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Bird species with wider geographical ranges have higher blood parasite diversity but not prevalence across the African-Eurasian flyway

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ABSTRACT

Avian blood parasites, from the genera *Plasmodium, Haemoproteus* and *Leucocytozoon*, are predicted to alter their range and prevalence as global temperatures change, and host and vector ranges shift. Understanding large-scale patterns in the prevalence and diversity of avian malaria and malaria-like parasites is important due to an incomplete understanding of their effects in the wild, where studies suggest even light parasitaemia can potentially cause rapid mortality, especially in naïve populations. We conducted phylogenetically controlled analyses to test for differences in prevalence and lineage diversity of haemoparasite infection (for *Plasmodium*, *Haemoproteus* and *Leucocytozoon*) in and between resident and migratory species along the African-Eurasian flyway. To test whether migratory strategy or range size drives differences in parasite prevalence and diversity between resident and migrant species, we included three categories of resident species: Eurasian only (n = 36 species), African only (n = 41), and species resident on both continents (n = 17), alongside intercontinental migrants (n = 64), using a subset of data from the MalAvi database comprising 27,861 individual birds. We found that species resident on both continents had a higher overall parasite diversity than all other categories. Eurasian residents had lower *Plasmodium* diversity than all other groups, and both migrants and species resident on both continents had higher *Haemoproteus* diversity than both African and Eurasian residents. *Leucocytozoon* diversity did not differ between groups. Prevalence patterns were less clear, with marked differences between genera. Both *Plasmodium* and *Leucocytozoon* prevalence was higher in species resident on both continents and African residents than in migrants and Eurasian residents. *Haemoproteus* prevalence was lower in Eurasian residents than species resident on both continents. Our findings contrast with previous findings in the North-South American flyway, where long-distance migrants had higher parasite diversity than residents and short-distance migrants, although we found contrasting patterns for parasite diversity to those seen for parasite prevalence. Crucially, our results suggest that geographic range may be more important than migratory strategy in driving parasite diversity within species along the African-Palaearctic flyway. Our findings differ between the three parasite genera included in our analysis, suggesting that vector ecology may be important in determining these large-scale patterns. Our results add to our understanding of global patterns in parasite diversity and abundance, and highlight the need to better understand the influence of vector ecology to understand the drivers of infection risk and predict responses to environmental change.

1. Introduction

Understanding the drivers of broad-scale patterns in parasite infection is vital in predicting alterations in geographical distribution due to global changes, or impacts on hosts through exposure to novel parasites (van Riper III et al., 1986; Goulson et al., 2015). Migratory species may be particularly important in this regard, because changing patterns of migration (Plummer et al., 2015) may either bring migratory species into contact with novel parasites (Morgan et al., 2007; Kubelka et al., 2022), or transfer parasites into novel areas (de Angeli Dutra et al., 2021b). Migratory species tend to host a more diverse range of parasites than their resident counterparts (Figuerola and Green, 2000; Koprivnikar and Leung, 2015; Jenkins et al., 2016; Shaw et al., 2018), although a recent global study found this pattern only for helminth species richness, not haemosporidian species richness (Gutiérrez et al., 2019). However, patterns for parasite prevalence are less consistent (Figuerola and Green, 2000), and

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can vary markedly between different parasite genera (Fecchio et al., 2021).

Migration is an energetically costly activity (Wikelski et al., 2003), and preparation for migration can cause a decreased investment in non-flight-related functions such as the immune system (Owen and Moore, 2006, 2008). Any effects of infection on migratory birds are mixed: Garvin et al. (2006), found negative associations between blood parasite infection and fat scores or body condition in only four of 54 bird species examined. Similarly, Cornelius et al. (2014) found little evidence that haemosporidian infection negatively affects three species of migratory songbirds, finding elevated leucocyte counts in one species, but with no significant effects on cellular immunity, body condition or fat reserves (Cornelius et al., 2014). Other earlier findings suggest that infection does not generally impact preparation for migration or migratory schedules (Santiago-Alarcon et al., 2013; Hahn et al., 2018). However, more recent studies found that juvenile birds infected by certain parasite lineages arrived later on breeding grounds (Ágh et al., 2022), and that birds with higher blood parasite infection intensities delayed the onset of autumn migration (Emmenegger et al., 2021).

