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Research article

Between- and within-population drivers of haemosporidian prevalence and diversity in American robins *Turdus migratorius*

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Avian haemosporidians are a diverse group of parasites that infect birds worldwide and have been a major focus of research for decades. Yet, few studies have identified the drivers of infection at the intraspecific host level. We aimed to study the drivers of prevalence and diversity of haemosporidian parasites infecting a common North American songbird species, the American robin *Turdus migratorius*, which breeds across most of the continent. We found little seasonal variation in haemosporidian prevalence in robins, although we detected a significantly positive relationship between robin breeding latitude and co-infection with different haemosporidian parasite lineages. Additionally, robins infected with *Plasmodium* had substantially better body condition than uninfected robins, which could be due to migratory culling. We detected 31 haemosporidian lineages among the robins we sampled, of which eight were novel. When matched against known haemosporidian lineages, our results suggest that robins harbor a higher diversity of haemosporidian parasites than previously known. The results of this study suggest that comparisons of common, widespread bird species such as robins across their range could help unveil novel aspects of the haemosporidian–host relationship and how such a relationship may change under current and future rapid environmental change.

Keywords: avian malaria, bird migration, latitude, *Leucocytozoon*, *Parahaemoproteus*, *Plasmodium*

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Introduction

Avian haemosporidians are a globally distributed group of parasites that infect a wide variety of bird taxa and are easily detectable in small blood samples. Thus, they provide an ideal model system for studying host–parasite interactions, including factors influencing host exposure, parasite impacts on host condition, host-parasite coevolution, and the role of hosts in parasite dispersal (e.g. Fecchio et al. 2020). Extensive research has explored the role of avian migration in the spread of haemosporidian parasites across Neotropical–Nearctic and Afrotropical–Palearctic flyways (Waldenström et al. 2002, Hellgren et al. 2007, Ricklefs et al. 2017, Pulgarín-R et al. 2019, Galen et al. 2024, Perrin et al. 2025), in host–parasite coevolution (Jenkins et al. 2012, Angeli Dutra et al. 2022), and the diversity and distribution of parasite lineages across avian host communities (Fecchio et al. 2019, Angeli Dutra et al. 2023). A large body of literature has also considered the reciprocal feedback between haemosporidian infections and migratory success (Hahn et al. 2018, Hegemann et al. 2018, Emmenegger et al. 2021, Ágh et al. 2022). Based on this research, bird migratory behavior has emerged as a driver of macroecological and macroevolutionary processes in haemosporidians, although these effects vary according to parasite taxa. For example, although migratory bird species harbor a greater diversity of *Leucocytozoon* lineages compared to resident bird species, only in resident species is there a signal of bird–parasite coevolution (Jenkins et al. 2012). In contrast, migratory behavior has no impact on bird–haemosporidian cophylogenetic congruence for *Haemoproteus* and *Plasmodium* (Angeli Dutra et al. 2022). Although the prevalence of *Leucocytozoon* across avian families increases with migration distance, migration distance has a varying or even an opposite effect on *Plasmodium* and *Haemoproteus* according to zoogeographical region (Fecchio et al. 2021).

A current gap in our knowledge of the susceptibility of avian hosts to haemosporidian parasites involves such individual-level host characteristics as demography, body condition, and breeding location. For example, most macroecological studies focusing on the relationship between infection probability and host migratory behavior sample a broad variety of avian host species, but often with little information about species-specific migratory routes, distance traveled, and time spent at migratory stopover, winter, and breeding sites. Such a bias may limit our ability to uncover the mechanisms driving dispersal of the parasite. For example, stopover duration may impact a migratory bird's ability to acquire or escape haemosporidian infection, as recently demonstrated for Chilean elaenia *Elaenia chilensis*. In this case, stopover time on the tropical wintering grounds may limit vector encounter rates between migratory elaenias and resident sympatric species, potentially resulting in limited transmission of *Leucocytozoon* parasites acquired by migrants on their Patagonian breeding grounds (Fecchio et al. 2022). More broadly, host life history strategy and social behavior may impact a parasite's prevalence and diversity at intra- and interspecific levels (Valenzuela-Sánchez et al. 2021). For example, prevalence of haemosporidians is positively related to parental care (Ganser et al. 2020) and gregariousness (Rodríguez-Hernández et al. 2021) in birds. Thus, host life history strategies, ecology, and behavior may predict individual- and population-level responses to pathogens, offering insights into the mechanisms driving parasite seasonal dynamics, distribution, and their ability to infect hosts across demographic states (reviewed by Valenzuela-Sánchez et al. 2021).

