Journal of Animal Ecology*, *80*, 19–38. https://doi.org/10.1111/j.1365-2656.2010.01742.x

Warburton, E. M., Pearl, C. A., & Vonhof, M. J. (2016). Relationships between host body condition and immunocompetence, not host sex, best predict parasite burden in a bat-helminth system. *Parasitology Research*, *115*, 2155–2164. https://doi.org/10.1007/s00436-016-4957-x

Zuk, M., & McKean, K. A. (1996). Sex differences in parasite infections: Patterns and processes. *International Journal for Parasitology*, *26*, 1009–1024. https://doi.org/10.1016/S0020-7519(96)80001-4

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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