

Research Article

Cite this article: Parsa F(Rose), Bayley S, Bell F, Dodd S, Morris R, Roberts J, Wawman D, Clegg SR, Dunn JC (2023). Epidemiology of protozoan and helminthic parasites in wild passerine birds of Britain and Ireland. *Parasitology* 1–14. <https://doi.org/10.1017/S0031182022001779>

Received: 30 July 2022
Revised: 14 December 2022
Accepted: 19 December 2022






Keywords:

Abundance; birds; British Isles; epidemiology; infection intensity; intestinal parasites; *Isospora*; prevalence; *Syngamus*

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Epidemiology of protozoan and helminthic parasites in wild passerine birds of Britain and Ireland

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Abstract

Avian endoparasites play important roles in conservation, biodiversity and host evolution. Currently, little is known about the epidemiology of intestinal helminths and protozoans infecting wild birds of Britain and Ireland. This study aimed to determine the rates of parasite prevalence, abundance and infection intensity in wild passerines. Fecal samples ($n = 755$) from 18 bird families were collected from 13 sites across England, Wales and Ireland from March 2020 to June 2021. A conventional sodium nitrate flotation method allowed morphological identification and abundance estimation of eggs/oocysts. Associations with host family and age were examined alongside spatiotemporal and ecological factors using Bayesian phylogenetically controlled models. Parasites were detected in 20.0% of samples, with corvids and finches having the highest prevalences and intensities, respectively. *Syngamus* (33%) and *Isospora* (32%) were the most prevalent genera observed. Parasite prevalence and abundance differed amongst avian families and seasons, while infection intensity varied between families and regions. Prevalence was affected by diet diversity, while abundance differed by host age and habitat diversity. Infection intensity was higher in birds using a wider range of habitats, and doubled in areas with feeders present. The elucidation of these patterns will increase the understanding of parasite fauna in British and Irish birds.

Introduction

Avian endoparasites play important roles in biodiversity, behaviour, ecology, host evolution and species conservation (Loye and Carroll, 1995; Richner, 1998; Asakawa *et al.*, 2002; Hudson *et al.*, 2006). It is therefore important to understand host–parasite associations in order to predict patterns of parasite emergence, transmission and pathogenicity (Poulin *et al.*, 2011). The pervasiveness and wide variety of parasites capable of infecting a host can have distinct implications for both inter- and intraspecific transmissions. More infected individuals can increase the probability of disease transmission in a community, underlining the importance of understanding the factors that influence parasite prevalence (Pérez-Tris and Bensch, 2005).

The intricate life cycles of certain helminths, such as *Fasciola* spp. have co-evolved with their hosts' complex food-webs due to their requirements of definitive, paratenic and intermediate hosts (Hoberg, 1996; Bakker *et al.*, 1997). As birds are globally widespread in nature and can act as reservoirs for various generalist parasites, they may play an important role in cross-species transmission (Ishtiaq and Renner, 2020); their high sociality can also have implications for disease transmission (Brown and Brown, 2004). Identifying the trends that occur in parasite emergence is also significant for the conservation of non-adapted species. Immunologically naïve animals are often more sensitive to infection due to the lack of coevolution with the introduced parasite, which may lead to the development of severe symptoms and mortality (Howe *et al.*, 2012; Vanstreels *et al.*, 2014). Therefore, determining the patterns of association of parasitic infections in wild bird populations is indispensable.

There is a dearth of epidemiological studies on the occurrence and distribution of intestinal parasites infecting wild passerine populations; elucidating these host–parasite associations is essential in understanding transmission, emergence and virulence (Waldenström *et al.*, 2002; Pérez-Tris and Bensch, 2005; Penczykowski *et al.*, 2016). Prior epidemiological research has often revolved around livestock, pets, humans and other mammalian wildlife (Hoque *et al.*, 2014; Minetti *et al.*, 2014), but only a few studies have examined both helminths and protozoa in wild birds (e.g. Wascher *et al.*, 2012). The only study conducted in Britain to include wild passerines solely examined coccidia (Brown *et al.*, 2010). There have been other studies examining the intestinal parasites of birds, including some in Asia and South America, that use a

wide range of detection techniques such as staining, sedimentation and sporulation (Badparva *et al.*, 2014; Hoque *et al.*, 2014); however, the majority examined domestic birds or those kept in zoological gardens (Pérez Córdón *et al.*, 2009). Therefore, observational epidemiological studies are integral in identifying the shared parasite fauna of wild birds.

Moreover, there is a scarcity of research on the potential effects of ecological variables, such as anthropogenic food availability, habitat and diet, on the prevalence, abundance and infection intensity of passerine intestinal parasites (but see Bandelj *et al.*, 2015). The effect of humans providing supplementary feeding to wildlife, such as through the use of supplementary bird seed, has been linked to the spread of *Trichomonas gallinae* protozoa, the aetiological agent of avian trichomonosis, to naïve hosts (e.g. Lennon *et al.*, 2013). Meanwhile, the diversity of the habitats and diets shared by passerines can impact their exposure to, or resistance against, parasites (Becker *et al.*, 2018; Strandin *et al.*, 2018); although these can be intertwined with other factors, such as migration, nutrition and feeding behaviour, they are still necessary to examine to elucidate whether they explain any trends observed in the rates of infections.

Coinfection, or the state of being infected by multiple pathogens simultaneously, is ubiquitous in nature, with various types of endoparasites often being detected together in wild vertebrates (Ezenwa, 2016). Coinfections can affect host health alongside influencing parasite transmission (Cox, 2001). A meta-analysis by Knowles (2011) demonstrated that helminths can influence immune system modulation of the murine (*Mus musculus*) host, leading to differing impacts on malaria infection dynamics. Despite the important dynamic effects multiple parasites can have on each other and the host (Thomas *et al.*, 2022), there is a scarcity of research into avian parasite epidemiology while taking coinfection into account.

Here, we determine the prevalence and abundance of helminths and coccidians infecting a range of wild avian hosts at 13 geographically separate sites across Britain and Ireland. We test whether parasite prevalence, abundance and infection intensity differ between avian host families, ages and spatiotemporally, and determine whether parasite genus influences the trends in parasite abundance and intensity; we also test the impacts of parasite genus on these variables separately. We also test whether the presence of feeders could act as a potential source of parasite transmission, predicting they will be linked with increased parasite prevalence and abundance. We also determine whether greater host habitat and diet diversity will increase both prevalence and abundance of gut parasites across avian hosts due to heightened exposure. Finally, we carry out rarefaction analyses to examine expected parasite diversity within each host species and test for under-sampling, and examine patterns of coinfection to test whether some commonly occurring parasites are detected together more or less often than would be expected.

Methods

Study sites

Fecal samples were collected from birds caught as part of regular ringing operations over 15 months, from March 2020 to June 2021 at 13 sites in England ($n=9$), Wales ($n=3$) and the Republic of Ireland ($n=1$). Sites consisted of garden ($n=6$), woodland ($n=2$) or farmland ($n=5$) habitats across 7 counties (Fig. 1).

Sample collection

Birds were caught using whoosh or mist nets on days with minimal wind or rain (time range: 6 am–4:30 pm; median: 9:47 am), fitted with a British Trust for Ornithology metal ring, and aged

and sexed, where possible, according to standard techniques (Svensson, 1992); only 1 bird, a blue tit, appeared in slightly poor condition with some facial feather loss. The presence or absence of feeders at each ringing site was also recorded. Birds were retained for a maximum of 10 min in sterile holding bags to allow for the production of a fecal sample prior to release. Feces were placed into clean, pre-labelled 1.5 mL tubes and refrigerated within 8 h in plastic bags until postage; the specimens were posted as soon as feasible for laboratory analysis (range: 2–14 days; median: 5 days).

Laboratory analysis

A conventional fecal flotation technique allowed for the detection of helminth eggs and protozoan oocysts using sodium nitrate flotation fluid with a specific gravity of 1.2 (Vetlab Supplies Ltd, Pulborough, West Sussex, UK) and the McMaster egg counting technique (Levecke *et al.*, 2011); the weights of the feces were measured (Supplementary Table 2) and scaled up to calculate the eggs/oocysts per g (EPG/OPG) to standardize the quantification of parasite abundance and intensity. Published keys assisted in morphological identification to the genus level based on colour, shape, size and other distinguishable features (Svobodová, 1994; Presswell and Lagrue, 2016; Gallo *et al.*, 2018).

Phylogenetically controlled mixed effects models

Statistical analyses were performed in R version 4.1.0 (R Core Team, 2021). Three phylogenetically controlled generalised linear mixed-effects models (PGLMMs) were constructed using the *MCMCglmm* package (Hadfield, 2010) for Bayesian analysis, alongside the *ape* package (Paradis *et al.*, 2004) to identify spatio-temporal and ecological associations with parasite prevalence, abundance and infection intensity when controlling for host phylogeny and time until analysis. The Markov chain Monte Carlo (MCMC) allows the analysis of complex models using a probabilistic sampling technique while controlling for fine-scale phylogenetic relatedness by treating avian phylogeny as a random variable. The phylogeny was obtained from BirdTree (Jetz *et al.*, 2012) using the Ericson All Species model. Due to systematic reclassifications of 2 former subspecies to distinct taxa, no data were available on BirdTree for *Corvus cornix* and *Acanthis cabaret*, so data for *Corvus corone* and *Carduelis flammula* were used as replacements due to being the most closely related species.

