**Bird migration** **connects regions but does not raise local prevalence and richness of avian haemosporidian parasites**

Daniela de Angeli Dutra¹\*, Antoine Filion¹, Alan Fecchio², Érika Martins Braga³, Robert Poulin¹

[danideangeli@live.com\*](mailto:danideangeli@live.com*) https://orcid.org/0000-0003-2341-2035

afilion90@gmail.com

[alanfecchio@gmail.com](mailto:alanfecchio@gmail.com) https://orcid.org/0000-0002-7319-0234

[embraga@icb.ufmg.br](mailto:embraga@icb.ufmg.br) <https://orcid.org/0000-0001-5550-7157>

[robert.poulin@otago.ac.nz](mailto:robert.poulin@otago.ac.nz) https://orcid.org/0000-0003-1390-1206

1.Department of Zoology, University of Otago, Dunedin, New Zealand

2.Programa de Pós-graduação em Ecologia e Conservação da Biodiversidade, Universidade Federal de Mato Grosso, Cuiabá, MT 78060-900, Brazil

3.Departamento de Parasitologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Brazil

**\*Correspondence:**

Daniela de Angeli Dutra

danideangeli@live.com

**Abstract** Migration has an important impact on the transmission of pathogens around the world. Certainly, migratory birds may disperse pathogens thought their routes, and may introduce pathogens to new areas and hosts. Indeed, haemosporidian parasites are among the most prevalent, diverse and important bird pathogens. South America provides an ideal opportunity to investigate the role of migration and parasite dispersal as it holds a great richness of resident and migratory birds (~3500 species). Here, we hypothesize that (1) migratory birds spread parasite lineages along their routes, and (2) localities crossed by more migratory routes have greater prevalence and richness of haemosporidians. For the first hypothesis, we tested whether parasite lineages found (i) only in migratory birds, (ii) in both migrants and residents, and (ii) only in residents, differ in their frequencies of occurrence among localities. For the second hypothesis, we tested for a relationship among localities between the overall local haemosporidian parasite richness and prevalence, and the proportion of migratory bird individuals passing through a locality. To this end, we combined a dataset on 13200 bird samples with data from the MalAvi database (overall total: ~2800 sequenced parasites comprising 668 distinct lineages, from 506 host species and 156 localities), and used Bayesian multi-level models to test the above hypotheses. Our results demonstrate that parasites shared by resident and migratory species are the most widespread, confirming the importance of migration for parasite dispersal. However, we observed no relationship for parasite richness, and a negative relation for prevalence per bird species, as a function of the proportion of migrants occurring in a locality. Therefore, we show that parasites are dispersed thought bird migration, however visiting migrants do not raise local prevalence and richness of avian haemosporidian parasites.

1.Introduction

Migration has an important impact on the transmission of disease across the world because migrant species can potentially disperse pathogens and parasites between two or more localities, and they are exposed to more infectious agents (Bauer and Hoye 2014). In this way, migrant species might play an important role in the evolution and distribution of parasites and promote the spread of pathogens to new areas and new hosts species. At the same time, human introduced pathogens and host species can decrease the fitness and survival of resident and native species, compromising the population abundance of local species and reducing community richness (Callaway and Ridenour 2004, Prenter et al. 2004). Conversely, the spread of pathogens might increase host richness by reducing competition pressures and, therefore, preventing competitive exclusion. Hence, pathogen spread might act as an environmental filter to new species colonization. Recent studies have demonstrated that migratory birds harbor a greater diversity of parasites than resident species (refs). In addition, several studies have documented the influence of migratory birds on the spread of important pathogens with some of these able to infect humans (Alekseev et al. 2001, Morshed et al. 2005, Poupon et al. 2006, Hellgren et al. 2007, Lindeborg et al. 2012, Ricklefs et al. 2017). Thus, the migratory behavior of birds may influence directly host local richness and population size.

Avian malaria parasites and related haemosporidians, could be used as geographical markers for migratory birds (Marzal 2012). Previous research has demonstrated differences in the timing of the main occurrence of haemosporidian infection in migrating birds. These studies have suggested that differences in haemosporidian lineages harbored could indicate whether birds had become infected in different areas (Marzal 2012). Since most haemosporidians cause life-long infections, parasites may travel across long distances with their bird host during migration. This would therefore allow them to infect new vectors and new avian hosts in novel environments (Fecchio et al. 2020). Indeed, migratory species are known for their potential to connect distant habitats and transfer large amounts of biomass and nutrients between ecosystems (Altizer et al. 2011). Furthermore, O’Connor et al. 2020 have demonstrated that migratory birds do not possess higher immune gene richness in wetter areas, which are usually associated with higher risk of avian malaria (Zamora-Vilchis et al. 2012, Gonzalez-Quevedo et al. 2014). Thereby, migratory birds may be more susceptible to pathogens in those regions. For this reason, it might also be expected that migratory birds harbor a more diverse range of parasites and might be more susceptible to parasite infections.