Many migratory birds move intercontinentally, likely encountering a wider variety of parasites than resident species on breeding, wintering and stopover grounds, potentially leading to a higher parasite diversity (de Angeli Dutra et al., 2021a). Infection by blood parasites can increase stopover time in migrants (Hegemann et al., 2018), which may potentially increase the likelihood of gaining further infections at stopover sites, although stopover can also allow birds to increase immune function (Eikenaar et al., 2020). Migratory birds may act as reservoirs of blood parasites and introduce them to resident species (Hellgren et al., 2007; Yoshimura et al., 2014; Pulgarín-R et al., 2019). However, parasite lineages have varying levels of host specificity, which may limit the role of migrants in their dispersal (Pulgarín-R et al., 2019; Soares et al., 2020). Indeed, any lineage sharing may strongly depend on the relatedness of migrant and resident species (Clark et al., 2016; Ricklefs et al., 2017). Whilst intercontinental migrants range seasonally over a wide geographic area, many resident species have been introduced beyond their native range, so will be exposed to a wide diversity of locally transmitted parasites across the entirety of their native and introduced range (Clark et al., 2015; Marzal et al., 2018). These species provide an ideal opportunity to test whether it is migratory strategy, or geographic range, that drives patterns of parasite diversity and prevalence at the continental scale.

Haemosporidian genera tend to differ in their degrees of host specialism, and consequently in their abilities to be transmitted between different host species (Hellgren et al., 2009). Within avian blood parasites, *Plasmodium* lineages tend to be more generalist, with *Haemoproteus* and *Leucocytozoon* more specialist (Gupta et al., 2019; Ellis et al., 2020), although there is significant inter-lineage variation within each genus (Moens et al., 2016; Ellis et al., 2020). Each parasite genus has distinct vectors, which may also influence patterns of host distribution, either through vector distribution, vector competence, or vector biting preferences (Valkiūnas, 2005).

Here, we expand on previous studies testing the drivers of large-scale patterns in blood parasite prevalence and diversity (de Angeli Dutra et al., 2021a), testing for the consistency of patterns between the Americas and those found in African-Palaearctic migrants by examining the prevalence and lineage diversity of *Plasmodium, Haemoproteus and Leucocytozoon* in African-Palaearctic migrants and resident birds. Compared with species found in the Americas, African-Palaearctic migrants tend to have longer migration distances, and migrants and African resident species tend to be more phylogenetically distinct than American species found together on wintering grounds (Ricklefs et al., 2017). The African-Palaearctic dataset also includes species resident across similar geographical ranges to migrant species, allowing us to directly test whether migratory strategy, or range size, might drive any observed differences. We tested two opposing hypotheses: i) migratory birds would have a higher parasite diversity and lineage richness than all three groups of resident species due to a combination of their exposure to infection on breeding, wintering and staging grounds; and ii) species resident on both continents would have similar parasite prevalence and diversity to migratory birds, and both would have higher prevalence and diversity than species resident in either Africa or Europe, due to similar overall geographic range. Furthermore, we predicted that these patterns may differ between parasite genera due to differing vector distributions.

2. Materials and methods

2.1. Data collection

Data were obtained from the 'Hosts and Sites Table' from the publicly accessible MalAvi database (Bensch et al., 2009). At the time of data extraction (26 September, 2019), MalAvi contained 373 studies on *Plasmodium*, *Haemoproteus* or *Leucocytozoon* parasites, providing an initial 11,125 host-parasite lineage combinations. Each combination provided information on parasite lineage, host species, host status (migratory or resident), host age (juvenile, adult or unknown), host environment (wild or captivity), location (from continent down to coordinates), number of hosts found to be infected, and number of individuals tested. Countries from which data were available and included are shown in Fig. 1.

2.2. Inclusion/exclusion criteria

We focused on birds found anywhere in the African-Eurasian flyway, removing any hosts found outside this region, and categorising hosts into one of four groups: 1) long-distance African-Palaearctic migrant (migratory); 2) resident in Africa only (African residents); 3) resident in Europe only (Eurasian residents) or 4) naturally resident in Africa and Eurasia (resident in both). The African-Eurasian flyway is defined by the African-Eurasian Migratory Landbirds Action Plan (AEMLAP) as containing "Africa, Europe (including all of the Russian Federation and excluding Greenland), the Middle East, Central Asia, Afghanistan, and the Indian subcontinent" (African-Eurasian Migratory Landbirds Working Group, 2014). From a total of 852 migratory species, 252 were identified in the MalAvi database using the species lists from the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA), the Convention on Migratory Species (CMS) Memorandum of Understanding on the Conservation of Migratory Birds of Prey in Africa and Eurasia (Raptors MOU) and AEMLAP (Raptor MOU, 2008; African-Eurasian Migratory Landbirds Working Group, 2014; Anon, 2018). Species resident in Africa and/or Eurasia (as previously defined) were identified using information from the International Union for Conservation of Nature Red List (IUCN, 2018). From 2,662 African residents, 271 were present in the MalAvi database, as were 239 out of 3,941 Eurasian residents. Species resident on both continents were recorded as a separate group unless studies were only conducted on one continent, in which case they were recorded as resident on that continent; intracontinental migrants were classified as resident on their respective continent for the purposes of these analyses.