The response variable for the parasite prevalence model comprised of the absence or presence (0 or 1) of any parasite genus within each host; this model comprised of a binomial PGLMM with a logit link. Parasite abundance and infection intensity were defined as the number of eggs/oocysts combined within each individual or each infected individual, respectively (Reiczigel *et al.*, 2019); these were each analysed using Poisson-distributed PGLMMs with a log link. Fixed effects in all 3 models comprised of bird family, host age (adult or juvenile/first year), season (a 4-level categorical variable: winter: December–February, $n=157$; spring: March–May, $n=196$; summer: June–August, $n=127$; autumn: September–November, $n=189$), geographic region [a 6-level categorical variable: region with 4 areas in England, 1 in Wales and 1 in Ireland (Fig. 1)], bird feeder presence or absence and diet and habitat diversity at the species level; these latter continuous variables were extracted from a Europe-wide dataset (Storchová and Hořák, 2018) and denote the total number of diets or habitats known to be used by the species (diet range: 1–6; habitat range: 1–5). Only families with samples from more than 10 individuals were included in the analyses, so Cettiidae ($n=1$), Certhiidae ($n=2$), Sittidae ($n=2$) and Regulidae ($n=5$) were removed from the dataset. To include host age in the analyses,

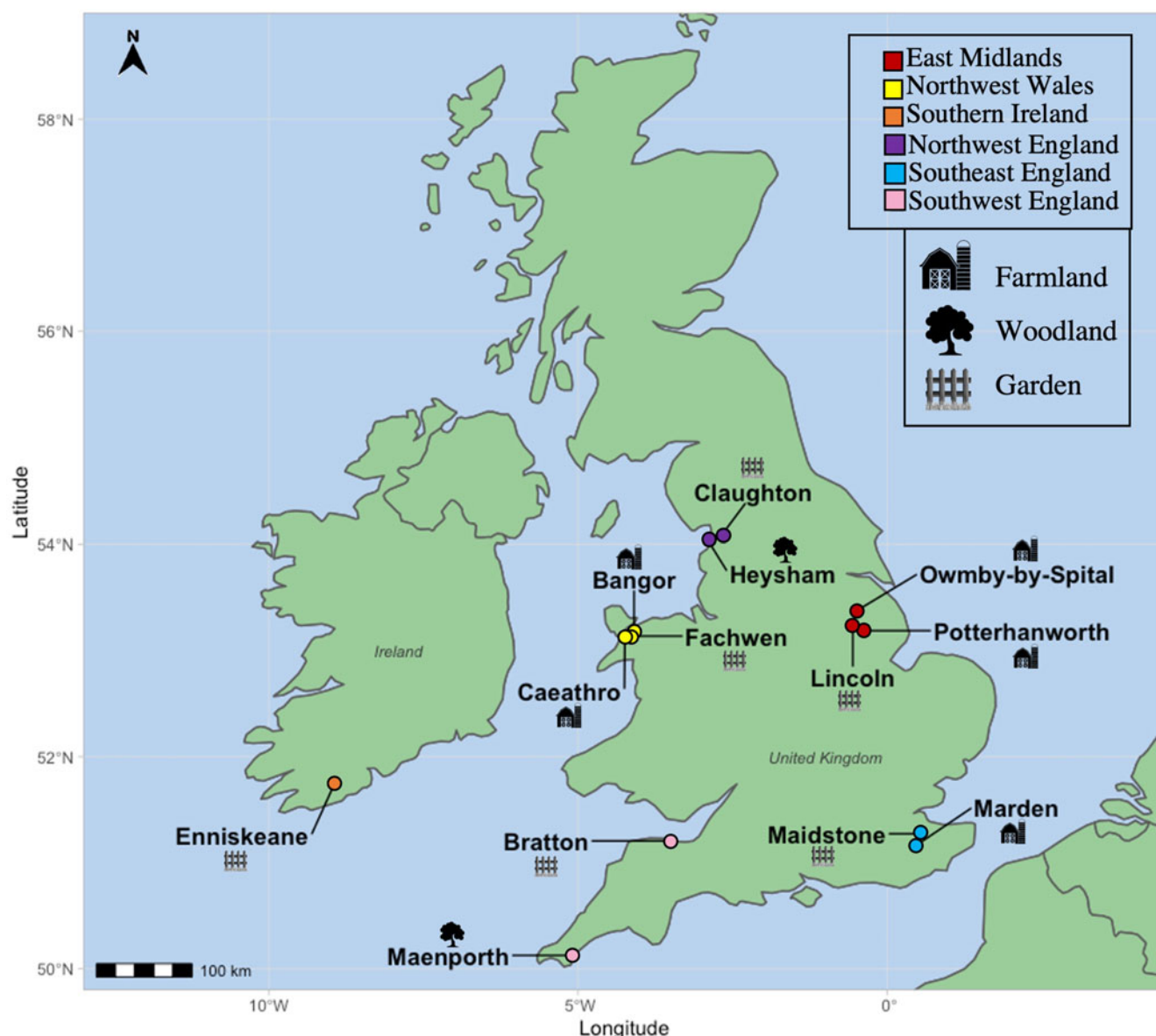


Fig. 1. Locations of avian fecal sampling sites throughout the British Isles, with the legends showing their characterization into geographical regions as well as symbols denoting the primary habitat type found at these areas.

specimens from *Aegithalos caudatus* ($n = 13$), *Passer montanus* ($n = 6$) and *Passer domesticus* ($n = 15$) were removed from the analysis as they undergo a complete post-juvenile moult and cannot be aged during ringing activities after the autumn; birds whose ages were not recorded ($n = 42$) were also removed from the analysis, resulting in final sample sizes of 669 (prevalence, abundance) and 138 (infection intensity) birds. For the abundance and infection intensity models, the analyses excluded Phylloscopidae ($n = 18$) as they were uninfected. The abundance and infection intensity analyses were also repeated to include parasite genus in the model to determine whether infection type influences parasite load. Host phylogeny and average time lapsed from sample collection until analysis (in days; range: 2.2–12.8 days) were included as a random effect in all models. Models were run for 500 000 iterations, with a 1000 burn-in period and a 500-thinning interval; the resulting effective sample sizes were similar amongst factors (~ 998).

Rarefaction analyses

To estimate how many parasites may have been missed due to under-sampling of hosts, rarefaction analyses were conducted

using the *vegan* package (Oksanen *et al.*, 2017), based on sampling without replacement. This allowed for quantification of any potential sampling biases by estimating the total parasite genera richness that was likely to be detected amongst the various avian host families based on observed samples (Gotelli and Colwell, 2001). Only families with more than 1 parasite genus observed ($n = 9$) were included. If asymptotic richness is shown to be reached by a host, then it can be concluded that the majority of parasite genera present within that host are likely to have been detected.

Co-occurrence analyses

The *cooccur* package (Griffith *et al.*, 2016) was used to test for patterns in parasite co-occurrence, and analyse whether multiple parasite genera were observed together at random or whether there were positive or negative correlations. This was performed by using the overall prevalence of each parasite and examining whether the observed rate of genus co-occurrence was higher or lower than expected (Griffith *et al.*, 2016). Trematodes were omitted from this analysis because they were underrepresented in the

data and to meet the assumption that only parasites present in more than 5% of positive samples are included.

Results

Samples were collected from 18 families of wild Passeriformes ($n = 755$), comprising 28 genera and 38 species. Sample sizes for each species range from 1 to 140 (mean \pm S.E.: 19.9 ± 4.2), with sample sizes per family varying from 1 to 228 (41.9 ± 13.2).

Parasite genera

Fourteen parasite genera were identified from microscopic analysis of fecal samples following fecal flotation. These comprised of gregarines (*Monocystis*), coccidians (*Eimeria*, *Isospora*), nematodes (*Capillaria*, *Porrocaecum*, *Syngamus*), cestodes (*Anonchotaenia*, *Dilepis*, *Passerilepis*, *Variolepis*) and trematodes (*Brachydistomum*, *Collyriclum*, *Echinostoma*, *Leucochloridium*) (Figs 2 and 3; Supplementary Fig. 1). Although mites and potential larvae-like stages were also detected in the samples, they were not included in fecal egg/oocyst counts.

Parasite prevalence

Intestinal parasites were identified in 20.0% (151/755) of all birds sampled (Fig. 4). Phylogenetically controlled analysis revealed that the prevalence of intestinal parasites differed between avian host families and amongst seasons, but not between sites (Table 2; Figs 5–7). Overall prevalence differed between families (range: 0–70%; mean \pm S.E.: $23.2 \pm 5.6\%$) with 6 avian families being uninfected (Figs 4 and 5; Table 2). The highest prevalences were observed in corvids, starlings and dunnocks (Figs 5 and 6); meanwhile, long-tailed tits and leaf warblers had the lowest prevalences. However, rarefaction curves suggested that asymptotic richness has only been reached amongst Acrocephalidae, Paridae and Turdidae (Supplementary Fig. 2). *Syngamus* spp. eggs (33.1%; 50/151), *Isospora* spp. oocysts (32.4%; 49/151) and *Capillaria* spp. eggs (27.2%; 41/151) were the most detected genera (Fig. 5). Birds sampled in the winter months had the highest prevalence ($26.1 \pm 3.4\%$) while those sampled in spring had the

lowest ($16.5 \pm 2.3\%$) (Fig. 7). Although there were no associations between parasite prevalence and feeder presence or habitat diversity (Supplementary Table 1), diet diversity and host age were strongly associated with prevalence (Table 2); in particular, infected birds had a greater mean diet diversity (2.7 ± 0.1) than those non-infected (2.6 ± 0.04), with species that were known to consume 6 diet types having the highest prevalence rates (75.0%; 6/8), followed by those with 4 (30.43%; 21/69), 2 (28.0%; 26/93), 1 (21.3%; 26/122) and 3 types (15.7%; 59/377). Juveniles had higher parasite prevalence of infection (22.4%; 89/397) than adults (17.9%; 51/285).

Parasite abundance

The mean abundance of parasitic EPG/OPG of feces across all birds was 1704.0 ± 504.8 . *Isospora* had the highest abundance overall (1485.2 ± 500.51 OPG) and trematodes the lowest (0.6 ± 0.2 EPG) with parasite genus driving trends in abundance (Table 3; Fig. 8). Phylogenetically controlled analyses found that parasite abundance varied between avian host families (Table 1; Fig. 6); specifically, abundances were higher in thrushes (1826.6 ± 905.6 EPG/OPG) than in starlings (234.6 ± 181.5 EPG). None of geographical region, diet diversity or feeder presence appears to influence abundance, but season, habitat diversity and age were strongly influential (Table 1; Fig. 7); specifically, birds sampled in winter had the highest mean abundance (6080 ± 2197.4 EPG/OPG) and those sampled in spring had the lowest (139.0 ± 46.1 EPG/OPG). Birds that were known to occupy 3 habitat types had the highest abundance (3350.0 ± 1254.9 EPG/OPG) followed by those with 5 (1092.3 ± 780.0 EPG/OPG), 4 (987.3 ± 367.2 EPG/OPG), 2 (215.2 ± 91.5 EPG/OPG) and 1 type (3.1 ± 2.2 EPG/OPG). Juveniles were infected to a higher degree (2565.0 ± 915.9 EPG/OPG) than adults (841.6 ± 327.3 EPG/OPG).

