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Migratory birds have higher prevalence and richness of avian haemosporidian parasites than residents

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ABSTRACT

Individuals of migratory species may be more likely to become infected by parasites because they cross different regions along their route, thereby being exposed to a wider range of parasites during their annual cycle. Conversely, migration may have a protective effect since migratory behaviour allows hosts to escape environments presenting a high risk of infection. Haemosporidians are one of the best studied, most prevalent and diverse groups of avian parasites, however the impact of avian host migration on infection by these parasites remains controversial. We tested whether migratory behaviour influenced the prevalence and richness of avian haemosporidian parasites among South American birds. We used a dataset comprising ~ 11,000 bird blood samples representing 260 bird species from 63 localities and Bayesian multi-level models to test the impact of migratory behaviour on prevalence and lineage richness of two avian haemosporidian genera (*Plasmodium* and *Haemoproteus*). We found that fully migratory species present higher parasite prevalence and higher richness of haemosporidian lineages. However, we found no difference between migratory and non-migratory species when evaluating prevalence separately for *Plasmodium* and *Haemoproteus*, or for the richness of *Plasmodium* lineages. Nevertheless, our results indicate that migratory behaviour is associated with an infection cost, namely a higher prevalence and greater variety of haemosporidian parasites.

1. Introduction

Migration can be defined as long-distance, regular movement of an animal population to and from a specific region, characterised by movement patterns that vary within and not between years (Teitelbaum and Mueller, 2019). Long-distance migrations are commonly observed in nature, occurring in a wide range of animals such as butterflies, fish and birds (Bauer and Hoye, 2014). In birds, migration occurs in almost 20% of species (~1850), including some of the best-studied species (Kirby et al., 2008). Nevertheless, many migrant species demonstrate partial migratory behaviour, when just a fraction of the population migrates while the remaining individuals reside in a single habitat during the whole year (Chapman et al., 2011). Migration exerts a strong influence on ecosystems since migrants can function as prey and predators in their new environment as well as carry parasites to new areas (Bauer and Hoye, 2014; Viana et al., 2016).

Migration imposes a substantial physiological cost for avian migrants, by consuming resources and causing physiological stress and muscle damage (Guglielmo et al., 2001; Jenni and Schaub, 2003; Altizer et al., 2011). In addition, migratory birds may be more exposed to parasites since they cross different regions along their route, which can expose them to a wider range of parasites during their phenological cycle (Jenkins et al., 2012; Koprivnikar and Leung, 2015; Teitelbaum et al., 2018). Further, the metabolic demands of migration such as fattening and strenuous activity are likely to decrease the amount of resources available to mount an immune response, which could lead to higher infection rates (Wikelski et al., 2003; Altizer et al., 2011). Therefore, we might expect that migratory birds harbour a more diverse range of parasites and might be more prone to infections. However, Møller and Erritzøe (1998) have demonstrated that migrant birds invest more in immune defence as a result of their higher exposure to parasite pressure. On the other hand, migration may provide a protective effect since migratory behaviour allows hosts to escape environments where infection risk is high (Altizer et al., 2011; Poulin et al., 2012; Satterfield et al., 2015; Fecchio et al., 2020b).

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Haemosporidians, vector borne protozoan parasites, are among the most prevalent, diverse and well-studied avian parasites. Indeed, these parasites are globally distributed and able to infect many avian clades (Valkiūnas, 2005; Marzal, 2012; Fecchio et al., 2020a). Haemosporidian parasites and their hosts are frequently used as ecological and evolutionary models, and have contributed to fundamental advances in our understanding of ecological processes associated with conservation and management of environment and wildlife (Marzal, 2012). Moreover, previous research suggests that differences in haemosporidian lineages harboured by individual birds may indicate whether they have become infected in different areas; thus, haemosporidians could be used also as geographic markers for bird migration (Marzal, 2012). Certainly, many factors such as climate, landscape conditions, local vector and avian richness, abundance and composition also explain variations in haemosporodian prevalence and diversity (Illera et al., 2017; Ferreira et al., 2017; Ferraguti et al., 2018; Pulgarín-R et al., 2018; Clark et al., 2020; Filion et al., 2020). Nevertheless, previous research also suggests that migratory behaviour may be positively related to infection status by haemosporidian parasites in avian species (Figuerola and Green, 2000; Illera et al., 2017).