South America comprises different types of biomes, which hold a great richness of native resident and migratory bird species, thus making it an ideal system to investigate such questions. Previous research has documented the prevalence of avian malaria in different regions of Brazil, and markedly different prevalence for *Plasmodium* spp have been reported between these regions (Braga et al. 2011). Indeed, the most prevalent avian haemosporidian parasite genus in this region is *Plasmodium* (Braga et al. 2011). *Plasmodium* parasites present higher host-shifting rates than other bird haemosporidians (Hellgren et al. 2007), which could certainly contribute to their increased dissemination by migratory birds into new areas. Indeed, host-shifting of a *Plasmodium* species from domestic chicken to wild and native birds has already been reported in South America (Ferreira-Junior et al. 2018).

Furthermore, the great avian richness (~3500 species) and abundance in South America (Remsen et al. in press) could also enhance the probability of parasite host-shifting between migratory and resident birds, given the likely presence of susceptible birds in any particular area. Besides that, the great richness and abundance of vectors (Consoli and Oliveira 1994) could also increase the chances of host-shifting between migratory and resident birds as it increases the chances of compatible vectors being present. Thus, these features make the South American avian haemosporidians a great model to investigate the putative transmission of pathogens via host migration in nature.

In this context, the main goal of this study is to evaluate the influence of migratory birds on the spread of haemosporidian parasites in South America. Specifically, we evaluated the hypothesis that (1) migratory birds spread parasite lineages along their migratory routes, and (2) localities crossed by more migratory routes have greater prevalence and richness of haemosporidian lineages. For the first hypothesis, we tested whether parasite lineages found (i) only in migratory birds, (ii) in both migrants and residents, and (ii) only in residents, differ in their frequency of occurrence among localities. Due to the fact migrants can carry parasites from many sites and potentially infect resident birds, we predicted that parasite lineages using migratory birds should occur in a greater percentage of localities than those using only resident birds. Moreover, migration behavior increases the exposure of birds to more parasite lineages and hence their contact with different parasites as migrants pass through regions that harbor different parasite communities. Therefore, we expect higher haemosporidian richness and prevalence in regions with more migratory birds. For the second hypothesis, we tested for a relationship among localities between the overall local haemosporidian parasite richness and prevalence, and the proportion of migratory birds passing through a locality.

2. Methods

2.1 Dataset

All analyses were performed using a dataset comprising ~13200 bird blood samples accounting for 916 species from 63 different localities sampled from 2005 to 2018 in South America, previously described in Lacorte et al. 2013, Ferreira et al. 2017, Fecchio et al. 2019 and supplemented with new, previously unpublished data. In addition, haemosporidian lineages from the MalAvi database (<http://130.235.244.92/Malavi/>, Bensch et al. 2009) were included from South American regions (Figure 1, Supplementary material). Combining both datasets, we obtained a total of ~2800 sequenced parasites representing 668 distinct lineages collected from 506 different host species and 156 localities (all lineages belonging to one of these three genera: *Plasmodium*, *Haemoproteus* and *Leucocytozoon*). Each locality was assigned to a biome based on the classification of Turchetto-Zolet et al. 2013. The parasite prevalence per bird species and locality was estimated using PCR diagnostic protocols described by Hellgren et al. 2004 and Fallon et al. 2003. The parasite lineages were identified by the PCR protocol described by Hellgren et al. 2004. This protocol produces a *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/>).

2.2 Potential correlates of prevalence and richness

*Spatial and temporal correlation*

All analyses were conducted in R (R Core Team, 2019). We determined whether there was significant spatial autocorrelation among localities for prevalence and parasite richness in our dataset by calculating the Moran Index value. In order to estimate this index, we combined the coordinates data into a matrix and employed the function “Moran.I” from the “Ape” package (Paradis and Schliep 2018). Temporal correlation analyses were performed using linear models, to determine whether prevalence or richness estimates varied throughout the sampling period (2005–2018). For parasite prevalence, we conducted a mixed linear model using the package “lme4” and the function “lmer” (Bates et al. 2015). Firstly, we grouped the data by year and location. Then, we compared the prevalence among years of collection considering number of birds collected and location as variables random variables. In order to test for a temporal correlation for parasite richness, we performed a simple linear model using the “lm” function.