Parasite infection intensity

The mean infection intensity of parasitic eggs and oocysts within the infected birds was 8407.0 ± 2420.0 /g of feces. *Isospora* had the highest maximum intensity overall (7327.5 ± 2417.7) and

Table 1. Significant results of phylogenetically controlled, Poisson MCMC GLMMs comparing the various factors affecting avian parasite abundance

		Estimate	95% CI		pMCMC
			Lower	Upper	
Intercept		−5.89	−68.21	60.26	0.812
Avian family					
Sturnidae	Troglodytidae	−25.69	−48.97	−2.46	0.014
Season					
Winter	Autumn	4.01	0.09	6.98	0.012
	Spring	7.94	4.08	11.99	<0.001
Ecological variables					
	Habitat diversity	0.24	−2.37	−2.08	0.024
Host variable					
	Age (juvenile vs adult)	2.53	0.36	5.06	0.032
Random effects					
	Host phylogeny	158.20	0.0023	793.70	
	Time until analysis	16 664	0.0030	4876	

Estimates, lower and upper 95% confidence interval (CI) values, and *P* values particle Markov chain Monte Carlo (pMCMC) have been included for the intercept, random effects and each level of the factors.

Table 2. Significant results of phylogenetically controlled, binomial MCMC GLMMs testing whether host and ecological factors influence avian parasite prevalence

		Estimate	95% CI		pMCMC
			Lower	Upper	
Intercept		−161.10	−1088.33	911.47	0.675
Avian family					
Acrocephalidae vs	Corvidae	767.12	0.58	1549.19	0.032
	Phylloscopidae	−2604.02	−6098.42	−80.49	0.018
Corvidae vs	Emberizidae	−694.84	−1221.29	−59.10	0.030
	Fringillidae	−767.33	−1266.14	−11.35	0.018
	Muscicapidae	−541.16	−1001.43	−37.98	0.034
	Paridae	−819.39	−1292.95	−149.24	0.016
	Phylloscopidae	−1456.88	−2471.92	−460.68	0.004
	Sylviidae	−718.54	−1219.41	−71.39	0.014
	Troglodytidae	−948.72	−1629.59	−173.59	0.006
Emberizidae vs	Phylloscopidae	−81.23	−163.16	−0.11	0.040
Fringillidae vs	Phylloscopidae	−381.50	−768.88	−74.62	0.004
	Prunellidae	105.74	0.13	228.02	0.028
	Sturnidae	167.36	9.79	353.28	0.030
	Turdidae	102.49	0.62	231.87	0.046
Paridae vs	Sturnidae	597.16	77.44	1061.17	0.024
Phylloscopidae vs	Prunellidae	−3271.88	−5012.14	−297.73	0.004
	Sturnidae	−1728.78	−3915.58	−267.10	0.008
	Turdidae	−336.47	−653.96	−5.81	0.016
Sturnidae vs	Troglodytidae	−966.31	−1725.63	−179.77	0.012
Troglodytidae vs	Turdidae	622.41	100.93	1120.12	0.006
Season					
Autumn vs	Spring	−145.35	−277.39	−8.82	0.026
	Winter	114.11	7.51	217.01	0.022
Spring vs	Winter	209.83	60.98	333.98	<0.001
Ecological variables					
	Diet diversity	−64.72	−181.32	−41.36	0.023
Host variable					
	Age (juvenile vs adult)	91.71	3.28	174.78	0.014
Random effects					
	Host phylogeny	42 829	0.003263	277 474	
	Time until analysis	5 399 675	0.002661	219 631	

Estimates, lower and upper 95% CI values, and *P* values (pMCMC) have been included for the intercept, random effects and each level of the factors.

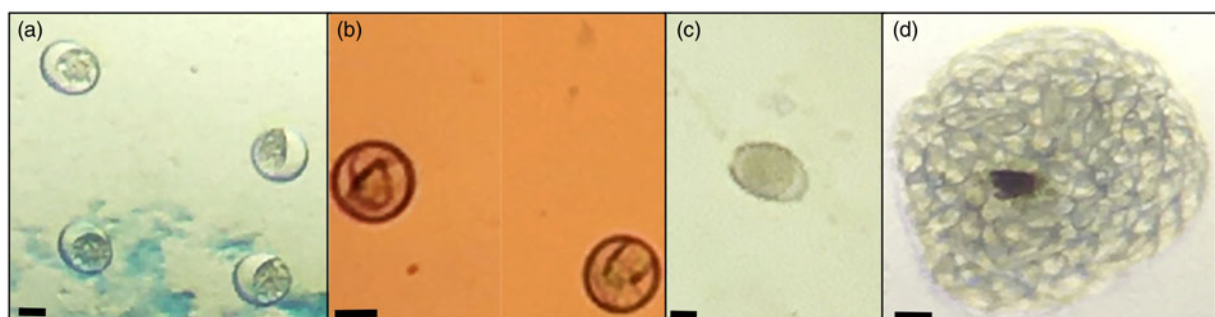


Fig. 2. Protozoa: (a) unsporulated and (b) sporulated *Isospora* sp. oocysts ($\sim 25 \times 23 \mu\text{m}^2$); (c) unsporulated *Eimeria* sp. oocyst ($\sim 25 \times 15 \mu\text{m}^2$) and (d) *Monocystis* sp. gametocyst ($\sim 185 \times 170 \mu\text{m}^2$) with enclosed sporozoites. Magnification is $10\times$ (a, c, d) and $20\times$ (b). Scale bar: $10 \mu\text{m}$.

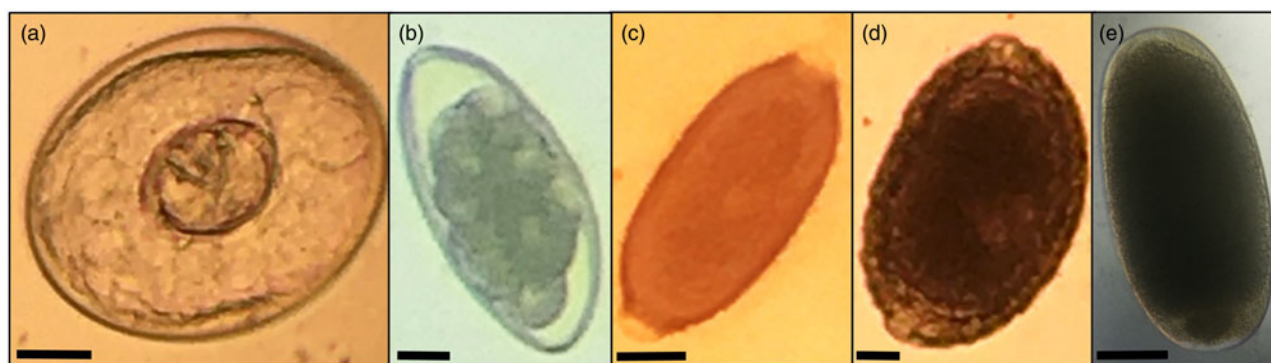


Fig. 3. Helminths: cyst of a cestode (a; $\sim 62 \times 40 \mu\text{m}^2$); eggs of *Syngamus* sp. (b; $\sim 80 \times 45 \mu\text{m}^2$), *Capillaria* sp. (c; $\sim 40 \times 23 \mu\text{m}^2$), *Porrocaecum* sp. (d; $\sim 97 \times 59 \mu\text{m}^2$) and a trematode (e; $\sim 53 \times 25 \mu\text{m}^2$). Magnification is $10\times$ (b, e) and $20\times$ (a, c, d). Scale bar: $10 \mu\text{m}$.

trematodes had the lowest maximum intensity (2.9 ± 0.9), with parasite genus driving trends in infection intensity (Table 4; Fig. 8). Phylogenetically controlled analyses found that infection intensity differed between avian host families (Table 5; Fig. 6); specifically, infection intensities were higher in finches ($37\,301.9 \pm 12\,331.8$ EPG) than in accentors (908.8 ± 471.1 EPG/OPG). Although neither season nor diet diversity appeared to influence infection intensity, geographical region, habitat diversity and feeder presence were strongly influential (Table 5; Fig. 7); in particular, birds sampled in northwest England and southwest England had the lowest (260.0 ± 120.4 EPG/OPG) and highest ($37\,688.0 \pm 12\,822.8$ EPG/OPG) average parasitic infection intensities, respectively (Fig. 7). Samples from areas with feeders had a greater infection intensity (9847.1 ± 2990.6 EPG/OPG) than those without (3894.1 ± 2370.9 EPG/OPG). Birds with 3 habitat types had the highest infection intensities ($22\,079.5 \pm 7752.1$ EPG/OPG), followed by those with 5 (4437.5 ± 3091.3), 4 (3184.7 ± 1142.0 EPG/OPG), 2 (1260.7 ± 451.7 EPG/OPG) and 1 habitat type (50.0 ± 0 EPG).

Rarefaction analyses

Rarefaction analyses on all samples suggest that we have detected over 80% of the parasite genera in Acrocephalidae, Muscicapidae, Paridae, Prunellidae and Turdidae (Supplementary Fig. 2). Analyses suggest we have detected 50% of parasite genera likely to be present in Corvidae, $\sim 65\%$ of parasite genera present in Emberizidae, $\sim 50\%$ of parasite genera present in Sturnidae and $\sim 70\%$ of parasite genera likely to be present in Sylviidae (Supplementary Fig. 2).

Coinfections and co-occurrence analyses

Most infected individuals had a solitary parasitic infection (87.4%; 132/151) while the remainder (12.6%; 19/151) had co-occurring infections; infection by 2 species was the most common (7.9%; 12/151), followed by 3 (2.0%; 3/151), 4 (2.0%; 3/151) and 5 (0.7%; 1/151). The most prevalent parasite genus, *Syngamus* spp., had the highest rates of co-occurring with *Capillaria* spp. in coinfections (Fig. 9). Co-occurrence analyses found both positive and negative associations between coinfecting parasite genera, with positive associations found only between *Monocystis* and *Syngamus*, and negative associations found amongst 6 pairs (Fig. 9). *Eimeria*, *Porrocaecum* and cestodes were only negatively associated with 1 other parasite while *Syngamus* and *Capillaria* had 2 negative correlations each and *Isospora* was negatively associated with 4 other parasites (Fig. 9).