Here, we examined whether the prevalence and diversity of haemosporidian parasites varies within a common North American songbird species, the American robin (*Turdus migratorius*; hereafter, robins). Robins breed across a broad range of latitudes, are common in a variety of habitats in North America (Vanderhoff et al. 2020), and vary in migratory behavior, with the occurrence of migratory and resident populations across the species' range (Jahn et al. 2019). Robins are also known to host various haemosporidian parasite lineages (Harl et al. 2020), with at least 48 lineages identified to date in the MalAvi database (11 *Plasmodium*, 19 *Parahaemoproteus*, 18 *Leucocytozoon*; Bensch et al. 2009). As such, they serve as an ideal model host to test predictions about how host body condition, individual life history variation, and seasonality may affect the probability of infection and lineage diversity. We evaluate whether haemosporidian diversity and prevalence vary across robin populations breeding at different latitudes. We also test whether haemosporidian prevalence in robins varies by season and robin body condition. We predict that haemosporidian prevalence is higher during the breeding season than in winter, as has been found in other songbirds (Hellgren et al. 2013, Sorensen et al. 2016, Pulgarín-R et al. 2019). Second, we predict that the diversity and prevalence of *Leucocytozoon* increases with robin breeding latitude, as has been found in other birds (Fecchio et al. 2020, 2023). Finally, we predict that the body condition of infected robins is lower than that of uninfected robins, since birds infected with haemosporidian parasites often lose weight during the acute phase of infection (Valkiunas 2004). We discuss how our results help fill the current gap in our knowledge of how host infection prevalence is related to individual-level host characteristics.

Material and methods

Bird capture and sampling

We sampled robins in Indiana across different seasons from January 2020 to September 2022 and in Alaska during the 2022 breeding season (May 2022). In Indiana, we captured robins on the campus of Indiana University-Bloomington and surrounding neighborhoods, primarily composed of mowed lawns with scattered trees. Our study site in Alaska was Joint Base Elmendorf-Richardson (JBER), near the city of Anchorage, where we sampled robins along forest edges adjacent to roads and mowed fields. Robins that breed in Bloomington are a mix of short-distance migrants and residents, with some robins migrating south beginning in

October and others remaining in Bloomington throughout winter (AEJ, unpubl.). Robins overwintering in Indiana may also breed in other regions of the continent. The migrants that leave Bloomington after breeding primarily overwinter in the southeastern USA, less than 1000 km distant, arriving in Bloomington after spring migration in March. Both resident and migratory robins breed in Bloomington from April to July (AEJ, pers. obs). Robins that breed at JBER are long-distance migrants, migrating over 5000 km to overwinter in the Great Plains of North America (EJW, unpubl.). They begin arriving in Alaska in May (AEJ, pers. obs) to breed.

We captured robins using polyester mist nets (3 × 18 m, 60 mm mesh; Avinet Research Supplies) from pre-dawn until late morning during appropriate weather conditions (i.e. no rain, no excessive heat or high wind). We banded each robin with a numbered band, and aged and sexed each bird based on plumage color, presence of juvenile plumage, and/or presence of a brood patch or cloacal protuberance (Pyle 1997). A subset of robins could not be sexed in the field, and PCR-based assessment of sex was not successful. We used Pyle (1997) to determine whether robins had hatched in the same calendar year as when we sampled them (classified as 'hatch year') or in previous calendar years (classified as 'after hatch year' and which we hereafter refer to as 'adults'). We define actively breeding robins as those with a cloacal protuberance or a brood patch. We measured unflattened wing chord and body mass (Ralph 1993) and collected a blood sample from each robin by puncturing the brachial vein with a sterile insulin needle and extracted ~ 150 ul blood with capillary tubes (Owen 2011). We stored whole blood in ethanol or without any buffer at −80°C until DNA extraction (Indiana only). We centrifuged other blood samples to separate plasma (Jahn et al. 2023), and stored the red blood cells at −80°C without buffer (both Indiana and Alaska). In 2020, we also collected the first secondary feather from robins in Indiana, each of which was stored in a paper envelope for subsequent analysis of stable hydrogen isotopes, to provide a broader sampling of breeding latitude of sampled robins. Robins molt their flight feathers on their breeding grounds before initiating fall migration (Vanderhoff et al. 2020), such that the feather hydrogen isotopic composition provides a reliable estimate of where they breed (Hobson et al. 2012, reviewed by Inger and Bearhop 2008).

Parasite detection and lineage identification

We extracted genomic DNA from avian blood using the Qiagen DNeasy 96 Blood and Tissue kit (Qiagen, Valencia, CA) following manufacturer protocols. We identified all parasite lineages using nested PCR, targeting a 477 bp fragment of the cytochrome-b (*cyt-b*) gene of the haemosporidian mitochondrial genome (Hellgren et al. 2004). We focused on PCR to diagnose haemosporidian infection, particularly given the need to characterize parasite diversity at the lineage level, acknowledging that this method can conflate chronic and active infection. Briefly, we used two nested PCR protocols for screening genomic DNA extracts for the three haemosporidian genera. First, to screen for *Plasmodium* and *Haemoproteus*, we used an initial PCR with primers (H332F and HaemNR2) that target a conserved region of the cyt-b gene. Next, we used a nested PCR (primers H350F and HaemR2). In a second set of nested PCR aimed at amplifying *Leucocytozoon*, we used primers HaemNF1 and HaemNR3 for an initial PCR and for nested PCR we used primers L350F and L890R. All PCR amplifications included positive and negative controls, with no evidence of possible contamination or false positives. Information on detailed reactions, reagents, and cycling conditions can be found in Hellgren et al. (2004) and Bell et al. (2015). Because variation in blood storage methods could affect DNA extractions and in turn parasite detection (Lynton-Jenkins et al. 2023), we ran a binomial generalized linear model (GLM) in R ver. 4.3 (www.r-project.org) to test whether the probability of infection differed between DNA extracted from whole blood or red blood cells, after accounting for sex, in the Indiana subset of robins. Our ability to detect infections did not vary between sample types ($\chi^2 = 0.68$, $p = 0.41$).