To reduce biases associated with analyses of parasite diversity data from small host sample sizes, we removed any data points where fewer than 10 individual hosts (in total, across studies) were

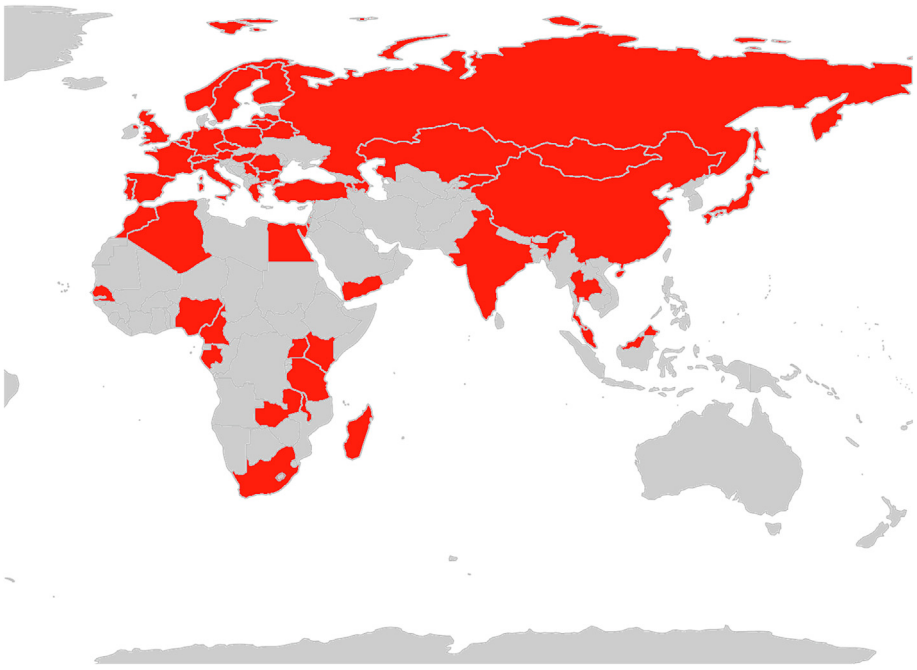

Fig. 1. Countries from which data were available and included within the analyses are shaded. Map created using the rworldmap package (South, 2011) in R.

screened for infection. For the analysis of parasite diversity, we then totalled the number of different lineages from each parasite genus found in each host species; for prevalence we totalled the number of infected and number of tested individuals of each species for each lineage across studies, dividing the total number of infected by the total number of tested individuals to calculate prevalence. To account for variation in sample size biasing estimates of parasite richness (i.e. fewer of the lineages present within a species being detected with smaller sample sizes), we conducted a bootstrap correction for our diversity data (Poulin, 1998; de Angeli Dutra et al., 2021a). Where data were not clear in MalAvi, or we identified inconsistencies in the database in the number of hosts sampled within a study between parasite genera, we referred to the sample sizes in the original publication to avoid double counting of individuals. Where we could not confirm the total host sample size tested from the original publication, we removed these data from our analysis.

Blood parasites that infect multiple host species tend to infect phylogenetically related subsets of available hosts (Fecchio et al., 2019), and host phylogeny also explains substantial variation in infection status across avian families (Barrow et al., 2019). Therefore, to control for any influence of phylogenetic relationships between host species on parasite prevalence and diversity, we downloaded phylogeny subsets from BirdTree (Jetz et al., 2012) to include in our phylogenetically controlled analyses. Where species were not available on BirdTree, we initially searched for synonyms and included these where available; those species not available under any synonym (n = 10; see Supplementary Data S1) were removed from our analysis. A phylogeny subset of 1000 trees was extracted from BirdTree using the option "Ericson All Species: a set of 10,000 trees with 9993 OTUs (operational taxonomic units) each" (Jetz et al., 2012). These were condensed into a single consensus tree for inclusion in the model using the '*phylo*' command in the *ape* package (Paradis and Schliep, 2018) in R v. 3.6.1. (R Core Team, 2021).

Our final host species totals for both parasite prevalence and parasite diversity analyses were 41 African residents, 36 Eurasian residents, 64 intercontinental migrants and 17 species resident on both continents, from 83 published papers. For the examination of parasite diversity, our datasets consisted of 27,861 birds sampled for *Plasmodium*, 22,907 for *Haemoproteus* and 13,080 for *Leucocytozoon*. For parasite prevalence, datasets consisted of 27,861 birds sampled for *Plasmodium*, 22,848 for *Haemoproteus* and 13,092 for *Leucocytozoon*.

2.3. Statistical analyses

Phylogenetically controlled analyses were conducted in R version 4.0.5 "Shake and Throw" for Mac (R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/) using the package *MCMCglmm* (Hadfield, 2010). We constructed two separate sets of models, examining parasite diversity (then repeating this analysis for bootstrap-corrected parasite diversity values) and parasite prevalence respectively, to test for differences between our four host groups while controlling for host phylogeny and sample size. Within each model set, we examined data for each parasite genus (*Plasmodium*, *Haemoproteus* and *Leucocytozoon*) separately; for parasite diversity, we also tested for differences within our overall dataset with all three genera combined. Due to the structure of the available data, which did not allow for the quantification of individuals infected by more than one genus simultaneously, we did not test for differences in overall parasite prevalence.