South America harbours the greatest richness of birds and vectors worldwide (Santiago-Alarcon et al., 2012; Remsen, J.V.J., Areta, J.I., Bonaccorso, E., Claramunt, S., Jaramillo, A., Pacheco, J.F., Robbins, M.B., Stiles, F.G., Stotz, D.F., Zimmer, K.J., n.d. A classification of the bird species of South America. Am. Ornithol. Soc. http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm), making it an ideal ecosystem in which to investigate the putative effect of migratory behaviour on bird infections by haemosporidian parasites. Therefore, we tested the impact of migratory behaviour on haemosporidian infections among South American birds. More specifically, we hypothesised that migratory behaviour increases the exposure of avian hosts to haemosporidian parasites, and predicted that migratory species would show higher prevalence of infection and greater richness of haemosporidian lineages than non-migrants. Firstly, we tested whether resident, partial migrant and full migrant species differed in their prevalences. Secondly, we determined whether resident, partial migrants and full migrants were infected by different numbers of haemosporidian species in order to evaluate whether parasite richness varies among species from distinct migratory host categories. When performing our analysis, we also considered other potential predictors of haemosporidian prevalence and lineage richness, such as bird phylogeny and bioclimatic factors, which influence the local abundance of vectors, in order to isolate the true effect of migratory behaviour.

2. Materials and methods

2.1. Dataset

All analyses were performed using a dataset comprising ~13,200 bird blood samples obtained from 896 avian species from 63 different localities comprising six different biomes - Amazonia, Atlantic Rain Forest, Brazilian Savanna, Temperate Grassland, Caatinga and Pantanal. The birds were sampled from 2005 to 2018, with a subset of those samples having previously been used in published research (Lacorte et al., 2013; Ferreira et al., 2017; Fecchio et al., 2019; Lopes et al., 2020) and the rest consisting of unpublished data (Fig. 1, see Supplementary Table S1). A total of 2078 sequenced parasites representing 578 distinct lineages were recovered from those blood samples, all belonging to one of two genera: *Plasmodium* and *Haemoproteus*. Haemosporidian prevalence per bird species was estimated as the number of positive samples out of all samples tested using PCR protocols described elsewhere

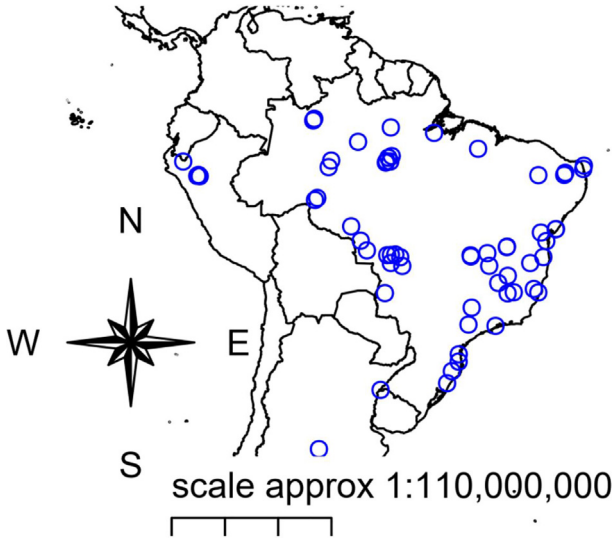

Fig. 1. Bird sampling localities across South America. A total ~ 11,000 individuals from 262 avian species were sampled from the 63 surveyed localities.