Discussion

Variation in the prevalence and abundance of intestinal parasites differed significantly between host families and between seasons; meanwhile, host family and geographical region appeared to affect parasitic infection intensity. Trends in parasite abundance and infection intensity were driven by parasite genus, specifically *Capillaria*, *Isospora* and *Syngamus*, although habitat diversity and host age also influenced abundance, and infection intensity was more than double at sites with feeders. Parasite prevalence was strongly affected by diet diversity and host age.

Previous epidemiological studies examining the distribution and intensity of endoparasitic infections in avian hosts have been carried out using a wide range of taxonomic groups, including Galliformes, Passeriformes and Psittaciformes (e.g. Masello *et al.*, 2006; Pérez Cordon *et al.*, 2009); although these have been performed in a wide range of countries, Britain and Ireland have not been thoroughly examined. Passerines can be parasitized by a diverse array of generalist and specialist protozoan and helminthic organisms, with varying pathogenicities (Brown *et al.*, 2010; Schoener *et al.*, 2012, 2013); the overall infection rate of 20% reported here is lower than those previously detected at 51.6, 34.8 and 29–48% from a range of birds in Spain, Iran and Bangladesh, respectively (Badparva *et al.*, 2014; Hoque *et al.*, 2014). However, these studies used larger amounts of feces and a wider range of diagnostic methods, and studied mainly domestic, as opposed to wild, birds, which may explain the lower prevalence rates we observed (Badparva *et al.*, 2014; Hoque *et al.*, 2014). Indeed, our findings are comparable to the prevalence of 20% detected in resident wild birds in Bangladesh (Hoque *et al.*, 2014). This variation of intestinal parasites amongst species could be due to coevolutionary adaptations caused by geographical and climatic variation or host immunological status and genetic resistance. Coevolution can be seen in birds that have adapted to be more tolerant to certain parasites and are known as natural hosts (Grantham and Williams, 2017); meanwhile, immune status may be affected by stressors, such as breeding, competition, nutrition and age (Hudson, 1986; Zuk *et al.*, 1990; Møller, 1991; Isomursu *et al.*, 2006; Bandelj *et al.*, 2015). In this study, juveniles had greater parasite prevalence and abundance rates than adults; this is different to prior studies on haemoparasitic infections in birds over time, with Piersma and van der Velde (2012) reporting malaria in 77% of adults but none in fledglings (Sanz *et al.*, 2001; Atkinson and Samuel, 2010). The variations seen here may be due to the immunological naivety of the host, with older birds developing robust responses to previously encountered infections (Isomursu *et al.*, 2006; Sorci, 2013; Bandelj *et al.*, 2015).

Spatiotemporal variation in endoparasitic infections have been reported from biogeographic and evolutionary studies exploring

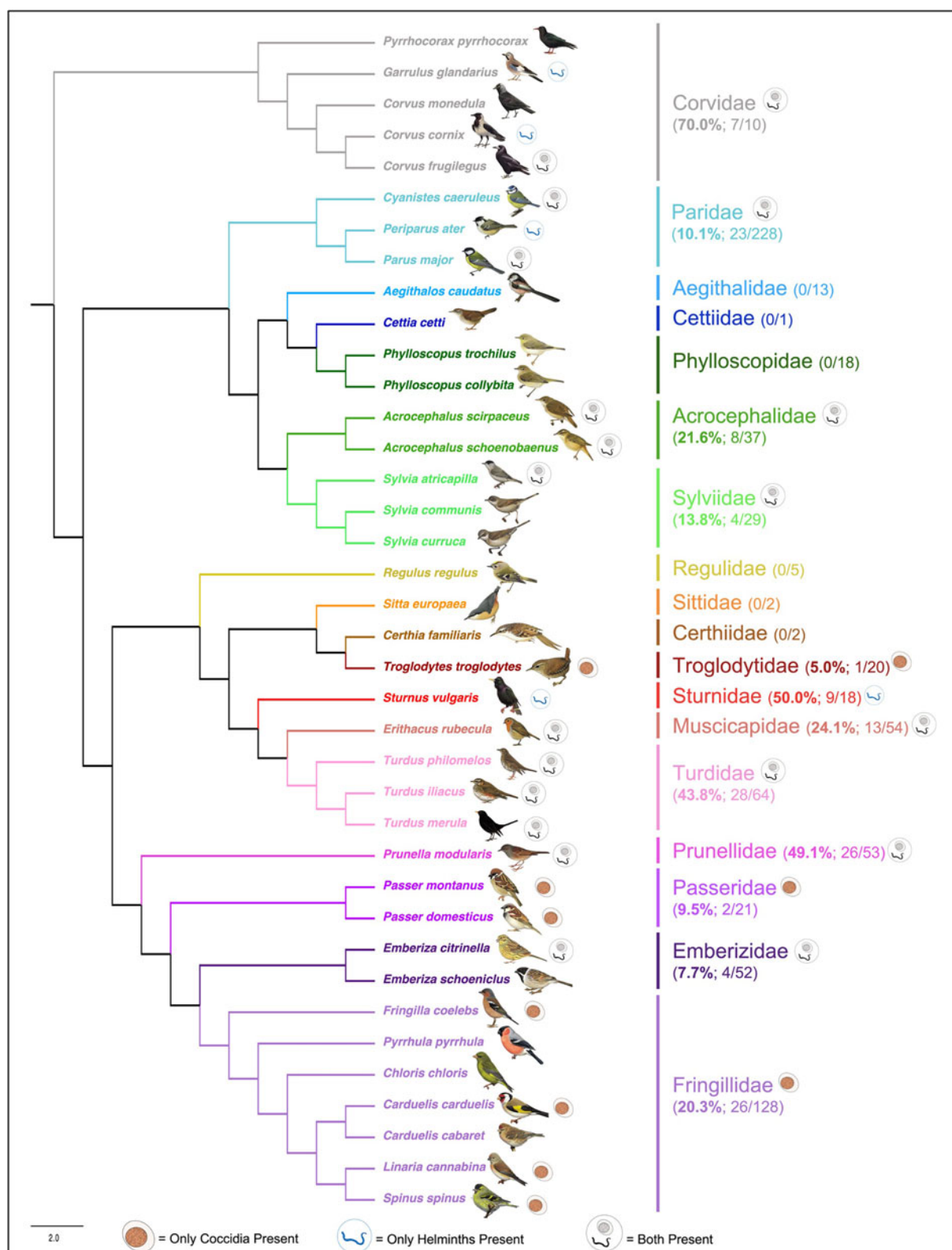


Fig. 4. Cladogram of avian species sampled and their presence of parasites, generated from BirdTree (Jetz *et al.*, 2012) and visualized in FigTree v1.4.4 (Rambaut, 2010). All bird images are from NatureGuides Ltd.

the prevalence and abundance of intestinal parasites (Santiago-Alarcon *et al.*, 2019; Bodawatta *et al.*, 2020); such studies explore the changes in parasite communities across defined time periods and spatial regions and can be essential in elucidating the shedding patterns of eggs and oocysts, such as the fecal excretion of *Isospora* spp. on a diurnal circadian cycle (Martinaud *et al.*, 2009; Dolnik *et al.*, 2011). The seasonal variation observed in the current

study may be due to temperature, humidity or precipitation; these have all been proven to affect the viability of parasites and, particularly, their infective stages when in the environment (Langkjær and Roepstorff, 2008; Maya *et al.*, 2012). The findings of the highest parasite prevalence in winter, often due to isosporiasis, and the lowest in spring, may have been due to existing infections that may persist in winter as birds may not have many

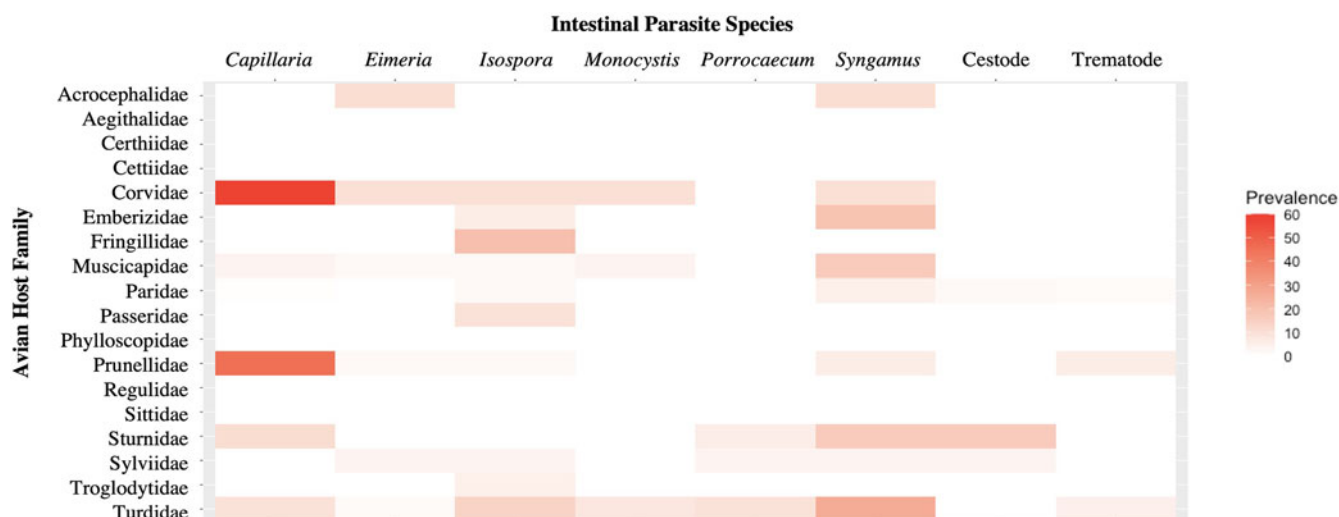


Fig. 5. Heat map showing the prevalence rates (0–60%) of the various types of intestinal parasites in the avian host families sampled.