Models were fitted using Bayesian phylogenetic mixed models, which account for non-independence among closely related species by using a Markov chain Monte Carlo (MCMC) estimation approach (see Section 2.4 for code availability). This included the consensus tree data from BirdTree as a random variable to control for phylogenetic relationships between host species. The prior distribution was defined using an R list (prior on the residual variance) and G list (random effects variance) with the parameters nu = 0.02 and V = 1, corresponding to an inverse-Gamma distribution.

For the first model set, we tested whether the migrant/resident category influenced the number of lineages found in each host species (diversity), using a Poisson model distribution and includ-

ing both phylogeny and the number of birds tested as random effects to control for interspecific relatedness and sample size, respectively. We then repeated these analyses using our bootstrapped estimates of lineage diversity to further account for sampling effort, using a log-transformed response variable and Gaussian model distribution. For the second model set, we tested whether the migrant/resident category influenced the prevalence of parasites within a species, accounting for the random effects of phylogeny as above, using a Binomial distribution. Here, we defined parasite prevalence at the species level as the number of individuals in the sample population (combining multiple studies, where appropriate) that tested positive for each parasite lineage found within that host species, controlling for sample size within our model by specifying the response variable as a two column variable containing the number of infected birds and the number of birds tested.

All models were run for 5,000,000 iterations with a burn-in phase of 1000 and a thinning interval of 500 (to avoid autocorrelation issues).

2.4. Data accessibility

All datasets and codes are available on Figshare. Diversity datasets, including raw data and bootstrap-corrected data, are available for overall parasite diversity (DOI: 10.6084/m9.figshare.23053472), *Plasmodium* (DOI: 10.6084/m9.figshare.23053475), *Haemoproteus* (DOI: 10.6084/m9.figshare.23053466) and *Leucocytozoon* (DOI: 10.6084/m9.figshare.23053463), with phylogenetic datasets for overall parasite diversity (DOI: 10.6084/m9.figshare.23051456) *Plasmodium* (DOI: 10.6084/m9.figshare.23051420) *Haemoproteus* (DOI: 10.6084/m9.figshare.23051432) and *Leucocytozoon* (DOI: 10.6084/m9.figshare.23051426) also provided. Prevalence datasets are available for *Plasmodium* (DOI: 10.6084/m9.figshare.23053394) *Haemoproteus* (DOI: 10.6084/m9.figshare.23053388) and *Leucocytozoon* (DOI: 10.6084/m9.figshare.23053397), with phylogenetic datasets for *Plasmodium* (DOI: 10.6084/m9.figshare.23053307) *Haemoproteus* (DOI: 10.6084/m9.figshare.23053304) and *Leucocytozoon* (DOI: 10.6084/m9.figshare.23053310) also provided.

Table 1
Summary results and full model outputs from phylogenetically-controlled mixed-effects models testing the effect of resident/migrant grouping on parasite diversity. Results are presented from the summary of the fixed effects, providing mean, upper and lower 95% confidence internals (CI), and effective sample size. Full model results include the significance of pairwise comparisons for analyses of parasite diversity.

Overall model	Mean	Lower CI	Upper CI	Effective sample size
All genera	0.212	0.033	0.414	9998
Plasmodium	0.048	0.002	0.150	9698
Haemoproteus	0.275	0.003	0.580	9564
Leucocytozoon	0.394	0.002	1.181	4896
All parasite genera	Estimate	Lower 95% CI	Upper 95% CI	*P*
Intercept	**1.937**	**1.244**	**2.658**	**<0.001**
A vs. E	−0.169	−0.583	0.290	0.443
A vs. I	0.143	−0.288	0.582	0.531
A vs. RB	**0.704**	**0.178**	**1.193**	**0.006**
E vs. I	0.310	−0.072	0.713	0.119
E vs. RB	**0.868**	**0.394**	**1.404**	**<0.001**
I vs. RB	**0.558**	**0.092**	**1.058**	**0.023**
Random: phylogeny	0.386	0.005	0.923	
Random: sample size	0.485	0.192	0.769	
Plasmodium				
Intercept	1.373	0.597	2.069	0.004
A vs. E	**0.820**	**0.294**	**1.317**	**0.002**
A vs. I	−0.225	−0.741	0.298	0.394
A vs. RB	−0.223	−0.787	0.351	0.440
E vs. I	**0.598**	**0.140**	**1.053**	**0.011**
E vs. RB	**−1.046**	**−1.651**	**−0.464**	**<0.001**
I vs. RB	−0.444	−1.009	0.137	0.126
Random: phylogeny	0.195	0.003	0.581	
Random: sample size	0.734	0.379	1.151	
Haemoproteus				
Intercept	0.758	−0.228	1.729	0.139
A vs. E	−0.256	−0.879	0.336	0.404
A vs. I	**0.891**	**0.284**	**1.461**	**0.003**
A vs. RB	**−1.154**	**−1.836**	**−0.470**	**<0.001**
E vs. I	**0.630**	**0.169**	**1.094**	**0.009**
E vs. RB	**−0.901**	**−1.483**	**−0.296**	**0.003**
I vs. RB	−0.271	−0.818	0.315	0.343
Random: phylogeny	0.862	0.103	1.973	
Random: sample size	0.175	0.002	0.448	
Leucocytozoon				
Intercept	0.767	−1.242	2.465	0.379
A vs. E	*0.740*	*−0.108*	*1.581*	*0.077*
A vs. I	−0.722	−1.647	0.123	0.103
A vs. RB	0.022	−1.042	1.086	0.959
E vs. I	0.025	−0.640	0.733	0.939
E vs. RB	*−0.731*	*−1.569*	*0.103*	*0.072*
I vs. RB	−0.704	−1.620	0.279	0.127
Random: phylogeny	3.154	0.002	8.040	
Random: sample size	0.460	0.002	1.185	