(Fallon et al., 2003; Hellgren et al., 2004; Bell et al., 2015). The parasite lineages were identified by a PCR protocol described earlier (Hellgren et al., 2004) which produces a cytochrome b (cyt b) fragment of 478 bp. The birds present in each locality were classified into three ecological classes: (1) resident; (2) partial migrant and (3) full migrant, according to the Brazilian Committee of Ornithology Records - CRBO 2014, Somenzari et al., 2018 and BirdLife International (https://www.birdlife.org/). For all analyses below, we considered only bird species with 10 or more individuals sampled, which represented ~ 11,000 bird individuals (Supplementary Table S2).

2.2. Phylogenetic signal

All analyses were conducted in R version 4.0 (R Core Team, 2019). Values for parasite prevalence and richness may be more similar among closely related bird species than among distantly related ones; such a 'phylogenetic signal' would create non-independence among species in the comparative analysis. In order to estimate the phylogenetic signal among prevalence and richness estimates for the bird species in our dataset, we downloaded a full avian phylogeny file from the AllBirdsHackett1.tre website (https://birdtree.org/), and used the "treeman" package (Bennett et al., 2017) to create a treeman file containing all trees from the original file. Then, we randomly selected 100 trees. This new file was converted from treeman to a phylo file, from which we extracted a consensus tree to account for phylogenetic uncertainty. We eliminated all bird species from the phylo tree which were not present in our dataset and using the "match" function from the "picante" package (Kembel et al., 2010), we matched the species between the tree and our dataset. Then, we calculated Pagel's λ to evaluate the phylogenetic signal among bird species in our dataset, for haemosporidian prevalence and parasite richness (Pagel, 1999). Values of λ can range between 0 and 1, equalling 1 when the trait has evolved consistently with a Brownian motion and trait values are similar among related species, and 0 when trait values are unrelated to phylogenetic closeness among species. In order to estimate λ, we applied the "phylosig" function from the "phytools" package (Revell, 2012). A phylogenetic tree was constructed to illustrate the avian phylogenetic relationships among species in our dataset (Supplementary Fig. S1).

2.3. Spatial autocorrelation

The species sampled differed between localities, therefore this may affect/bias the estimates of prevalence and richness. To evaluate the potential impact of proximity among localities on our results, we evaluated the spatial autocorrelation among localities for total prevalence (i.e., number of infected individuals/total number of individuals sampled, all bird species combined) and parasite richness (total number of parasites lineages, across all bird species combined) in our dataset by calculating the Moran Index value. Index values range between −1.0 and +1.0, with 0 indicating no spatial autocorrelation and −1.0 or +1.0 high spatial autocorrelation. To compute this index, we filtered the data for species sampled 10 or more times and combined the coordinates data into a matrix, and employed the function "Moran.I" from the "Ape" package (Paradis and Schliep, 2018).

2.4. Climate variables

Similarly, environmental variables vary among localities, and may influence the local abundance or diversity of insect vectors of haemosporidians. Since individuals of different avian species were not all sampled from exactly the same localities, local climatic variables likely to influence vectors must be incorporated into the analyses. We used annual mean precipitation (variable BIO15) and annual mean temperature (variable BIO1, °C) as predictors in the Bayesian models since temperature and precipitation are known to be related to haemosporidian infections (Illera et al., 2017; Clark et al., 2020). We extracted these climate variables from the Worldclim database (https://worldclim.org/version2) using the package "raster" in R. Then, we selected the data for the 63 localities included in our dataset with 10 min resolution.

2.5. Bayesian analyses

We constructed two Bayesian models using the "brms" package (Bürkner, 2017) to evaluate whether migratory species (partial or full) harbour a higher prevalence and a higher lineage richness of haemosporidians than residents. In both models, we created a matrix with phylogenetic distances between bird species and used the function "cov_ranef" to account for phylogenetic influence on parasite prevalence and richness. By controlling for bird phylogeny, and because most host traits are phylogenetically conserved, our models take into account the possible effects of various host traits on parasite prevalence and richness. This was an important step in the present analyses since we observed strong phylogenetic signals in our dataset (see section 3).