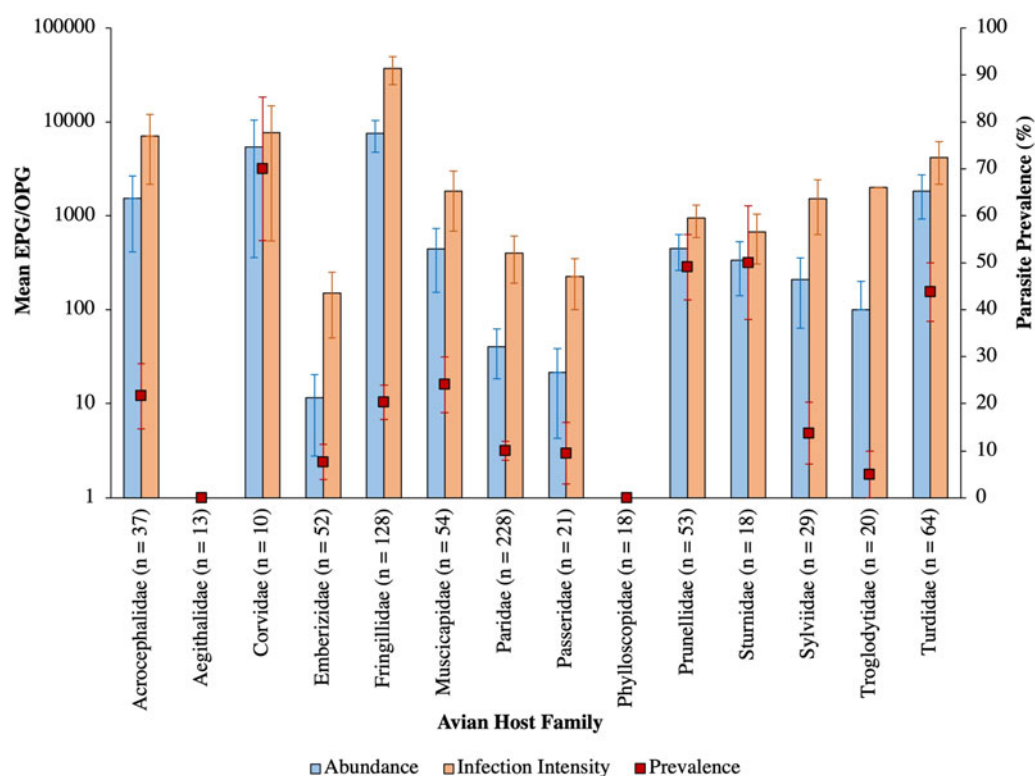


Fig. 6. Mean abundance (\pm s.e.), infection intensity (\pm s.e.) and prevalence (\pm s.e.), represented by blue bars, orange bars and red square points, respectively, of intestinal parasites amongst avian families. Sample sizes are denoted in parentheses.

resources to invest in immunity over this period or be due to the increased sociality of birds forming groups in winter (Nord *et al.*, 2020). Meanwhile, birds sampled in spring may have had reduced prevalence and abundance of parasites due to decreased rainfall or moisture content in the air; eggs and oocysts can desiccate faster under dryer conditions, as seen in ascarid helminths (Senecal *et al.*, 2020), but recording of specific weather conditions would be required to test this.

The geographical variation may be due to the type of habitat the birds reside in as well as the availability of food, which may be affected by anthropogenic activities (Aponte *et al.*, 2014). The ubiquity of wild birds allows them to inhabit an array of habitats, from urban to rural landscapes (Bairlein, 1983). Although the

passerine species in this study were sampled in farmland, woodland or garden sites, the diversity of their habitat use varies (Storchová and Hořák, 2018). Host habitat diversity, in particular, was found to have a strong influence on parasite abundance and infection intensity, with observed overall trends of greater abundance and infection intensity rates as mean habitat diversity increased, aside from the several *Isospora*-infected finches leading to the abnormally high rates seen in birds that occupy 3 habitat types. These findings may also have contributed into the overall significance of geographical variation in avian parasite epidemiology; for example, prior research has confirmed the importance of ecology in spatial distribution of haemoparasites (Cornuault *et al.*, 2013). Meanwhile, food availability is known to affect

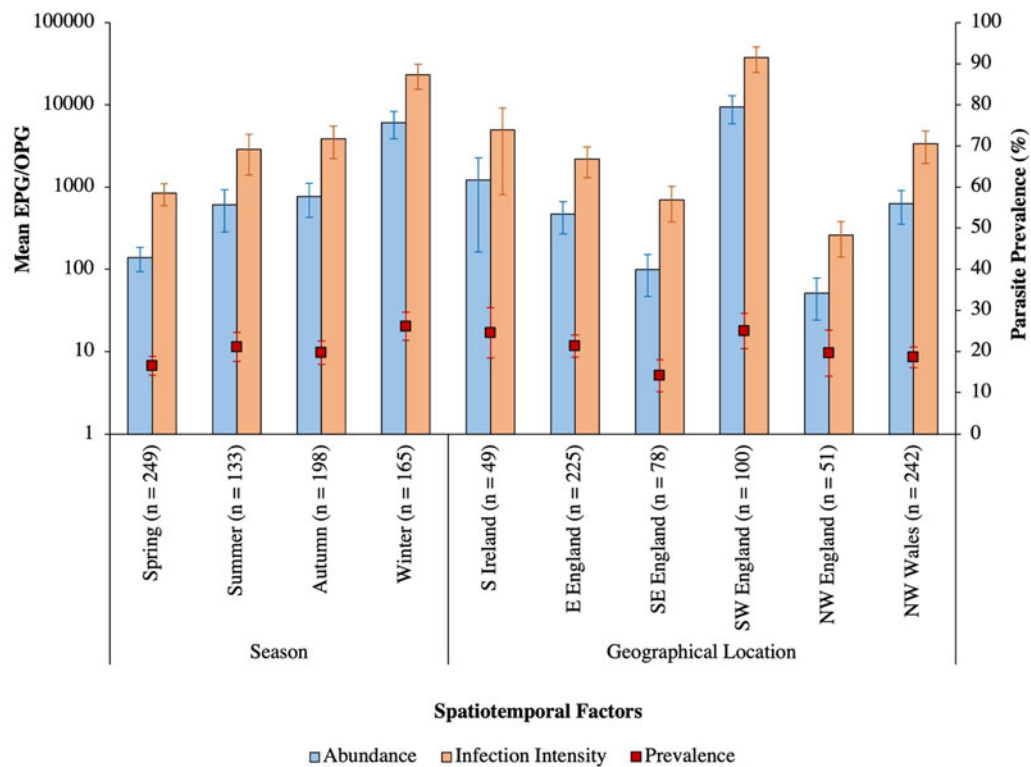


Fig. 7. Mean abundance (\pm s.e.), infection intensity (\pm s.e.) and prevalence (s.e.), represented by blue bars, orange bars and red square points, respectively, of intestinal parasites amongst the sampled seasons and sites across the British Isles. Sample sizes are denoted in parentheses. N, north; E, east; W, west; S, south; EPG/OPG, eggs/oocysts per g.

Table 3. Significant results of phylogenetically controlled, Poisson MCMC GLMMs comparing the various avian parasite genera on abundance

		Estimate	95% CI		pMCMC
			Lower	Upper	
Intercept		−73.94	−110.52	−23.75	<0.001
Parasite genus					
Capillaria vs	Cestode	−10.37	−15.35	−5.39	<0.001
	Eimeria	−8.29	−12.90	−3.73	<0.001
	Isospora	4.65	1.39	8.31	0.006
	Monocystis	−8.92	−13.62	−4.33	<0.001
	Porrocaecum	−9.38	−14.03	−4.37	<0.001
	Syngamus	3.58	0.18	6.87	0.036
	Trematode	−9.00	−13.48	−4.39	<0.001
Isospora vs	Cestode	−10.29	−22.43	−4.84	<0.001
	Eimeria	−9.90	−21.07	−4.37	<0.001
	Monocystis	−10.50	−22.49	−5.27	0.040
	Porrocaecum	−10.92	−22.55	−5.10	<0.001
	Syngamus	1.68	−8.42	−5.95	<0.001
	Trematode	−11.08	−19.61	−6.14	<0.001
Syngamus vs	Cestode	14.81	3.23	20.24	0.017
	Eimeria	14.61	3.38	20.79	<0.001
	Monocystis	15.31	3.99	21.52	<0.001
	Porrocaecum	15.33	3.59	21.01	<0.001
	Trematode	−8.91	−20.46	−3.61	0.029
Random effects					
	Host phylogeny	9.43	0.003138	44.59	
	Time until analysis	16 946	0.002174	62.77	

Estimates, lower and upper 95% CI values, and *P* values (pMCMC) have been included for the intercept, random effects and each level of the factors.