A, African residents; E, Eurasian residents; I, intercontinental migrants; RB resident in both; Significant pairwise comparisons ($P < 0.05$) are highlighted in bold; marginally different comparisons ($0.05 < P < 0.1$) are in italic font.

Analysis code is available in R code format (DOI: 10.6084/m9.figshare.23053487) and text format (DOI: 10.6084/m9.figshare.23053520).

3. Results

3.1. Parasite diversity is highest in species resident on both continents

When controlling for both host phylogeny and sample size, species resident on both continents had a higher overall parasite diversity than all other groups (Table 1; Fig. 2A; mean ± 1 S.E. parasite lineages: species resident on both continents: 16.18 ± 3.74; African residents: 5.29 ± 0.72; Eurasian residents: 6.83 ± 1.39; intercontinental migrants: 9.41 ± 1.36). This pattern was consistent between raw diversity data and bootstrap estimates of diversity (Table 2; Supplementary Fig. S1); values for mean ± S.E. are presented from the raw data throughout.

Patterns in parasite diversity differed between the three parasite genera, but all statistically significant differences were consistent between raw diversity data (Table 1) and bootstrap estimates of parasite diversity (Table 2). Eurasian residents had a lower *Plasmodium* lineage diversity than all other groups (Eurasian residents: 2.05 ± 0.45; African residents: 3.22 ± 0.39; intercontinental migrants: 4.69 ± 0.82; species resident on both continents: 5.44 ± 1.37), with no difference between African residents, migrants or those resident on both continents (Fig. 2B). *Haemoproteus* diversity was higher in both species resident on both continents and intercontinental migrants (species resident on both continents: 5.87 ± 1.33; intercontinental migrants: 3.92 ± 0.60) than either African or Eurasian residents (Fig. 2C; African residents: 1.50 ± 0.27; Eurasian residents: 2.18 ± 0.44). *Leucocytozoon* diversity did not differ between groups (Fig. 2D).

3.2. Patterns of parasite prevalence differ between genera

The three parasite genera all showed statistically significant, but different, patterns between host groups when controlling for host phylogeny. *Plasmodium* prevalence was lowest in intercontinental migrants and Eurasian residents (Fig. 3A; Table 3; intercontinental migrants: 0.14 ± 0.02; Eurasian residents: 0.16 ± 0.03). Prevalence in African residents was higher than in Eurasian residents, but only marginally higher than intercontinental migrants (Fig. 3A; Table 3; African residents: 0.27 ± 0.03). Species resident on both continents had higher *Plasmodium* prevalence than both Eurasian residents and intercontinental migrants (Fig. 3A; species resident on both continents: 0.35 ± 0.06).

Eurasian residents had lower *Haemoproteus* prevalence than species resident on both continents (Eurasian residents: 0.15 ± 0.04; species resident on both continents: 0.31 ± 0.08); neither group differed in *Haemoproteus* prevalence from African residents or intercontinental migrants (Table 3; Fig. 3B; African residents: 0.13 ± 0.04; intercontinental migrants: 0.21 ± 0.03).