For the first model, we analysed the prevalence per bird individual as a function of their migratory category (resident; partial migrant and full migrant, reference level = resident). For this, we considered the infection status of individuals birds as our dependent variable (binary response: 0 for uninfected, 1 for infected), and migratory category as our independent variable. Temperature and precipitation were also retained as fixed factors whereas locality was considered a random factor. We employed the Bernoulli distribution family, using four chains with 4000 total iterations per chain (2000 for warm-up, 2000 for sampling).

In our second Bayesian model, we considered parasite richness per bird species and bird category (resident; partial migrant and full migrant, reference level = resident) as our dependent and independent variables, respectively. Parasite prevalence per bird species, number of localities in which the bird species was sampled, and number of bird individuals per species sampled, were also employed as fixed factors. As we analysed parasite richness by grouping all individuals per species regardless of where they were sampled, it was not possible to include local bioclimatic data. The random factors used in the previous model were not included here, since the analysis of parasite richness is not locality-based but combines data across localities for each bird species. Here, we applied the negative binomial distribution family and again we used four chains with 4000 total iterations per chain (2000 for warm-up, 2000 for sampling). We chose our priors using the "get_prior" function. The models' results were plotted using the "conditional_effects" function to visualise the predictions of the population-level effects.

In addition, we repeated the analyses for parasite richness using bootstrap extrapolated richness values and the Gamma distribution family (Poulin, 1998). Among several non-parametric estimators of 'true' richness, i.e. accounting for parasite lineages likely to have been missed by insufficient sampling, the bootstrap is generally more conservative: it improves the richness estimate beyond the number of lineages observed, but is unlikely to overshoot 'true' richness (Poulin, 1998). Bootstrap correction was calculated following the formula below:

$$S_B = S_o + \sum \left[\, 1 \; - \; \left(h_j / H \right) \,\right]^H$$

where h_j is the number of infected individuals sampled per species, H is the total number of host individuals per species, S_o is the observed parasite richness per species and S_B is the bootstrap corrected parasite richness. Further, after running the above analyses for all haemosporidian genera combined, we ran separate models for *Plasmodium* and *Haemoproteus* parasites for both (prevalence and parasite richness) dependent variables.

2.6. Data accessibility

A part of the data that support the findings of this study is openly available at https://onlinelibrary.wiley.com/doi/10.1111/mec.15094. The other portion of the data that support our findings can be shared by Prof. Érika Martins Braga under reasonable request.

3. Results

3.1. General avian and parasite data description

We analysed 260 different avian species, consisting of five fully migratory species (n = 389 individuals), 17 partial migratory species (n = 1277) and a majority of resident species (238 species, 9346 individuals). Most birds (89% of all individuals) were passerines, with Columbiformes being the second most frequently sampled order (6.5%) in our dataset. Across all samples, 98 bird individuals presented mixed infections, i.e. the presence of more than one haemosporidian lineages in the same bird, which we observed mainly in resident birds (97 out of 98 cases).

Distinct haemosporidian lineages (473) were recovered in our study, with most present only in resident birds. We observed 72 lineages infecting migrant species, consisting of 22 lineages found in full migrant and 55 in partial migrant species, of which 11 and 18 occurred exclusively in full and partial migrants, respectively. However, nine of out of the 11 parasites exclusively found in full migrant hosts were observed in only one migrant species (*Vireo olivaceus*). We observed that full migrants and residents shared 11 lineages whereas partial migrants and residents shared 37 lineages. Only five parasite lineages were detected in all three bird categories.

3.2. Phylogenetic signal and spatial autocorrelation

We detected considerable phylogenetic signals among bird species for both prevalence (λ = 0.49) and parasite richness (λ = 0.17),

justifying the inclusion of avian phylogeny into our models. Additionally, the spatial autocorrelation analyses revealed there was no substantial effect of space on parasite richness, however we observed moderate spatial autocorrelation for prevalence (Moran Index = 0.16), which our models account for by including locality of sampling as a random factor. Local temperature and precipitation had no effect on parasite prevalence (Table 1).