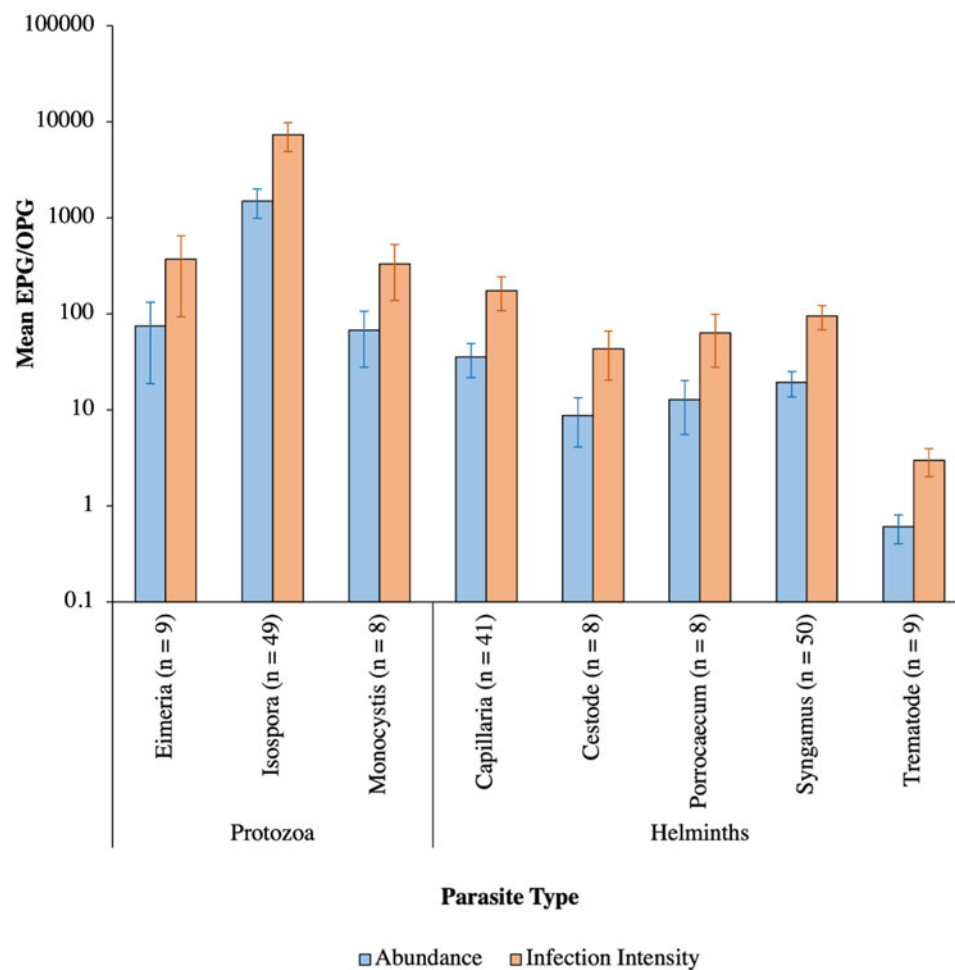


Fig. 8. Mean abundance (\pm s.e.) and infection intensity (\pm s.e.) represented by blue and orange bars, respectively, of the various parasite genera in all or infected hosts. The number of individual hosts each parasite was detected in are denoted in parentheses. EPG/OPG, eggs/oocysts per g.

avian life-history traits, such as reproductive success and body mass (Récapet *et al.*, 2017). The effect of humans on wildlife is multifaceted due to urbanization and can include outwardly positive actions, such as the widespread use of bird feeders to provide supplementary food to wild animals and which appear to have been responsible for some variation in infection intensity (Delgado-V and French, 2012; Becker *et al.*, 2018); however, they can act as a source of parasite transmission, such as in trichomoniasis (Lennon *et al.*, 2013).

Variation in diet can lead to certain birds having a greater likelihood of ingesting potential intermediate hosts, such as parasitized earthworms (Aponte *et al.*, 2014), as evidenced by the potential case of pseudoparasitism by *Monocystis*, an earthworm parasite, we detected. Diet has the potential to influence the immune system by creating a stronger response to infection following the consumption of foods with antiparasitic activity; a variety of animals ingest items due to the therapeutic action of the secondary metabolites, such as parrots (Masello *et al.*, 2018). The diverse feeding behaviours of passerines, which is dependent on their diet and includes ground foraging, can also contribute to parasite transmission (Willson, 1974), and further work should examine the potential relationship between diet and parasitic infection. For example, birds such as corvids, that consume anthropogenic foods may have fewer parasites; ring-billed gulls (*Larus delawarensis*) were found to have fewer trophically transmitted protozoa and helminths when their diet was formed primarily by these foods rather than aquatic intermediate hosts, such as fish or invertebrates (Aponte *et al.*, 2014). Some diets

might provide birds with more resources or energy that can be placed into mounting an immune response, or vice versa if the food is of poor quality (Strandin *et al.*, 2018), and diet choice can also contribute to parasite transmission (Willson, 1974), which may explain the overall trend of greater parasite prevalence rates with increasing mean diet diversity seen here. Birds, such as most thrushes (Turdidae) and dunnocks (*Prunella modularis*), have a higher exposure to trophically transmitted eggs and oocysts through the wider range of foods they eat, which may explain the high incidences detected here (Dolnik *et al.*, 2010); in the Netherlands, omnivorous passerines such as starlings (Sturnidae) were more heavily parasitized by helminths than seed eaters, such as finches (Fringillidae) (Borgsteede *et al.*, 2000). Our finding of higher infection intensities in birds at sites with feeders highlights the potential risks of supplementary feeding for parasite transmission (e.g. Lennon *et al.*, 2013).

Co-occurrence analyses demonstrated a positive association between *Monocystis* and *Syngamus* spp., which may be explained by earthworms serving as a definitive host and paratenic vector to both, respectively (Clapham, 1934; Field *et al.*, 2003). Negative associations between *Isospora* and the 4 helminthic genera may be due to the varying immunological responses that occur within a host, particularly if they are bottom-up controls or resource-based competition of host nutrients from blood (Graham, 2008); meanwhile, *Isospora* and *Eimeria* spp. could be negatively associated due to their high relatedness leading to heterologous, or cross-protective, immunity (Smith *et al.*, 2001). Moreover, host-mediated responses could explain the opposing correlation between

Table 4. Significant results of phylogenetically controlled, Poisson MCMC GLMMs comparing the various avian parasite genera on infection intensity

		Estimate	95% CI		pMCMC
			Lower	Upper	
Intercept		−9.34	−21.48	3.89	0.082
Capillaria vs	Cestode	−9.18	−13.57	−4.21	<0.001
	Eimeria	−8.89	−12.94	−4.41	<0.001
	Monocystis	−9.51	−13.86	−4.64	<0.001
	Porrocaecum	−9.77	−14.37	−5.41	<0.001
	Trematode	−9.30	−14.18	−5.14	<0.001
Isospora vs	Cestode	−11.98	−16.94	−7.74	<0.001
	Eimeria	−11.59	−15.57	−7.27	<0.001
	Monocystis	−12.19	−17.00	−8.17	<0.001
	Porrocaecum	−12.61	−17.06	−8.00	<0.001
	Trematode	−12.17	−16.47	−7.69	<0.001
Syngamus vs	Cestode	13.13	8.73	17.35	<0.001
	Eimeria	12.93	8.88	17.89	<0.001
	Monocystis	13.63	9.48	18.63	<0.001
	Porrocaecum	13.65	9.09	18.11	<0.001
	Trematode	−10.59	−14.96	−6.51	<0.001
Random effects					
	Host phylogeny	12.11	0.003134	60.18	
	Time until analysis	15 367	0.001573	59.87	

Estimates, lower and upper 95% CI values, and *P* values (pMCMC) have been included for the intercept, random effects and each level of the factors.

Table 5. Significant results of phylogenetically controlled, Poisson MCMC GLMMs comparing the various factors affecting avian parasitic infection intensity

		Estimate	95% CI		pMCMC
			Lower	Upper	
Intercept		6.86	−1.66	13.75	0.070
Avian family					
Fringillidae	Prunellidae	−2.40	−4.90	−0.19	0.048
Geographical region					
Northwest England	Southeast England	−0.39	−10.54	−10.46	0.034
	Southwest England	−0.51	−9.22	−8.03	0.041
Ecological variables					
	Habitat diversity	0.71	−1.33	−0.02	0.048
	Feeder presence (yes vs no)	−0.55	−2.50	−1.73	0.044
Random effects					
	Host phylogeny	1.52	0.002338	6.99	
	Time until analysis	15 937	0.002696	64.89	

Estimates, lower and upper 95% CI values, and *P* values (pMCMC) have been included for the intercept, random effects and each level of the factors.

Syngamus and *Capillaria* spp. or cestodes, as often infections with 1 type of helminth have led to protection against others (Cox, 2001); despite the first 2 species often being present in samples together, this negative association could be indicative of opposing abundances due to the clearing of secondary infections. Despite finding multiple associations between co-occurring parasites, we can only speculate as to whether these are due to genuine interactions.

While these potential mechanisms may underlie our observations, our rarefaction analyses suggest that we may have detected most intestinal parasite fauna in only 5 bird families, so further sampling to confirm parasite species richness is required. Additionally, we only used morphological analysis to identify species, using a single detection technique. The detection of trematode and eimeriid species could have been improved through

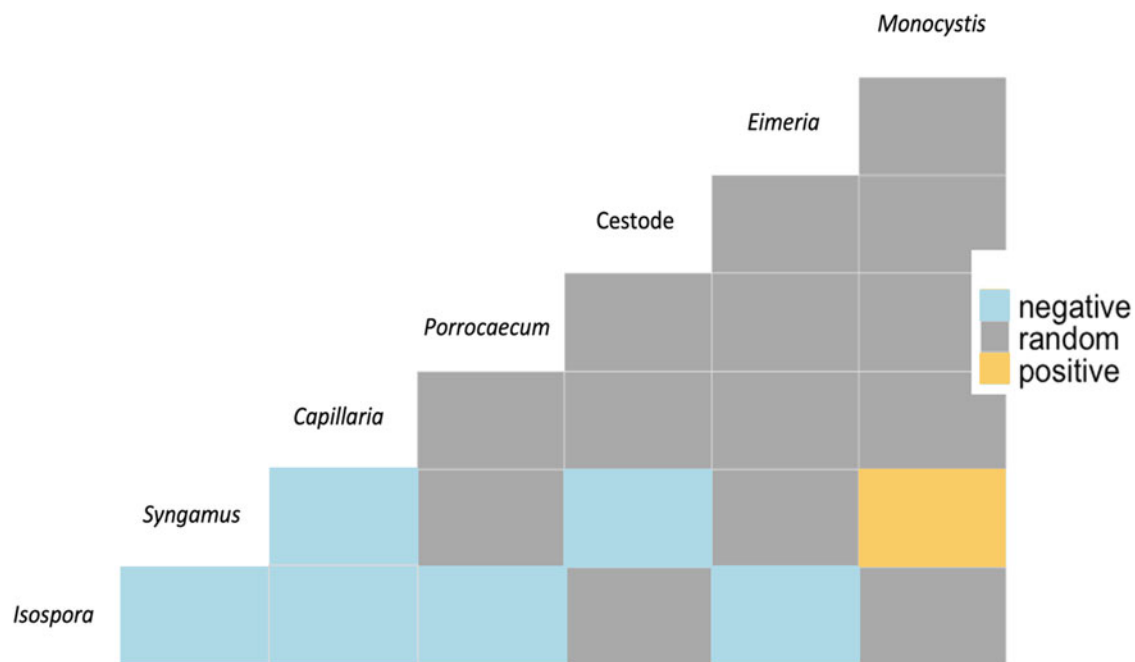


Fig. 9. Co-occurrence matrix for intestinal parasite genera demonstrating non-random associations between helminths and protozoa in passerine samples. Yellow and blue denote positive and negative interactions, respectively, while grey represents random associations.

sedimentation with salt or sugar solutions and sporulation, respectively, and may explain our low rates of detection of these taxa (Lobos-Ovalle *et al.*, 2021; Abdu *et al.*, 2022). More sensitive identification techniques, such as polymerase chain reaction followed by sequencing, used alongside morphological analyses, would allow the identification of specific parasite strains to confirm whether cross-species parasite transmission may be occurring (Nadler and De León, 2011; Perkins *et al.*, 2011). Sampling throughout the day may increase the likelihood of detecting parasites in the prepatent stage; for example, egg excretion of helminths has been seen to occur during certain patterns in a day in natural or experimental avian infections (Villanúa *et al.*, 2006; Wongrak *et al.*, 2015). Thus, future studies should explore the epidemiology of these organisms in more controlled settings, such as regular sampling in the same site at a similar time every day.