Amplicons from PCR positives were purified using ExoSAP-IT (Affymetrix, Santa Clara, CA, USA) and sequenced using BigDye terminator v3.1 cycle sequencing kit (Applied Biosystems, Foster City, CA, USA). Forward and reverse sequences were visualized, assembled, and reconciled using Geneious v8.1.8 (Kearse et al. 2012). Sequence identities were verified with a local BLAST against the MalAvi database (Bensch et al. 2009) using BioEdit v.7.2.0 (Hall 1999), and identified lineages were assigned to the genera *Plasmodium*, *Leucocytozoon*, and *Haemoproteus* (specifically the subgenus *Parahaemoproteus*). Chromatograms that showed the presence of multiple infections were scored as co-infections and underwent additional PCR amplification and sequencing to split out lineages. Any remaining co-infections were split using the protocol described in Orlofske et al. (2024). New lineages were named TURMIG16–TURMIG23 following standard protocol for avian malaria parasites (Bensch et al. 2009). All sequences have been deposited in MalAvi and GenBank (PQ477990-8020), and accession numbers can be found in the raw dataset (Supporting information). For downstream statistical analyses, we derived infection status for each haemosporidian taxon, overall infection status, and haemosporidian richness (number of lineages per individual robin).

Feather stable isotope analysis

Feathers were cleaned using a 2:1 chloroform:methanol solution to remove external oils and contaminants. To control for the effect of exchangeable hydrogen, cleaned and homogenized feathers were forced into isotopic equilibration with a water vapor of known isotopic composition in a flow-through chamber system at 115°C (Schimmelmann 1991, Sauer et al. 2009). We then analyzed equilibrated feather samples using a thermal conversion elemental analyzer coupled with a ThermoFinnigan Delta Plus XP isotope ratio mass spectrometer at the Indiana University Stable Isotope Research Facility. Feathers were run in replicate for quality control and sample averages are reported. We report δ^2H feather values in

standard per mil notation (‰) relative to Vienna Standard Mean Ocean Water using two reference materials: USGS77 (polyethylene powder) and hexatriacontane 2 (C_{36} n-alkane 2). Analytical precision is ± 2.2‰ for δ^2H values and reported values represent the isotopic composition of non-exchangeable hydrogen per sample (Schimmelmann 1991, Sauer et al. 2009).

We then conducted geographic assignments for individual birds during breeding months based on their δ^2H values using the 'assignR' package in R (www.r-project.org) (Bowen et al. 2014, Ma et al. 2020). To rescale the growing season precipitation isoscape (Bowen et al. 2005) to a feather isoscape best reflecting robin ecology, we used known values from members of a ground-foraging bird guild, including *Turdus migratorius*, *Hylocichla mustelina*, *Catharus fuscescens*, *C. guttatus*, and *C. ustulatus* (Hobson et al. 2012). The recalibration model had an intercept value of −23.4‰ and explained 70% of the isotopic variation in resident individuals. We estimated geographic assignment based on the top 10% highest posterior probability. From these probability maps, we determined maximum estimated breeding latitude per individual robin using the 'raster' package (Hijmans 2023).

Statistical analysis

All data analyses were limited to only the first capture record of any recaptured robin to limit pseudoreplication. For our analyses, we defined breeding latitude as either the latitude at which a robin was captured during the breeding season or the estimated maximum latitude based on a robin's feather stable isotopic signature. We defined the season when a robin was sampled based on Vanderhoff et al. (2020) and personal observations: breeding was defined as occurring from April to July, molt from August to mid October, fall migration from late October to November, winter from December to February, and spring migration during March. We estimated body condition separately for males, females, and individuals of unknown sex using the residuals of sex-specific linear models that regressed wing chord on body mass (Labocha and Hayes 2012).