3.3. Migratory behaviour and other predictors for haemosporidian parasite prevalence and richness

We found that bird migratory behaviour is associated with increased haemosporidian prevalence and haemosporidian richness (Fig. 2A and B). Resident bird species had an average prevalence of 14.3% whereas full migrants and partial migrants had prevalence rates of 38.6% and 15.7%, respectively (Fig. 2A). Prevalence was significantly higher for fully migratory than for resident species (Table 1). However, no difference was observed when evaluating the prevalence of *Plasmodium* and *Haemoproteus* lineages separately (Supplementary Tables S3 and S4).

A similar pattern was observed for parasite richness, whose model showed that fully migratory species presented higher parasite richness when considering all haemosporidian lineages combined (Table 2). In other words, residents and partial migrants harboured similar numbers of parasite lineages per host species while fully migratory species hosted a greater number of parasite lineages (Fig. 2B). In addition, parasite richness was influenced by overall prevalence and the number of localities in which the birds were collected (Table 2). However, when analysing parasite richness separately for each haemosporidian genus, we observed no difference in parasite richness among bird migratory categories for *Plasmodium*, whereas full migrants harboured on average higher parasite richness for *Haemoproteus* (Supplementary Tables

Table 1
Parameter estimates, standard errors, and confidence intervals for the Bayesian model testing the difference in haemosporidian prevalence among host migratory categories. Estimates whose confidence intervals do not overlap 0 are considered significant.

	Estimate	Standard error	Confidence Interval (95%)	
Intercept	−1.82	0.96	−3.70	0.08
Full migrant	1.32	0.45	0.46	2.22
Partial migrant	0.11	0.26	−0.39	0.61
Temperature	0.00	0.00	−0.01	0.01
Precipitation	−0.01	0.00	−0.01	0.00

Table 2
Parameter estimates, standard errors, and confidence intervals for the Bayesian model testing the difference in haemosporidian richness among host migratory categories. Estimates whose confidence intervals do not overlap 0 are considered significant.

	Estimate	Standard error	Confidence Interval (95%)	
Intercept	0.03	0.15	−0.28	0.31
Full migrant	0.60	0.20	0.20	1.00
Partial migrant	−0.09	0.14	−0.36	0.17
Prevalence	2.38	0.19	2.01	2.75
Number of individual birds	0.00	0.00	0.00	0.00
Number of localities	0.06	0.01	0.04	0.07