Epidemiological studies are essential to further the understanding required for species conservation as well as research into host–parasite biodiversity, evolution and the transmission of parasitic disease to other organisms. Although most avian endoparasites can be non-pathogenic for healthy, adapted hosts, transmission to naïve bird species can decimate populations; for instance, non-adapted little penguins (*Eudyptula minor*) infected by avian malaria introduced by other hosts in New Zealand (Cannell *et al.*, 2013; Sijbranda *et al.*, 2017). Anthropogenic activities, such as habitat fragmentation through urbanization and climate change causing vector migration, can lead to increased stress on passerine hosts, which can decrease their immunological status to a level where these infections become fatal (Laurance *et al.*, 2013). These studies can be helpful to the One Health approach currently gaining traction worldwide, due to the global distribution of passerines and increasing incidence of infectious and/or zoonotic diseases; however, the intrinsic value of the opportunistic nature of this kind of epidemiological research is in understanding the parasite faunas shared by disparate avian hosts from a variety of locations over time.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0031182022001779>.

Data availability. Data will be available on open access upon acceptance of manuscript.

Acknowledgements. The authors thank the anonymous reviewers for their time and helpful feedback that has improved this manuscript.

Author's contributions. F. R. P. and J. C. D. conceived and designed the study. Sample collection was carried out by F. B., S. B., S. D., R. M., J. R., D. W. and J. C. D. F. R. P. performed laboratory and statistical analyses and wrote the article with assistance from J. C. D. and S. R. C.

Financial support. This research did not receive any specific grant from funding agencies in the public, commercial or not-for-profit sectors.

Conflict of interest. The authors declare there is no conflict of interest.

Ethical standards. Sample collection from wild birds was approved by the University of Lincoln Research Ethics Committee (LEAS3818) and was carried out under British Trust for Ornithology ringing permits issued to F. B., S. B., S. D., R. M., J. R., D. W. and J. C. D.

References

- Abdu S, Chimento M, Alarcón-Nieto G, Zúñiga D, Aplin LM, Farine DR and Brandl HB (2022) The performance of field sampling for parasite detection in a wild passerine. *Ecology and Evolution* **12**, 1–14.
- Aponte V, Gentes M, Verreault J, Locke S, Giroux J, Marcogliese D and McLaughlin D (2014) Effect of habitat use and diet on the gastrointestinal parasite community of an avian omnivore from an urbanized environment. *Canadian Journal of Zoology* **92**, 629–636.
- Asakawa M, Nakamura S and Brazil M (2002) An overview of infectious and parasitic diseases in relation to the conservation biology of the Japanese avifauna. *Journal of the Yamashina Institute for Ornithology* **34**, 200–221.
- Atkinson C and Samuel M (2010) Avian malaria *Plasmodium relictum* in native Hawaiian forest birds: epizootiology and demographic impacts on 'apapane *Himatione sanguinea*. *Journal of Avian Biology* **41**, 357–366.
- Badparva E, Ezatpour B, Azami M and Badparva M (2014) First report of birds infection by intestinal parasites in Khorramabad, west Iran. *Journal of Parasitic Diseases* **39**, 720–724. doi: 10.1007/s12639-014-0427-5
- Bairlein F (1983) Habitat selection and associations of species in European passerine birds during southward, post-breeding migrations. *Ornis Scandinavica* **14**, 239–245.

- Bakker T, Mazzi D and Zala S (1997) Parasite-induced changes in behavior and color make *Gammarus pulex* more prone to fish predation. *Ecology* **78**, 1098–1104.
- Bandelj P, Blagus R, Trilar T, Vengust M and Vergles Rataj A (2015) Influence of phylogeny, migration and type of diet on the presence of intestinal parasites in the faeces of European passerine birds (Passeriformes). *Wildlife Biology* **21**, 227–233.
- Becker D, Hall R, Forbes K, Plowright R and Altizer S (2018) Anthropogenic resource subsidies and host–parasite dynamics in wildlife. *Philosophical Transactions of the Royal Society B: Biological Sciences* **373**, 20170086.
- Bodawatta K, Synek P, Bos N, Garcia-del-Rey E, Koane B, Marki P, Albrecht T, Lifjeld J, Poulsen M, Mundlinger P, Sam K and Jönsson K (2020) Spatiotemporal patterns of avian host–parasite interactions in the face of biogeographical range expansions. *Molecular Ecology* **29**, 2431–2448.
- Borgsteede F, Okulewicz A and Okulewicz J (2000) A study of the helminth fauna of birds belonging to the Passeriformes in the Netherlands. *Acta Parasitologica* **45**, 14–21.
- Brown C and Brown M (2004) Empirical measurement of parasite transmission between groups in a colonial bird. *Ecology* **85**, 1619–1626.
- Brown M, Ball S and Snow K (2010) Coccidian parasites of British wild birds. *Journal of Natural History* **44**, 2669–2691.
- Cannell B, Krasnec K, Campbell K, Jones H, Miller R and Stephens N (2013) The pathology and pathogenicity of a novel *Haemoproteus* spp. infection in wild little penguins (*Eudyptula minor*). *Veterinary Parasitology* **197**, 74–84.
- Clapham P (1934) Experimental studies on the transmission of gapeworm (*Syngamus trachea*) by earthworms. *Proceedings of the Royal Society B: Biological Sciences* **115**, 18–29.
- Cornuault J, Khimoun A, Harrigan R, Bourgeois Y, Milá B, Thébaud C and Heeb P (2013) The role of ecology in the geographical separation of blood parasites infecting an insular bird. *Journal of Biogeography* **40**, 1313–1323.
- Cox F (2001) Concomitant infections, parasites and immune responses. *Parasitology* **122**, S23–S38.
- Delgado-V C and French K (2012) Parasite–bird interactions in urban areas: current evidence and emerging questions. *Landscape and Urban Planning* **105**, 5–14.
- Dolnik O, Dolnik V and Bairlein F (2010) The effect of host foraging ecology on the prevalence and intensity of coccidian infection in wild passerine birds. *Ardea* **98**, 97–103.
- Dolnik O, Metzger B and Loonen M (2011) Keeping the clock set under the midnight sun: diurnal periodicity and synchrony of avian *Isospora* parasites cycle in the High Arctic. *Parasitology* **138**, 1077–1081.
- Ezenwa VO (2016) Helminth–microparasite co-infection in wildlife: lessons from ruminants, rodents and rabbits. *Parasite Immunology* **38**, 527–534.
- Field S, Schirp H and Michiels N (2003) The influence of *Monocystis* sp. infection on growth and mating behaviour of the earthworm *Lumbricus terrestris*. *Canadian Journal of Zoology* **81**, 1161–1167.
- Gallo S, Ederli N and Oliveira F (2018) Endoparasites and ectoparasites of rheas (*Rhea americana*) from South America. *Tropical Biomedicine* **35**, 684–695.
- Gotelli N and Colwell R (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**, 379–391.
- Graham A (2008) Ecological rules governing helminth–microparasite coinfection. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 566–570.
- Grantham C and Williams D (2017) Avian malaria, body condition, and blood parameters in four species of songbirds. *The Wilson Journal of Ornithology* **129**, 492–508.
- Griffith D, Veech J and Marsh C (2016) Cooccur: probabilistic species co-occurrence analysis in R. *Journal of Statistical Software* **69**, 1–17.
- Hadfield J (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* **33**, 1–22.
- Hoberg E (1996) Faunal diversity among avian parasite assemblages: the interaction of history, ecology, and biogeography in marine systems. *Bulletin of the Scandinavian Society for Parasitology* **6**, 65–89.
- Hoque M, Hassan M, Haque E, Shaikat A, Khan S, Alim A, Skerratt L, Islam A, Tun H, Dissanayake R, Day T, Debnath N and Yamage M (2014) A survey of gastro-intestinal parasitic infection in domestic and wild birds in Chittagong and Greater Sylhet, Bangladesh. *Preventive Veterinary Medicine* **117**, 305–312.
- Howe L, Castro I, Schoener E, Hunter S, Barraclough R and Alley M (2012) Malaria parasites (*Plasmodium* spp.) infecting introduced, native and endemic New Zealand birds. *Parasitology Research* **110**, 913–923.
- Hudson P (1986) The effect of a parasitic nematode on the breeding production of red grouse. *Journal of Animal Ecology* **55**, 85–92.
- Hudson P, Dobson A and Lafferty K (2006) Is a healthy ecosystem one that is rich in parasites? *Trends in Ecology and Evolution* **21**, 381–385.
- Ishtiaq F and Renner S (2020) Bird migration and vector-borne parasite transmission. In Santiago-Alarcon D and Marzal A (eds), *Avian Malaria and Related Parasites in the Tropics*. Springer, Cham, New York City: Springer International Publishing, pp. 513–526.
- Isomursu M, Rätti O, Helle P and Hollmén T (2006) Sex and age influence intestinal parasite burden in three boreal grouse species. *Journal of Avian Biology* **37**, 516–522.
- Jetz W, Thomas G, Joy J, Hartmann K and Mooers A (2012) The global diversity of birds in space and time. *Nature* **491**, 444–448.
- Knowles S (2011) The effect of helminth co-infection on malaria in mice: a meta-analysis. *International Journal for Parasitology* **41**, 1041–1051.
- Langkjær M and Roepstorff A (2008) Survival of *Isospora suis* oocysts under controlled environmental conditions. *Veterinary Parasitology* **152**, 186–193.
- Laurance S, Jones D, Westcott D, Mckeown A, Harrington G and Hilbert D (2013) Habitat fragmentation and ecological traits influence the prevalence of avian blood parasites in a tropical rainforest landscape. *PLoS ONE* **8**, e76227.
- Lennon R, Dunn J, Stockdale J, Goodman S, Morris A and Hamer K (2013) Trichomonad parasite infection in four species of Columbidae in the UK. *Parasitology* **140**, 1368–1376.
- Leveck B, Behnke J, Ajjampur S, Albonico M, Ame S, Charlier J, Geiger S, Hoa N, Ngassam R, Kotze A, McCarthy J, Montresor A, Periago M, Roy S, Tchuente L, Thach D and Vercruysse J (2011) A comparison of the sensitivity and fecal egg counts of the McMaster egg counting and Kato-Katz thick smear methods for soil-transmitted helminths. *PLoS Neglected Tropical Diseases* **5**, 1–10. doi: 10.1371/journal.pntd.0001201
- Lobos-Ovalle D, Navarrete C, Navedo JG, Peña-Espinoza M and Verdugo C (2021) Improving the sensitivity of gastrointestinal helminth detection using the Mini-FLOTAC technique in wild birds. *Parasitology Research* **120**, 3319–3324.
- Loye J and Carroll S (1995) Birds, bugs and blood: avian parasitism and conservation. *Trends in Ecology & Evolution* **10**, 232–235.
- Martinaud G, Billaudelle M and Moreau J (2009) Circadian variation in shedding of the oocysts of *Isospora turdi* (Apicomplexa) in blackbirds (*Turdus merula*): an adaptive trait against desiccation and ultraviolet radiation. *International Journal for Parasitology* **39**, 735–739.
- Masello J, Choconi R, Sehgal R, Tell L and Quillfeldt P (2006) Blood and intestinal parasites in wild Psittaciformes: a case study of burrowing parrots (*Cyanoliseus patagonus*). *Ornitologia Neotropical* **17**, 515–529.
- Masello J, Martínez J, Calderón L, Wink M, Quillfeldt P, Sanz V, Theuerkauf J, Ortiz-Catedral L, Berkunsky I, Brunton D, Díaz-Luque J, Hauber M, Ojeda V, Barnaud A, Casalins L, Jackson B, Mijares A, Rosales R, Seixas G, Serafini P, Silva-Iturriza A, Sipinski E, Vásquez R, Widmann P, Widmann I and Merino S (2018) Can the intake of anti-parasitic secondary metabolites explain the low prevalence of hemoparasites among wild Psittaciformes? *Parasites & Vectors* **11**, 1–15.
- Maya C, Torner-Morales F, Lucario E, Hernández E and Jiménez B (2012) Viability of six species of larval and non-larval helminth eggs for different conditions of temperature, pH and dryness. *Water Research* **46**, 4770–4782.
- Minetti C, Taweanan W, Hogg R, Featherstone C, Randle N, Latham S and Wastling J (2014) Occurrence and diversity of *Giardia duodenalis* assemblages in livestock in the UK. *Transboundary and Emerging Diseases* **61**, e60–e67.
- Møller A (1991) Parasite load reduces song output in a passerine bird. *Animal Behaviour* **41**, 723–730.
- Nadler SA and De León GPP (2011) Integrating molecular and morphological approaches for characterizing parasite cryptic species: implications for parasitology. *Parasitology* **138**, 1688–1709.
- Nord A, Hegemann A and Folkow L (2020) Reduced immune responsiveness contributes to winter energy conservation in an Arctic bird. *Journal of Experimental Biology* **223**, 1–11.
- Oksanen J, Blanchet F, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin P, O'Hara R, Simpson G, Solymos P, Stevens M, Szoecs E and Wagner H (2017) vegan: community ecology package. R package version 2.4-5. Available at <https://CRAN.R-project.org/package=vegan>.