*Phylogenetic Signal*

In order to estimate the phylogenetic signal among prevalence and richness estimates for the bird species in our dataset, we downloaded the file AllBirdsHackett1.tre from <https://birdtree.org/> website. Using the “treeman” package (Bennett et al. 2017), we created 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 one single random tree. We grouped our data per species and eliminated all bird species from the phylo tree which were not present in our dataset. 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 lambda (λ) to evaluate the phylogenetic signal among bird species in our dataset, for both haemosporidian prevalence and parasite richness. Values of λ can range between 0 (no phylogenetic signal) and 1 (strong phylogenetic signal). In order to estimate lambda (λ), we applied the “phylosig” function from the “phytools” package (Revell 2012).

*Climate variables*

We used mean precipitation seasonality, and annual mean temperature (ºC) as predictors in the mixed models. We used R to extract these climate variables from the Worlclim database (<https://worldclim.org/version2>). Using the package “raster”, we extracted the data using the “getData” function, then we selected only the data from the 63 localities included in our original dataset since climate variables were applied only in mixed model analyses, for which the MalAvi data was not employed.

2.3 Statistical Analyses

The spatial and temporal autocorrelation analyses revealed there was no substantial effect of time or space on parasite richness, however, for prevalence, we observed a Moran Index effect of 0.15, and for this reason, locality was used as a random effect in our second mixed model to control for idiosyncratic characteristics of localities. Likewise, considerable phylogenetic signals were observed among bird species for prevalence (0.49) and parasite richness (0.17). Considering this, phylogenetic covariation was added in Bayesian analyses and we analysed the prevalence using species as a fixed factor in the second mixed model.

*Bayesian model*

In order to determine whether migratory birds spread parasite lineages along their migratory routes and to evaluate the parasite connectivity among localities due to migratory behavior, we used multi-level modeling (MLM) with the “brms” package (Bürkner 2017) to evaluate the percentage of localities in which haemosporidian lineages occurred depending on whether they were found only in resident birds, only in partial migrant and fully migrant birds, or in both residents and migrants. We decided to use this approach as it allows to control for host phylogeny and to statistically estimate the percentage of localities among which lineages are distributed according to their host status.

Firstly, using the “ape” package (Paradis and Schliep 2018), we computed the phylogenetic expected variances and covariances from our bird species and incorporated this to control for phylogenetic effects in our Bayesian model. Secondly, we applied the “get\_priors” function to fit the priors for our model. We considered as independent and dependent variables bird migratory categories and percentage of localities in which each lineage was present, respectively, and res as reference level. As our Moran Index value for spatial autocorrelation of parasite richness among localities was low (-0.0008), we did not consider locality as a variable in our model and also did not use model correction for locality coordinates. Thus, we ran the model applying the “Beta” family, 4 chains with 2000 total iterations per chain and 1000 of warmup interactions. The model results were plotted using the “conditional\_effects” function to visualize the predictions of the population-level effects. We ran three models: one for all three parasite genera combined, one for *Plasmodium* lineages only, and one for *Haemoproteus* lineages only. Finally, we ran the “loo\_model\_weights“ to account for the effect of host richness and number of hosts infected per lineage in our dataset.

*Mixed models*

Two mixed models were performed to estimate whether localities with more migratory birds have greater prevalence and richness of haemosporidian lineages. We chose to use mixed models since we are analysing localities and we could not have enough data for a robust Bayesian model. fixed effects and evaluate those variables into the models. With this objective, we employed the “lmer” function from the “lme4” package (Bates et al. 2015). In the first model, we considered parasite richness as the dependent variable and percentage of migratory bird individuals (i.e., percentage of migratory individuals out of all individual birds sampled in a locality) as the independent variable. Local host richness (i.e., number of bird species sampled per locality), prevalence across all birds sampled), percentage of migratory species and number of migrant individuals were considered fixed variables. Further, number of individual birds tested for infection per site, biome, mean precipitation and temperature were set as random variables. In this model, we did not use data from the MalAvi database, but only our dataset described above since it provides more information regarding the localities, such as prevalence data and host richness. We ran three models: one for all three parasite genera combined, one for *Plasmodium* lineages only, and one for *Haemoproteus* lineages only.