We fitted GLMs with binomial error distributions to evaluate how the probability of infection by haemosporidians was related to breeding latitude (i.e. the latitude at which a sampled robin breeds) for adult robins. We ran three different binomial GLMs. In the first model, we filtered the data to analyze only adult robins (n = 182) sampled during the breeding season, and we added breeding latitude (based on the latitude where a robin was captured during the breeding season), sex (reference level = female), breeding condition (i.e. males with a cloacal protuberance or females with a brood patch), robin body condition, and sampling year (reference level = 2020) as explanatory variables. In the second model, we only analyzed data from adult robins for which we had feather stable isotope data (n = 113, only robins sampled in Indiana during 2020), which provided data from robins breeding across a broad geographic range, since robins sampled in Indiana could breed elsewhere. This GLM considered maximum breeding latitude (based on feather stable isotope composition), season (e.g. breeding, molt, winter, spring migration and fall migration, reference level = molt), sex (reference level = female), and body condition as explanatory variables. In our third model, we combined our data from Alaska and Indiana with previously published data on robin infection (n = 84) from Alaska, New York, and Pennsylvania (Fecchio et al. 2023). The combined dataset was filtered to include only robins sampled during the breeding season (n = 242). We ran a GLM using latitude and year as our explanatory variables due to the lack of individual-level traits, such as age and sex, in the additional robin dataset (Fecchio et al. 2023). Thus, this model included robins of all ages, including those of unknown age. Importantly, latitude and year were only weakly correlated (ρ = 0.26). We also ran each of these models for each of the three haemosporidian taxa (*Plasmodium*, *Parahaemoproteus*, and *Leucocytozoon*) separately when the number of infections or co-infections for each taxon individually was higher than 20.

We ran a separate model to evaluate latitudinal effects on haemosporidian richness, using the above-mentioned combined breeding season-only dataset (Alaska, Indiana, New York, and Pennsylvania). We derived site-level haemosporidian richness and used bootstrap correction to account for possible sampling biases (Smith and van Belle 1984, Poulin 1998), where S_B is the bootstrap-corrected richness, S_O is the observed richness, h is the number of infected hosts, and H is the number of total hosts:

$$S_B = S_O + \sum \left[1 - \left(h / H\right)\right]^H$$

We then ran a generalized linear mixed model (GLMM) using the bootstrapped-corrected haemosporidian richness as our response variable and the Tweedie distribution family with the 'glmmTMB' package (Brooks et al. 2017). We added latitude as our primary explanatory variable controlling for the number of infections (i.e. sampling effort). Reproductive origin (i.e. Alaska, Indiana, New York, and Pennsylvania) was included as a random effect to account for local biases when estimating haemosporidian richness.

To evaluate latitudinal differences in parasite composition, we created an incidence matrix between latitude and parasite lineages, assigning a latitude to sites where data were collected in Alaska and eastern USA (i.e. Indiana, New York, Pennsylvania). We then calculated a dissimilarity matrix (Bray–Curtis) for parasite taxonomic composition among different degrees of latitude using the 'vegan' package (Dixon 2003). We also compared dissimilarity in parasite taxonomic composition among geographic categories (i.e. Alaska versus eastern USA) using a permutational multivariate analysis of variance (PERMANOVA) for homogeneity of multivariate dispersions with 999 permutations, again using the 'vegan' package.

Finally, to test whether the phylogenetic diversity of haemosporidian parasites is structured by geographic distance between our Indiana and Alaska sampling sites, we used a

Mantel test as implemented in the 'vegan' package (Dixon 2003). We used the 'geosphere' package to calculate pairwise distances (km) between these sampling sites and the 'ape' package to compute pairwise phylogenetic distances between each haemosporidian lineage (Paradis and Schliep 2019). We based the phylogenetic dissimilarity matrix on a phylogeny of robin-associated haemosporidian lineages constructed in MrBayes 3.2 (Ronquist et al. 2012), using *Leucocytozoon fringillinarum* (ZOLEU02 – GenBank accession FJ168563) as an outgroup. We built the Bayesian tree with 10 million Markov chain Monte Carlo generations and a GTR + I + G nucleotide substitution model (Abadi et al. 2019). To accommodate birds with multiple infections, we separated analyses by haemosporidian taxa. In scenarios where a single bird was infected with multiple lineages from the same haemosporidian taxon (n = 18), we randomly selected the lineage included in the respective test. The Mantel tests used a Pearson method and 1000 permutations to correlate the geographic and phylogenetic dissimilarity matrices.

Results

We sampled a total of 389 robins across a gradient spanning ~ 22 degrees latitude, with 238 individual robins infected with haemosporidians (61, 95% CI: 56–66%; Fig. 1). *Plasmodium* was present in 201 robins (52, 95% CI: 47–57%), *Parahaemoproteus* was present in 40 robins (10, 95% CI: 8–14%), and *Leucocytozoon* was present in five robins (1.3, 95% CI: 0.6–3%). We detected a total of 31 parasite lineages (Supporting information) belonging to *Plasmodium* (n = 17), *Parahaemoproteus* (n = 10), and *Leucocytozoon* (n = 4). Of the 31 lineages detected, eight (25.8%) were novel, according to MalAvi. These included five *Plasmodium* lineages (TURMIG16,18-20,23), one *Parahaemoproteus* lineage (TURMIG22), and two *Leucocytozoon* lineages (TURMIG17,21). Of the robins sampled, 24 (6, 95% CI: 4–9%) were co-infected with more than one distinct haemosporidian lineage (either within or across parasite genera).