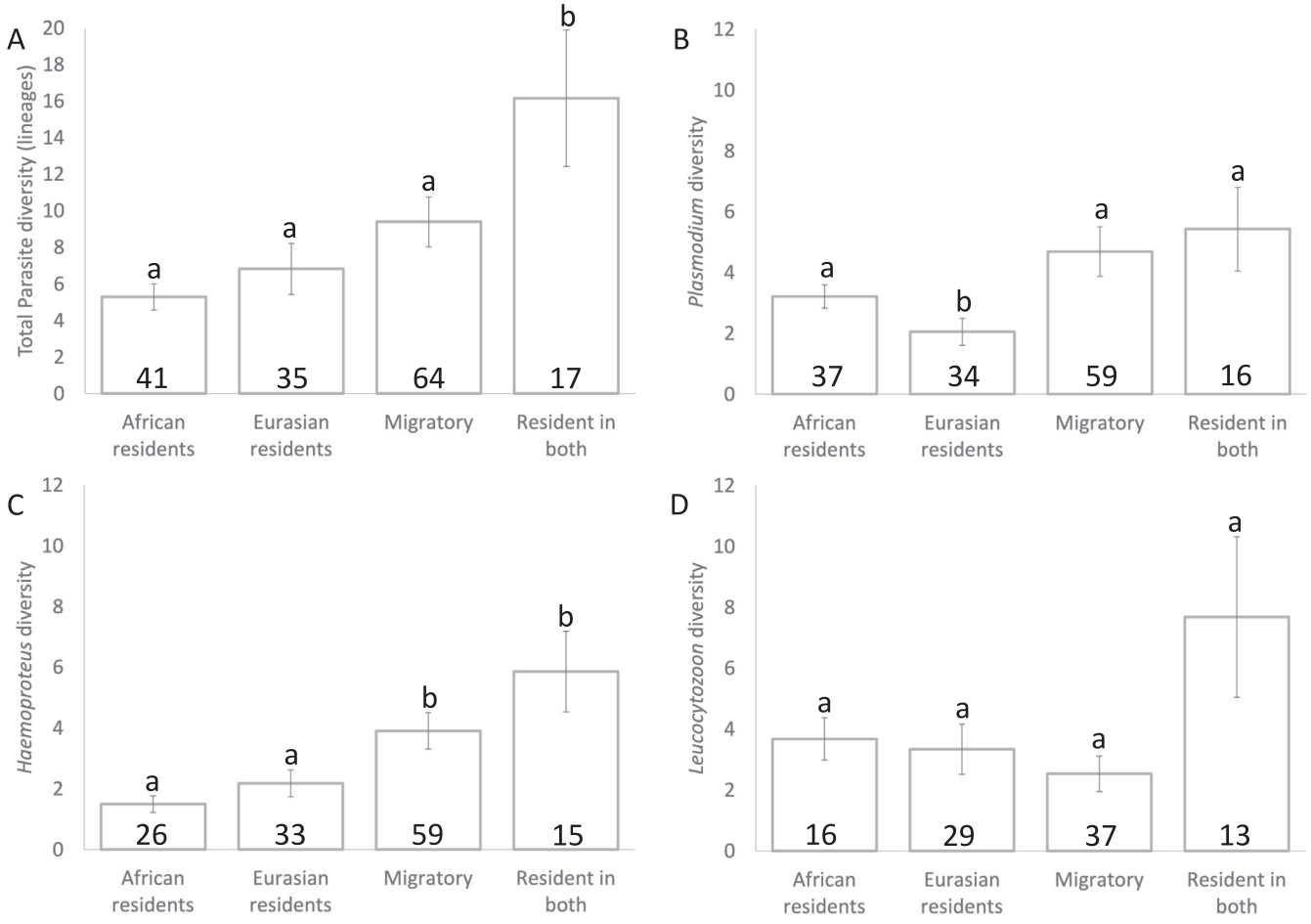

Fig. 2. Mean numbers of (A) total parasite lineages in all genera (*Haemoproteus*, *Leucocytozoon* and *Plasmodium*) combined by host group; (B) *Plasmodium* parasite lineages by group; (C) *Haemoproteus* parasite lineages by host group; (D) mean number of *Leucocytozoon* parasite lineages by host group. Different letters indicate significant differences in mean lineages as indicated by phylogenetically controlled mixed models ($P < 0.05$).

Table 2
Summary results and full model outputs from phylogenetically-controlled mixed-effects models testing the effect of resident/migrant grouping on bootstrap-corrected estimates of parasite diversity. Results are presented from the summary of the fixed effects, providing mean, upper and lower 95% confidence internals (CI), and effective sample size. Full model results include the significance of pairwise comparisons for analyses of bootstrap-corrected estimates of parasite diversity.