In the second model, we analysed the prevalence of infection in each bird species among localities. For this, we considered local prevalence in each bird species as our dependent variable and local percentage of migratory bird individuals as our independent variable. Parasite richness, number of migrants and percentage of migrant species were employed as fixed variables. Further, we used biome, locality, number of birds per species and mean precipitation and temperature as random variables. In this model, we filtered our data in order to include only species with 10 or more bird individuals analysed. For this second model we again used only our dataset described above and excluded data from the MalAvi database, since the latter presents only positive and sequenced samples. Again, we ran three models: one for all three parasite genera combined, one for *Plasmodium* lineages only, and one for *Haemoproteus* lineages only.

3. Results

Our Bayesian model analyses revealed the lineages shared by resident and migratory species are the most widespread spatially, as they are found in a higher percentage of localities (Figure 2, Table 1). When considering all haemosporidian genera together, we observed that the lineages shared by all three categories (resident, partial migrant and full migrant) are the most widespread, followed by those shared between residents and either type of migratory species. Nevertheless, despite the fact lineages shared by migratory species and residents are more widely distributed, lineages present in only residents, migratory or partially migratory species presented similar spatial distribution in our model. We also observed that host richness had the highest weight in parasite dispersal, followed by the number of birds infected and then host status (0.807, 0.102, 0.091).

When repeating these analyses separately for the two main parasite genera, we observed differences in the pattern of distribution between *Plasmodium* and *Haemoproteus*. For *Plasmodium* parasites, we observed a much greater spatial distribution of lineages shared by all three host categories, followed by the lineages shared by migrant or partial migrant and residents (Figure 3, Table 2). *Plasmodium* spp. lineages occurring in the three bird categories were present in 12.6% (SE = ±1.2%) of localities, a much higher value than for other lineages. However, for *Haemoproteus* lineages, we observed greater spatial distribution of lineages shared only by migrant or partial migrant and resident birds. The lineages shared by all three bird categories and those occurring in only one bird category had similar distributions among localities (Figure 4, Table 3).

Our first null model revealed that there is positive correlation between the percentage of migratory bird individuals per locality and local parasite richness (p = 0.002, Figure 5, Table 4). We also observed positive effect of the percentage of migratory bird individuals on parasite richness for *Plasmodium*, but not for *Haemoproteus* infections were treated separately (p = 0.004, p = 0.15, respectively; Figure S1 and S2, Table S1 and S2). Nevertheless, in all models we observed significant effects on parasite richness for the other two predictors: host richness and prevalence.

For the second model, in which we analysed the relationship between local prevalence per bird species and local percentage of migratory bird individuals, we observed a positive correlation between the relative occurrence of migrants and prevalence of haemosporidian parasites per species (p = 0.03, Figure 6, Table 5). However, when we repeated the analysis separately for only *Plasmodium* or *Haemoproteus* lineages, we observed no relation between percent of migrants and prevalence per host species (p = 0.26, p = 0.65, Figure S3 and S4, Table S3 and S4). Temperature had no significant effect on prevalence per bird species, whether when considering all haemosporidian lineages (Table 5), or only *Plasmodium* or *Haemoproteus* lineages (Tables S3 and S4).

**4. Discussion**

Animal migrations can play important roles in both the geographical dispersal of disease agents, and in the local epidemiology of diseases for both resident and migratory species (refs). Here, we demonstrated that bird migratory behavior can disperse parasite lineages through their migratory routes, such that lineages infecting migrants are spread to more localities. Despite migration leading to lineages dispersal in South America, we did not observe higher parasite richness nor higher prevalence of infection in localities with higher proportions of migratory birds. Indeed, haemosporidian prevalence decreased as the proportion of migratory individuals rose across localities. Nevertheless, parasite richness per locality was positively related to local host species richness, prevalence and number of migrant individuals, which may indicate a positive relationship between the absolute number of migratory birds per region and local parasite richness. Thus, migrant birds play an important role in the ecology and evolution of haemosporidian dispersal in South America.

Further, when analyzing lineages of the genera *Plasmodium* and *Haemoproteus* separately, we observed that lineages present in resident, partial and full migrants display different distributional patterns. While *Plasmodium* lineages showed a much wider distribution than other lineages, we observed a spread rate similar to the one observed in resident birds for *Haemoproteus* parasites. It is known some *Plasmodium* parasites are highly generalist and able to infect a broad range of bird and vector hosts. For instance, *Plasmodium relictum* is able to infect at least 26 different species of Culicidae vectors and birds from many different orders (Valkiūnas 2005). The degree to which a parasite can shift between hosts certainly facilitates the putative dispersal of these organisms into new regions. Meanwhile, *Haemoproteus* spp. are, in general, more specialist parasites (Valkiūnas 2005, Okanga et al. 2014, Fecchio et al. 2020) which may reduce their ability to successfully establish in new regions with different ranges of vectors and bird species. In addition, despite the fact lineages shared by resident and migratory species presented the highest frequency of occurrence among localities, parasites infecting only full or partial migrant birds were present in a similar proportion of localities as those infecting only resident avian hosts. We believe insufficient sampling of certain migrant avian species in many areas could lead to the low percentage of localities in which lineages infecting only partial and full migrant birds were found, since lineages infecting only migrant hosts may be specialist parasites. Besides, no single migrant species passes through all localities, reducing their likelihood of sampling parasite lineages from all areas.