Our initial set of GLMs found varying effects of latitude on haemosporidian infection. Our first model, which was designed to test whether haemosporidian prevalence in robins varies by latitude, detected a positive effect of latitude and body condition on the probability of infection of all adult robins sampled when combining haemosporidian taxa, with no effect of sex, breeding condition, or year (Table 1). There was also a marginally positive effect of body condition on the probability of infection by *Plasmodium*, a positive effect of latitude on the probability of infection by *Parahaemoproteus* and of co-infection by any two parasite lineages, but no effect of any of the other variables we tested (Table 1). We did not consider a separate model for *Leucocytozoon* given the very low prevalence.

Our second model, which only included data for adult robins with feather stable isotopic signatures, detected a negative effect of latitude on the probability of infection when

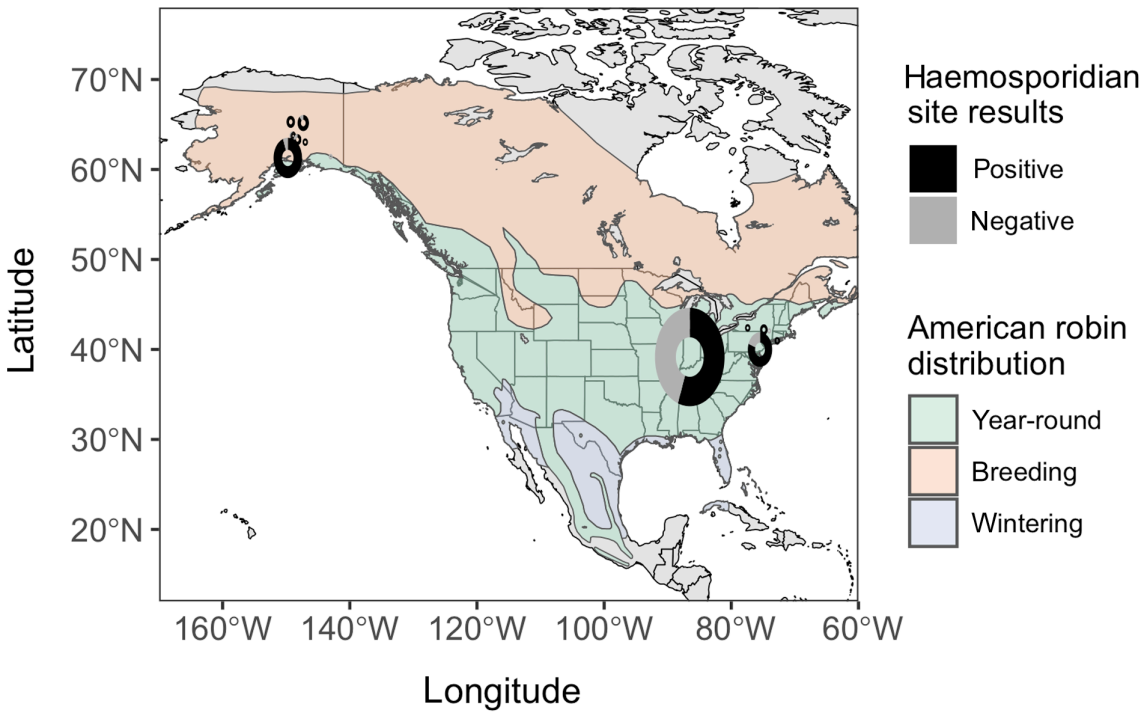

Figure 1. Sampling sites of American robins across North America, where sites are shown as donut charts of the overall proportion of haemosporidian-positive hosts as determined by PCR. Point size is scaled by the overall number of birds sampled per site. Overlaid is the American Robin geographic distribution provided through the International Union for the Conservation of Nature, stratified by the year-round range, breeding range, and wintering range.

Table 1. Results of generalized linear models with a binomial error structure on the effects of breeding latitude, body condition, sex, breeding condition (males with cloacal protuberance or females with brood patch), and year on the probability of infection by haemosporidian parasites in American robins. Statistically significant effects (i.e., $p \leq 0.05$) are shown in bold.