Overall model	Mean	Lower CI	Upper CI	Effective sample size
All genera	0.346	0.222	0.492	9998
Plasmodium	0.164	0.094	0.246	9998
Haemoproteus	0.269	0.165	0.380	9131
Leucocytozoon	0.210	0.059	0.381	9998
All parasite genera	Estimate	Lower 95% CI	Upper 95% CI	*P*
Intercept	**2.050**	**1.505**	**2.568**	**<0.001**
A vs. E	−0.067	−0.410	0.304	0.699
A vs. I	0.127	−0.230	0.468	0.486
A vs. RB	**0.704**	**0.257**	**1.136**	**0.002**
E vs. I	0.196	−0.121	0.522	0.230
E vs. RB	**0.770**	**0.325**	**1.216**	**0.002**
I vs. RB	**0.574**	**0.164**	**1.016**	**0.008**
Random: phylogeny	0.198	0.002	0.523	
Random: sample size	0.322	0.103	0.545	
Plasmodium				
Intercept	**1.617**	**1.205**	**1.989**	**<0.001**
A vs. E	**−0.341**	**−0.611**	**−0.059**	**0.020**
A vs. I	−0.030	−0.324	0.280	0.813
A vs. RB	0.283	−0.086	0.637	0.127
E vs. I	**0.312**	**0.066**	**0.560**	**0.012**
E vs. RB	**0.622**	**0.264**	**0.971**	**<0.001**
I vs. RB	*0.310*	*−0.035*	*0.653*	*0.080*
Random: phylogeny	0.080	0.002	0.244	
Random: sample size	0.364	0.174	0.564	
Haemoproteus				
Intercept	**1.096**	**0.572**	**1.664**	**<0.001**
A vs. E	0.152	−0.167	0.479	0.359
A vs. I	**0.431**	**0.098**	**0.751**	**0.010**
A vs. RB	**0.699**	**0.286**	**1.101**	**<0.001**
E vs. I	**0.282**	**0.031**	**0.553**	**0.033**
E vs. RB	**0.550**	**0.187**	**0.923**	**0.003**
I vs. RB	0.264	−0.089	0.617	0.143
Random: phylogeny	0.215	0.010	0.565	
Random: sample size	0.061	0.002	0.162	
Leucocytozoon				
Intercept	**1.778**	**0.745**	**2.866**	**0.005**
A vs. E	*−0.391*	*−0.804*	*0.028*	*0.067*
A vs. I	*−0.378*	*−0.815*	*0.081*	*0.098*
A vs. RB	0.010	−0.549	0.601	0.974
E vs. I	0.017	−0.303	0.356	0.912
E vs. RB	*0.404*	*−0.016*	*0.851*	*0.064*
I vs. RB	0.392	−0.098	0.875	0.111
Random: phylogeny	1.01	0.007	2.229	
Random: sample size	0.131	0.003	0.309	

A, African residents; E, Eurasian residents; I, intercontinental migrant; RB, resident in both. Significant pairwise comparisons ($P < 0.05$) are highlighted in bold; marginally different comparisons ($0.05 < P < 0.1$) are italicised.

Leucocytozoon prevalence was higher in African residents and species resident on both continents (African residents: 0.39 ± 0.08; species resident on both continents: 0.30 ± 0.06) than in Eurasian residents and intercontinental migrants (Table 3; Fig. 3C; Eurasian residents: 0.19 ± 0.05; intercontinental migrants: 0.12 ± 0.04).

4. Discussion

Overall, we found no evidence to support our first hypothesis, that migratory species would have a higher parasite diversity and prevalence than all resident species. Instead, although patterns differ between parasite genera, our results provide partial support for our second hypothesis, suggesting that species resident on both continents have a higher parasite diversity – but not prevalence – than all other groups. This suggests that it may be geographic range, rather than migratory strategy, that drives patterns in parasite distribution in African-Palaearctic species.

Haemosporidian diversity was higher in species resident on both continents than in any other group, with no difference between migrants and either African or Eurasian residents. This contrasts with previous findings in the Americas, where fully migrant species (but not partial migrants) had higher parasite diversity than residents (de Angeli Dutra et al., 2021a). Whilst we do not distinguish between partial or intra-continental migrants and resident species in our analyses, this would be worth testing on the African-Palaearctic flyway as more data become available. However, in our study, species resident on both continents had a higher parasite diversity than species resident on only one continent. This suggests that instead of migratory strategy leading to increased parasite diversity (de Angeli Dutra et al., 2021a), a larger geographic range may increase parasite diversity. This contrasts to the findings of Gutiérrez et al. (2019), where no relationship was found between haemosporidian species richness and either range size or migration distance (Gutiérrez et al., 2019). Studies of avian gut parasites have suggested that migratory species have a greater species richness of nematode parasites (Koprivnikar and Leung, 2015; Gutiérrez et al., 2019), although a separate study found helminth species richness was linked more to the diversity of habitats used by hosts, rather than to migration distance (Gutiérrez et al., 2017). In avian haemosporidians, recent