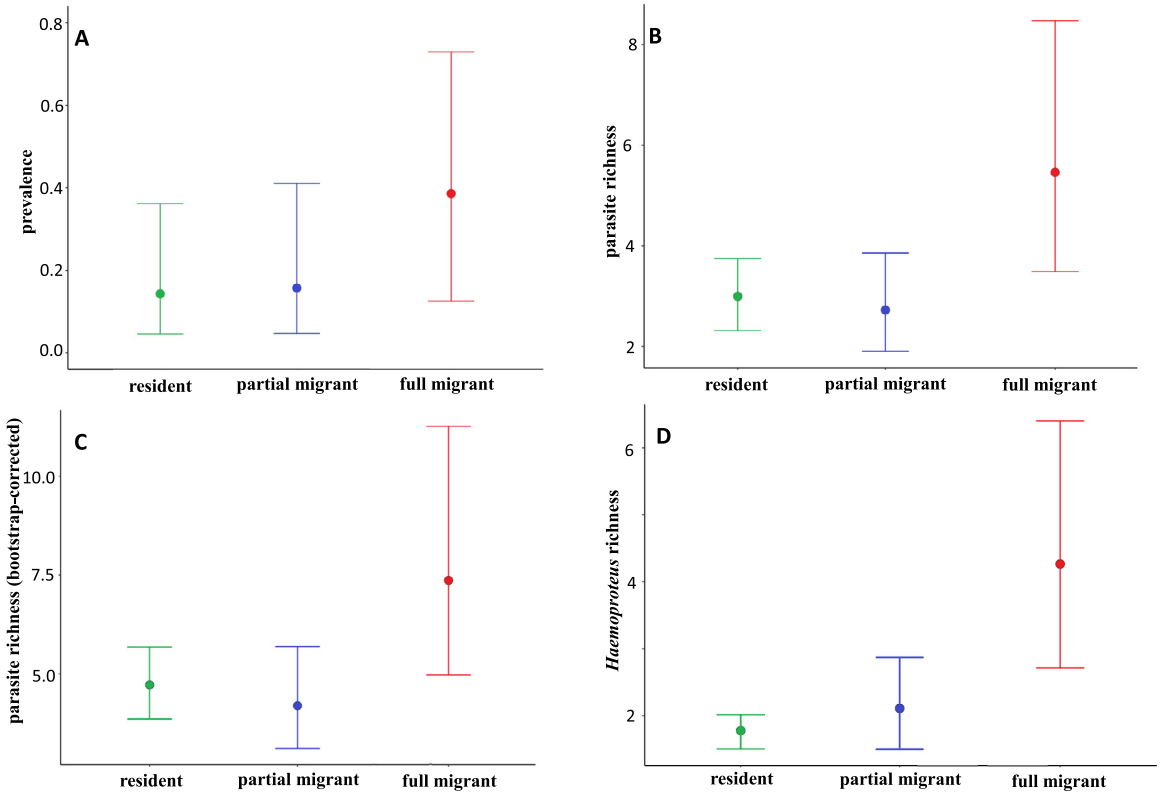

Fig. 2. Haemosporidian prevalence and richness among bird migratory categories. (A) Mean (±standard error) haemosporidian prevalence for each host migratory category. (B) Mean (±standard error) haemosporidian lineage richness for each host migratory category. (C) Mean (±standard error) bootstrap-corrected haemosporidian lineage richness for each host migratory category. (D) Mean (±standard error) *Haemoproteus* lineage richness for each host migratory category.

S5 and S6, Supplementary Fig. S2, Fig. 2D). Indeed, fully migratory species present the highest richness of haemosporidian parasites (5.5 lineages on average), followed by residents (3.0) and partial migrants (2.7). Further, when using bootstrap corrected estimates of parasite richness, we again demonstrated that fully migratory bird species harbour more haemosporidian and *Haemoproteus* parasite lineages (Supplementary Tables S7–S9, Fig. 2C, Supplementary Fig. S2).

4. Discussion

Migration may expose hosts to a greater range of parasites, it can act as an energetic challenge that culls infected individuals from the population, and it can provide a mechanism to escape from environments presenting a high infection risk (Altizer et al., 2011; Poulin et al., 2012). Our results indicate that among South American birds, individuals of fully migratory species are more frequently infected by haemosporidian parasites than residents and, at the same time, migratory species as a whole carry a greater number of parasite lineages. However, partial migrants appear to be equally infected by haemosporidians as resident hosts. Furthermore, we also demonstrate that the higher infections by haemosporidian parasites may apply only to some parasite groups since we did not observe a greater parasite richness in migratory species when only considering *Plasmodium* lineages. Also, it is important to note that we did not observe differences in haemosporidian prevalence between migratory categories when analysing *Plasmodium* and *Haemoproteus* genera separately. Moreover, our results may indicate haemosporidian infracommunities (i.e. all infections within individual hosts) are potentially more diverse in resident birds since those hosts account for the majority of mixed infections. Nevertheless, overall migratory behaviour is associated with greater infections by haemosporidian parasites, in terms of both prevalence and richness.