Variable	Estimate	SE	*Z*	p
All haemosporidian parasites				
Intercept	−2.70	1.39	−1.94	**0.05**
Latitude	0.11	0.03	3.59	**< 0.001**
Body condition	0.60	0.23	2.65	**0.01**
Sex (male)	0.08	0.41	0.19	0.85
Sex (unknown)	−0.66	0.93	−0.71	0.48
Breeding	−0.48	0.59	−0.81	0.42
Year (2021)	−0.81	0.58	−1.40	0.16
Year (2022)	−0.75	0.50	−1.50	0.13
Plasmodium				
Intercept	1.32	0.94	1.41	0.16
Latitude	−0.01	0.02	−0.57	0.57
Body condition	0.36	0.19	1.93	**0.05**
Sex (male)	0.19	0.36	0.52	0.60
Sex (unknown)	−0.20	0.78	−0.26	0.80
Breeding	−0.32	0.46	−0.69	0.49
Year (2021)	−0.39	0.55	−0.72	0.47
Year (2022)	−0.79	0.47	−1.68	0.09
Parahaemoproteus				
Intercept	−6.79	1.36	−4.99	**< 0.001**
Latitude	0.10	0.02	4.31	**< 0.001**
Body condition	0.09	0.27	0.32	0.75
Sex (male)	−0.20	0.54	−0.36	0.72
Sex (unknown)	0.50	1.30	−0.38	0.70
Breeding	0.21	0.62	0.34	0.73
Year (2021)	−15.98	1186.44	−0.01	0.99
Year (2022)	0.46	0.86	0.54	0.59
Co-infection				
Intercept	−6.29	1.77	−3.56	**< 0.001**
Latitude	0.09	0.04	2.58	**0.01**
Body condition	−0.02	0.31	−0.07	0.94
Sex (male)	0.27	0.64	0.42	0.68
Sex (unknown)	−15.34	1269.81	−0.01	0.99
Breeding	−0.17	0.72	−0.24	0.81
Year (2021)	0.05	1.05	0.04	0.97
Year (2022)	−0.77	1.03	−0.74	0.46

combining haemosporidian taxa (Fig. 2), although body condition, sex, and season had no significant effect (Supporting information). Similarly, we found a negative effect of latitude on the probability of infection by only *Plasmodium* (Supporting information). This model was not applied to other parasite genera, given rare positives in this subset of the data (one positive for each of *Parahaemoproteus* and *Leucocytozoon*).

Our third model, which combined our data with that of other avian malaria surveys in robins (Fecchio et al. 2023), detected a positive effect of latitude on the probability of infection when combining all haemosporidian taxa, as well as for *Parahaemoproteus* and *Leucocytozoon* when we analyzed those parasite taxa separately (Fig. 3, Supporting information). We also detected a negative effect of latitude on the probability of infection by *Plasmodium* and a positive effect of latitude on the probability of co-infection (Fig. 3, Supporting information). These results were robust when accounting for year, and we observed declines in the probability over time for *Leucocytozoon* and co-infections (Supporting information).

Our secondary analyses focused on haemosporidian diversity. In our Tweedie GLMM, neither latitude nor sampling effort had significant effects on bootstrap-corrected haemosporidian lineage richness; reproductive origin also had no effect (Supporting information). In our PERMANOVA of lineage composition, we also found no effect of Alaska or eastern USA grouping ($F_{1,6} = 0.67$, $p = 0.44$). The results of the Mantel test indicated the phylogenetic distance between parasite lineages was weakly correlated with the geographic distance between sampling sites for *Plasmodium* ($r = 0.15$, $p < 0.01$) but not *Parahaemoproteus* ($r = -0.05$, $p = 0.87$). *Leucocytozoon* was not analyzed due to the small number of infected robins.

Discussion

Overall, we detected little seasonal variation in haemosporidian prevalence in robins, with little support for the predictions that haemosporidian prevalence is higher during the breeding season than in winter or that body condition of infected robins is lower than that of uninfected robins. We also found that prevalence of *Plasmodium* decreases with breeding latitude in robins, that *Leucocytozoon* and *Parahaemoproteus* increases with breeding latitude, and that there is a positive relationship between robin breeding latitude and co-infection.

We detected a positive relationship between breeding latitude and probability of infection when combining haemosporidian taxa after sampling robins at specific breeding sites (our first model), but the opposite pattern when we inferred breeding latitude using feather stable isotopes (our second model). This could be due to having sampled robins that breed across a broader geographic range when using feather stable isotopes, which we cannot directly quantify, due to high uncertainty in the longitude of the breeding site when using this technique. Thus, inferring patterns across regions may require more detailed continental-level sampling.

The positive relationship between robin body condition and infection by haemosporidians that we detected in our first model may be attributable to a variety of factors, including migratory culling of infected robins with poor body condition (Bradley and Altizer 2005). Furthermore, we may have sampled robins during the chronic phase of infection, which may have less of an impact on host condition months after the primary infection occurred (Bensch et al. 2007). Research on another partially migratory bird, the American kestrel *Falco sparverius* and its haemosporidians, shows that habitat type can impact parasite transmission dynamics (Frixione and Rodríguez-Estrella 2023). Given that robins are capable of using a variety of habitats, depending on region and time of year (Vanderhoff et al. 2020), the impacts of habitat- and community-related drivers of exposure to parasites (Tamayo-Quintero et al. 2023), and resulting ability to acquire food resources (thereby impacting body condition) are difficult to disentangle.