- Paradis E, Claude J and Strimmer K (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics (Oxford, England)* **20**, 289–290.
- Penczykowski R, Laine A-L and Koskella B (2016) Understanding the ecology and evolution of host–parasite interactions across scales. *Evolutionary Applications* **9**, 37–52.
- Pérez-Tris J and Bensch S (2005) Dispersal increases local transmission of avian malarial parasites. *Ecology Letters* **8**, 838–845.
- Pérez Cerdón G, Hitos Prados A, Romero D, Sánchez Moreno M, Pontes A, Osuna A and Rosales M (2009) Intestinal and haematic parasitism in the birds of the Almuñecar (Granada, Spain) ornithological garden. *Veterinary Parasitology* **165**, 361–366.
- Perkins S, Martinsen E and Falk B (2011) Do molecules matter more than morphology? Promises and pitfalls in parasites. *Parasitology* **138**, 1664–1674.
- Piersma T and van der Velde M (2012) Dutch house martins *Delichon urbicum* gain blood parasite infections over their lifetime, but do not seem to suffer. *Journal of Ornithology* **153**, 907–912.
- Poulin R, Krasnov B, Mouillot D and Thieltges D (2011) The comparative ecology and biogeography of parasites. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**, 2379–2390.
- Presswell B and Lagrue C (2016) Assessing parasite infections from avian faecal samples: the old methods are still the best. *Notornis* **63**, 32–36.
- Rambaut A (2010) *FigTree v1.3.1*. Edinburgh: Institute of Evolutionary Biology, University of Edinburgh.
- R Core Team (2021) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Core Team.
- Récapet C, Bize P and Doligez B (2017) Food availability modulates differences in parental effort between dispersing and philopatric birds. *Behavioral Ecology* **28**, 688–697.
- Reiczigel J, Marozzi M, Fábán I and Rózsa L (2019) Biostatistics for parasitologists – a primer to quantitative parasitology. *Trends in Parasitology* **35**, 277–281.
- Richner H (1998) Host–parasite interactions and life-history evolution. *Zoology* **101**, 333–344.
- Santiago-Alarcon D, MacGregor-Fors I, Falfán I, Lüdtké B, Segelbacher G, Schaefer H and Renner S (2019) Parasites in space and time: a case study of haemosporidian spatiotemporal prevalence in urban birds. *International Journal for Parasitology* **49**, 235–246.
- Sanz JJ, Arriero E, Moreno J and Merino S (2001) Interactions between hemoparasite status and female age in the primary reproductive output of pied flycatchers. *Oecologia* **126**, 339–344.
- Schoener E, Howe L, Charleston T and Castro I (2012) Helminths in endemic, native and introduced passerines in New Zealand. *New Zealand Journal of Zoology* **39**, 245–256.
- Schoener E, Alley M, Howe L and Castro I (2013) Coccidia species in endemic and native New Zealand passerines. *Parasitology Research* **112**, 2027–2036.
- Senecal J, Nordin A and Vinnerås B (2020) Fate of *Ascaris* at various pH, temperature and moisture levels. *Journal of Water and Health* **18**, 375–382.
- Sijbranda D, Hunter S, Howe L, Lenting B, Argilla L and Gartrell B (2017) Cases of mortality in little penguins (*Eudyptula minor*) in New Zealand associated with avian malaria. *New Zealand Veterinary Journal* **65**, 332–337.
- Smith W, Pettit D and Smith S (2001) Cross-protection studies with gut membrane glycoprotein antigens from *Haemonchus contortus* and *Teladorsagia circumcincta*. *Parasite Immunology* **23**, 203–211.
- Sorci G (2013) Immunity, resistance and tolerance in bird–parasite interactions. *Parasite Immunology* **35**, 350–361.
- Storchová L and Hořák D (2018) Life-history characteristics of European birds. *Global Ecology and Biogeography* **27**, 400–406.
- Strandin T, Babayan S and Forbes K (2018) Reviewing the effects of food provisioning on wildlife immunity. *Philosophical Transactions of the Royal Society B: Biological Sciences* **373**, 1–11. doi: 10.1098/rstb.2017.0088
- Svensson L (1992) *Identification Guide to European Passerines*. Thetford: British Trust for Ornithology.
- Svobodová M (1994) *Isospora*, *Caryospora* and *Eimeria* (Apicomplexa: Passeriform birds from Czech Republic Eimeriidae) in Milena. *Acta Protozoologica* **33**, 101–108.
- Thomas R, Dunn J, Dawson D, Hipperson H, Horsburgh G, Morris A, Orsman C, Mallord J, Grice P, Hamer K, Eraud C, Lormée H and Goodman S (2022) Assessing rates of parasite coinfection and spatio-temporal strain variation via metabarcoding: insights for the conservation of European turtle doves *Streptopelia turtur*. *Molecular Ecology* **31**, 2730–2751.
- Vanstreels R, Kolesnikovas C, Sandri S, Silveira P, Belo N, Ferreira Jr. F, Epiphanyo S, Steindel M, Braga É and Catao-Dias J (2014) Outbreak of avian malaria associated to multiple species of *Plasmodium* in magellanic penguins undergoing rehabilitation in southern Brazil. *PLoS ONE* **9**, e94994.
- Villanúa D, Pérez-Rodríguez L, Gortázar C, Höfle U and Viñuela J (2006) Avoiding bias in parasite excretion estimates: the effect of sampling time and type of faeces. *Parasitology* **133**, 251–259.
- Waldenström J, Bensch S, Kiboi S, Hasselquist D and Ottosson U (2002) Cross-species infection of blood parasites between resident and migratory songbirds in Africa. *Molecular Ecology* **11**, 1545–1554.
- Wascher C, Bauer A, Holtmann A and Kotschal K (2012) Environmental and social factors affecting the excretion of intestinal parasite eggs in graylag geese. *Behavioral Ecology* **23**, 1276–1283.
- Willson M (1974) Avian community organization and habitat structure. *Ecology* **55**, 1017–1029.
- Wongrak K, Gauly M and Daş G (2015) Diurnal fluctuations in nematode egg excretion in naturally and in experimentally infected chickens. *Veterinary Parasitology* **208**, 195–203.
- Zuk M, Thornhill R, Ligon J and Johnson K (1990) Parasites and mate choice in red jungle fowl. *Integrative and Comparative Biology* **30**, 235–244.