Dispersal of haemoporidians might be an important step toward parasite diversification for local community composition since parasites, after establishing in new regions, can evolve into new separate parasite lineages (Ellis et al. 2019, Fecchio et al. 2019). Indeed, Ellis et al. 2019 demonstrated that South America presents the greatest proportion of sympatric nodes for *Plasmodium* spp. and one of the greatest *Haemoproteus* diversification rates, indicating high rates of parasite diversification in this region. Hence, considering the contribution of migrant birds toward parasite dispersal, these hosts might play a fundamental role in parasite evolution and diversification in South America. Indeed, many species migrate during the breeding season and relapses mainly occurs after this period (Valkiūnas 2005), thus facilitating parasite dispersal to new regions. However, we did not observe a clear relation between the presence of migrant birds and haemosporidian richness since our data suggests only the absolute number of migrants per locality, but not the proportion of migrant species and individuals, influences parasite richness. Indeed, the fact that most of our lineages were observed only in resident birds could explain the weak relationship between avian migrants and haemosporidian richness, since the greatest haemosporidian diversity occurs in resident avian species. In addition, Hellgren et al. 2007 also suggest that new haemosporidian introductions into resident bird faunas are not common evolutionary events. Moreover, we observed that other factors such as host richness and overall local prevalence also influence parasite richness. Therefore, it seems environmental and host features could be more important to determine parasite richness than dispersal patterns.

We also demonstrated that where the percentage of migrant birds in a community is high, local haemosporidian prevalence is low, indicating the presence of migrant birds can decrease parasite prevalence in bird communities. In fact, migration often allows species to escape environments with higher risks of infection, decreases infection levels, and could favor the evolution of less-virulent pathogens (Altizer et al. 2011). These facts could lead to reduced haemosporidian prevalence in localities with higher proportions of migrant birds since long-distance migratory behavior can remove infected individuals from bird communities as diseased animals are less likely to successfully migrate because of the physiological requirements of migration and the energetic costs of disease (Bradley and Altizer 2005, Altizer et al. 2011). However, Hahn et al. 2018 experimentally verified that low intensity haemosporidian infections do not affect the capacity of birds to migrate, thus, most infected birds could still migrate and potentially spread their parasites into new areas. Meanwhile, the fact that migration filters highly and moderately infected birds, which are the most likely to infect new vectors (Pigeault et al. 2015), allows community prevalence to remain low. Certainly, further research will be required to confirm the importance of migration behavior in mitigating haemosporidian community prevalence.

Thus, despite the fact previous research has suggested a modest influence of bird migration on parasite dispersal between Europe and Africa (Hellgren et al. 2007) or North America and the Caribbean (Soares et al. 2019), we demonstrated that South American migrants can play an important role in parasite dispersal and, consequently, in their evolution and diversity. Nevertheless, as observed by Ricklefs et al. 2017, most lineages are not shared between resident and migrant species, indeed, most of our parasite lineages were observed only in resident birds, demonstrating that resident host species harbour the greatest parasite richness in our study system. We also demonstrated that, despite the fact migrants can carry haemosporidians to new localities, migration of itself may not affect parasite richness. In addition, migrants appear to possess a certain “protector effect” for bird communities in our study system, as their presence seems to be related to lower community-wide prevalence of infection. By comparing the distribution of different pathogen lineages, our analyses demonstrate that migrants carry haemosporidians and possibly other pathogens throughout their migration routes, thereby contributing to the spread of disease on a continental scale.

**Funding**

D. de Angeli Dutra and A. Filion were supported by doctoral scholarships from the University of Otago. During the project, Alan Fecchio was supported by a postdoctoral fellowship (PNPD scholarship) from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES).

**Acknowledgments**

We thank the MalAvi curators for maintaining the database and for making all data available, as well as all researchers who shared their data. We are also grateful to all funding agencies that made this research possible.

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