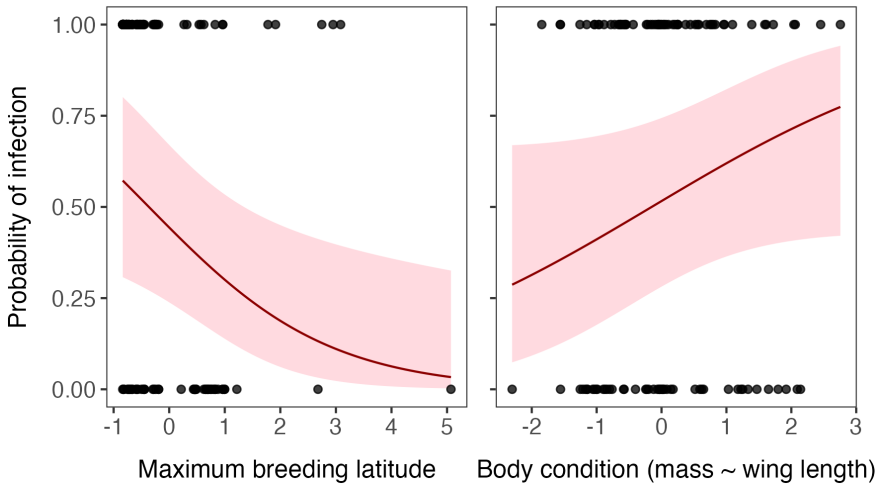

Figure 2. Probability of haemosporidian infection (combining all parasite taxa) as a function of maximum breeding latitude (estimated using feather hydrogen isotopes and rescaled with a center of zero), and body condition in adult American robins. Fitted values are shown from the corresponding GLM with 95% confidence intervals, overlaid with raw positivity data.

The positive relationship between co-infection and latitude that we found in robins is a pattern that has been previously found for songbirds and their haemosporidians across the Americas (Fecchio et al. 2020, 2023) and specifically for close relatives of robins, the *Catharus* thrushes (Starkloff and Galen 2023). The co-infections reported in these two studies are primarily based on *Leucocytozoon* infection, whereas the co-infections we detected are by *Plasmodium* and *Parahaemoproteus*. One possible reason for this difference could be that robins are more resistant to *Leucocytozoon* lineages across their range, even in boreal bird communities such as Alaska, where single infections and co-infections are dominated by this haemosporidian genus (Galen et al. 2019, Fecchio et al. 2023). The trends and causes of co-infection in wildlife remains an understudied topic, although co-infection by parasites generally is likely more the rule than the exception across host taxa (Hoarau et al. 2020).

We found little evidence of latitude-dependent diversity for haemosporidian parasites hosted by robins, which supports previous findings at a global scale (Clark 2018) – but see Fecchio et al. (2019) – and which could be attributable to a variety of taxon- and regional-specific factors. Trends in parasite diversity may also be taxon-specific. *Leucocytozoon* diversity, for example, exhibits a positive relationship with latitude and seems to follow vector diversity rather than avian host diversity (Fecchio et al. 2020). However, *Leucocytozoon* was

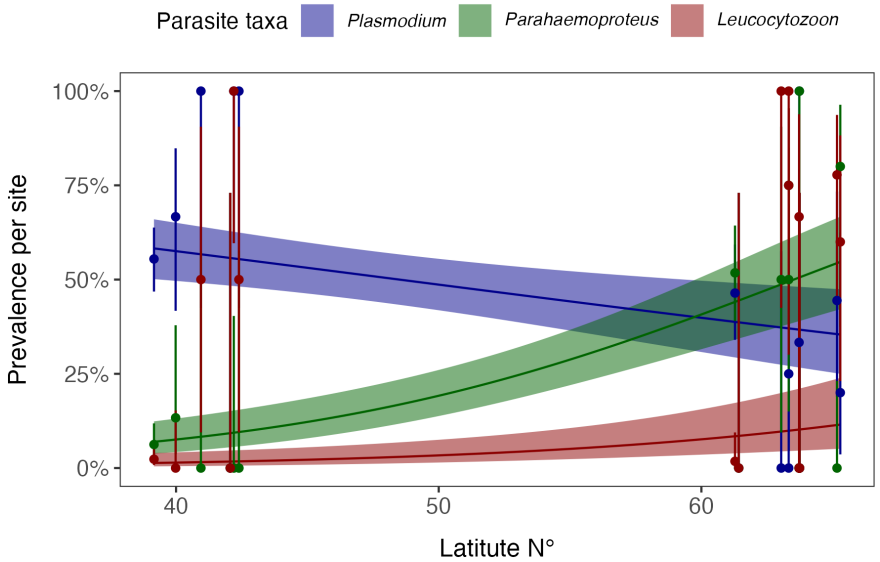

Figure 3. Prevalence of infection by *Plasmodium*, *Parahaemoproteus*, and *Leucocytozoon* in American robins as a function of breeding latitude using data from Alaska and Indiana (present study) and from Alaska, New York, and Pennsylvania, from a previous study (Fecchio et al. 2023). Fitted values from each parasite taxon-specific GLM are shown with 95% confidence intervals, with site-level prevalence data overlaid (confidence intervals were calculated using the Wilson interval for small sample sizes).

scarce in the robin populations that we studied, suggesting differential resistance by robins to these parasites or lack of exposure to competent vectors for this haemosporidian genus. Notably, a previous study (Fecchio et al. 2023) found that only two in 10 American robins sampled in Alaska were infected with *Leucocytozoon*. Furthermore, haemosporidian diversity is positively related to avian diversity (Angeli Dutra et al. 2023, Tamayo-Quintero et al. 2023) and avian host composition (Fecchio et al. 2019). The high fraction of novel haemosporidian parasite lineages that we detected in robins (> 25%) shows that they harbor a higher diversity of haemosporidian parasite lineages than previously known. Given that few haemosporidian lineages have been matched to known morphospecies, robins could be a model system to study the relationship between molecular and morphological diversity using recently developed techniques (Galen et al. 2018).