Since migrants may harbour a greater richness of certain parasites, they can influence directly the local communities they visit and temporarily inhabit. It is important to note that a few earlier studies have reported the same pattern as the one presented here, with migrant species carrying a greater richness of parasites than resident ones (Figuerola and Green, 2000; Jenkins et al., 2012; Koprivnikar and Leung, 2015; Teitelbaum et al., 2018). Naturally, host migration can benefit parasites by expanding their distribution due to the potential of migrants to transmit parasites to new regions across their route, providing also opportunities for parasite host-switching (Poulin and de Angeli Dutra, 2021). Indeed, migratory behaviour seems to impact haemosporidian diversity in South America (Fecchio et al., 2019). On the other hand, partial migrants do not show higher prevalence nor richness of haemosporidian parasites, therefore, their impact on parasite dispersal may not be as prominent as that of fully migratory species. Moreover, since parasites consume resources from their hosts, partial migrants may choose to migrate only when there is no additional cost of haemosporidian infection. Similarly, partial migrants also present shorter migration distances, hence, they could still invest enough resources in parasite defence.

Haemosporidian parasites, which are vector-borne parasites with different life cycles and transmitted by distinct vectors depending on their genus (Valkiūnas, 2005), may respond differently to abiotic and biotic influences, including their use of migratory hosts. Being infected by specialist lineages might be one reason why fully migrant species harbour greater parasite richness and possibly prevalence than residents, which is particularly true for *Vireo olivaceus*. We observed that this species was infected by eight (two *Plasmodium* spp. and six *Haemoproteus* spp.) distinct parasite lineages that were not found in any other species. We also found a more prominent effect of migratory behaviour leading to higher parasite diversity in migrant hosts for *Haemoproteus* parasites. The high cost of migration may increase host susceptibility by increasing their chances of being infected and favouring the specialisation of some parasites, a pattern which seems more pronounced for *Haemoproteus* spp.. Further, since *Haemoproteus* vectors (e.g., biting midges of the genera *Culicoides*) display strong phylogenetic conservatism in feeding preferences (Martínez-de la Puente et al., 2015), parasite specialisation on a small range of bird species may be beneficial and further enhance parasite richness in migratory species. Thus, it is possible that haemosporidian vectors play an important role in the infection patterns of avian haemosporidians in migrant species. Certainly, further research should investigate the factors associated with the ability or inability of vector-borne parasites to be spread to new avian communities.

In this study, we demonstrate that fully migratory avian species are more infected by haemosporidians than non-migratory and, consequently, migratory behaviour increases avian risk of infection to these parasites, possibly mediated by differences in exposure to various vectors and parasite lineages. Escaping haemosporidian infections is unlikely to be a pressure favouring migration in avian hosts. Previous research suggests the cost of migration can increase exposure to parasites in migrant individuals, whereas in other cases it may instead provide a mechanism to escape from parasites (Figuerola and Green, 2000; Jenkins et al., 2012; Poulin et al., 2012; Koprivnikar and Leung, 2015; Illera et al., 2017; Teitelbaum et al., 2018; Fecchio et al., 2020b). It is possible that parasite escape does not always compensate the high cost of migration, leading to divergent infection rates between resident and fully migrant hosts. In addition, because low intensity haemosporidian infections do not impact bird migration ability (Hahn et al., 2018), the culling of infected hosts during migration and consequent reduction in parasite prevalence in the migrants' next habitats may not occur in this system. At the same time, many bird species harbour long-lasting haemosporidian infections with mild consequences (Valkiūnas, 2005); therefore, the additional resource use required by migration combined with exposure to a wider range of parasites should influence bird infection rates and parasite richness in migrant species.

In summary, we demonstrated that migratory behaviour increases host infection rate and parasite richness by haemosporidians generally. It is important to stress that *Plasmodium* richness does not seem to be influenced by migration. Furthermore, partial migrants present values for prevalence and parasite richness that do not differ from those of residents. Thus, it is possible that migratory behaviour only impacts avian exposure to haemosporidians when a large portion of the population migrates across long distances since species with partial migration do not show higher infection rates nor parasite richness. In addition, it is possible partial migrants undertake migration only if there is no extra cost of infection. We also observed no impact of climatic variables on general haemosporidian prevalence, suggesting that at least in our dataset, the effect of migratory behaviour eclipses that of climatic factors. Further research should aim to establish why migration influences parasite richness differently for different parasite taxa.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijpara.2021.03.001.

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