We found little evidence that haemosporidian prevalence in robins is higher during the breeding season than in winter. This may be a result of our sampling in a single location (Indiana), resulting in population-specific drivers, such as the local climate, seasonality, and age structure of that population. Mixing of resident and migrant robins during winter could also homogenize the prevalence rates we observed, potentially masking seasonal differences. Additionally, the robins we studied migrate within temperate latitudes, whereas the previous studies finding higher haemosporidian prevalence during the breeding season focused on migratory birds overwintering at tropical latitudes (Hellgren et al. 2013, Sorensen et al. 2016, Pulgarín-R et al. 2019). Thus, the environmental conditions robins experience during winter may lead to a disparate pattern relative to birds that overwinter at tropical latitudes. Another contributing factor may be the high sensitivity of PCR as a diagnostic method, which could conflate low-parasitemia chronic infections in winter with active infections in the breeding season (Fallon and Ricklefs 2008). Supplementing molecular diagnostics with methods to quantify parasite intensity, such as quantitative PCR or microscopy, could reveal more predictable patterns of seasonality in active infections, and help to determine whether haemosporidian lineages infecting robins are capable of infecting vectors to complete their life cycle and how likely they are to be transmitted locally among other avian species.

Given the highly variable migration distances exhibited by robins across North America (Jahn et al. 2019, Vanderhoff et al. 2020), they could be a useful model to study the mechanisms underlying the tradeoffs involved in the dispersal of parasites by songbird hosts (Becker et al. 2022). The conditions under which migratory birds disperse parasites are not well understood and are likely molded by a suite of ecological and evolutionary constraints to dispersal and transmission, which themselves vary according to the host's taxon and physiology, region, and time of year (Sorensen et al. 2016, Fecchio et al. 2019, Poulin and de Angeli Dutra 2021). For example, the prevalence and diversity of haemosporidian parasites of grey-cheeked thrush *Catharus minimus*, which shares few lineages of parasites with other species of birds it overlaps with in winter, is season-dependent (Pulgarín-R et al. 2019). Such temporal patterns in prevalence profiles are also likely to be lineage-specific due to, for example, the coevolution of the host with a given set of parasite lineages (Hellgren et al. 2013).

Comparisons of closely related taxa with different movement strategies (e.g. short- versus long-distance migration) promises novel insights into how migratory animals and pathogens interact in different contexts (Shaw et al. 2023). At the intraspecific level, future research could reveal whether long-distance migrant robins may face a greater risk of paying higher physiological costs or even mortality via migratory culling by their parasites, as has been found in other migratory taxa (Bradley and Altizer 2005, Slowinski et al. 2018). Such work could include assessing the relationship between infection intensity and migration distance, which can be nonlinear (Shaw et al. 2023). Explicit quantification of immune tradeoffs, such as those experienced by short- versus long-distance migrants, would also be informative. Little consensus exists on the impacts of haemosporidian parasites on the condition and survival of their avian hosts, with some studies finding no significant effects on body condition (Young and Proudfoot 2014) or fitness (Bensch et al. 2007), while some instead find positive effects on fitness (Zylberberg et al. 2015).

Robins and other common bird species may also serve as sentinels of how pathogens are moving into new regions as global climate change progresses. If mosquitos begin to emerge earlier at northerly latitudes than they do currently (Hoover and Barker 2016), robins that arrive in spring may be at greater risk of infection by mosquito-borne pathogens, such as *Plasmodium*. Given that some migratory robins have already advanced the timing of their spring migration (Oliver et al. 2020), they may serve as reliable sentinels of the pathogen-associated risks to climate change faced by migratory songbirds. Furthermore, given that urban birds often exhibit a suppressed stress response (Partecke et al. 2006), comparisons of rural versus urban robins may reveal the impacts of urbanization on their health, and whether robins can be useful as sentinels of the presence of avian pathogens or harmful contaminants in cities (Zahor et al. 2024).

The present study is one of the first to evaluate the complex suite of intra-specific drivers at inter- and intra-population levels that impact the probability of haemosporidian infection and diversity in a common bird host. Further intraspecific comparisons in avian hosts promise insights into the drivers of parasite–host relationships in different contexts and how avian parasites may react to ongoing, rapid environmental change.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.mcvdnck8z (Jahn et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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