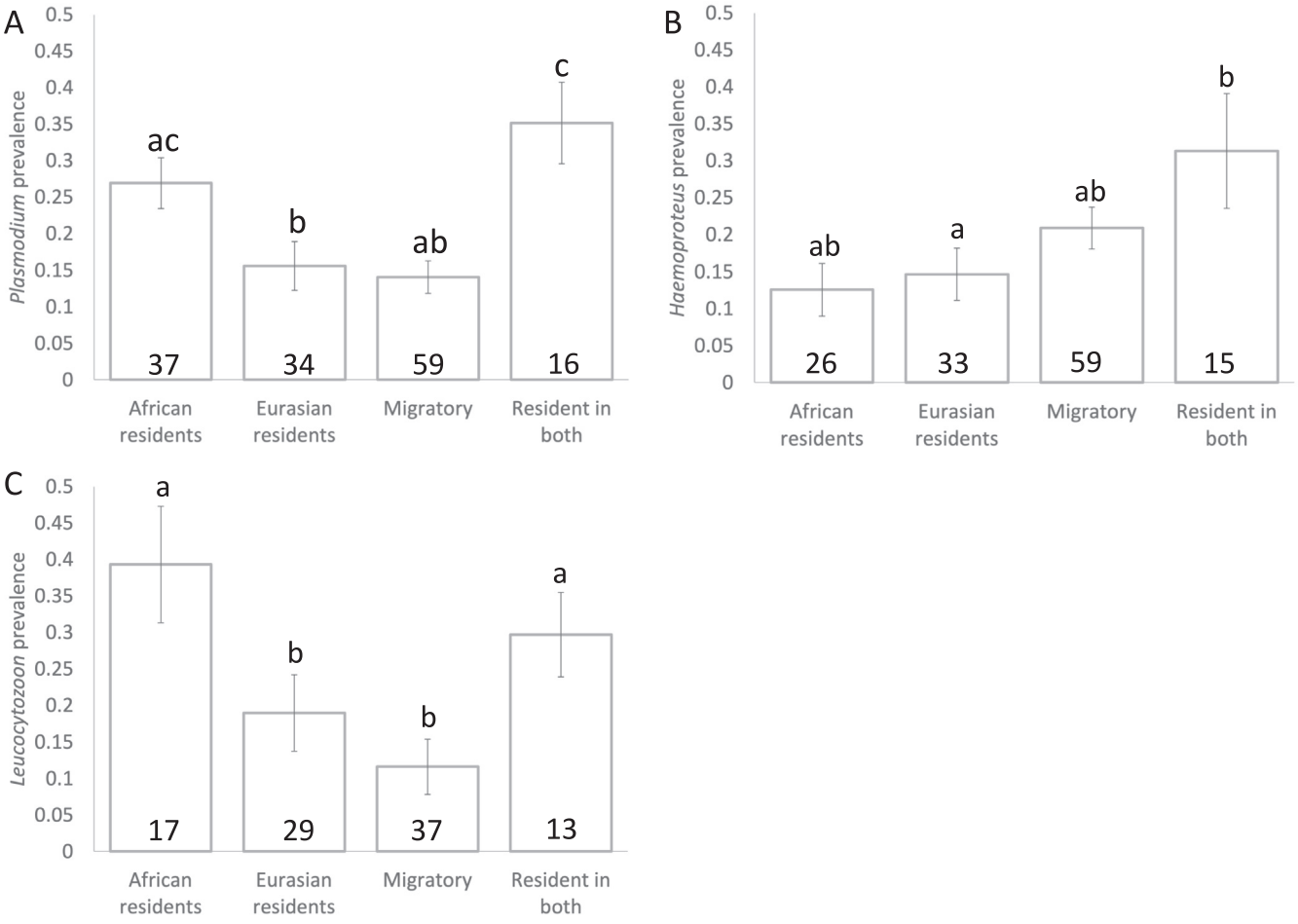

Fig. 3. Prevalence of parasite infection by (A) *Plasmodium*, (B) *Haemoproteus*, (C) *Leucocytozoon*. Letters above bars indicate significant differences; bars with the same letter do not differ from one another. Numbers in bars indicate sample sizes (host species).

evidence as to whether migratory species are facilitating the spread of blood parasites is conflicting: data from the Caribbean indicate that host switching between sympatric species at the overwintering grounds is rare, despite close phylogenetic relationships (Soares et al., 2020). Conversely, data from South America suggest that migrants have significant potential to transmit haemosporidians across their range (de Angeli Dutra et al., 2021b), which may be predicted by taxonomic similarity (Ricklefs et al., 2017).

The observed patterns in parasite diversity differed between the three parasite genera. *Plasmodium* diversity was lower in Eurasian residents than in all other groups. Whilst avian *Plasmodium* is widespread in temperate regions (Clark et al., 2014), this observation may be driven by a higher *Plasmodium* diversity in tropical African regions, despite lower sampling effort (Clark et al., 2014), being reflected in all groups bar Eurasian residents. This may be related to vector distribution, or the nature of parasite-vector relationships: *Plasmodium* is transmitted by mosquitoes (Culicidae), which reach their highest species richness near the equator (Foley et al., 2007). If parasite-vector relationships are specialist, as demonstrated in some European mosquito species (Gutiérrez-López et al., 2020), then a higher vector diversity may lead to a higher diversity of *Plasmodium* lineages in those avian groups whose range includes Africa.

Haemoproteus diversity was lower in both Eurasian and African residents than both other groups, suggesting a straightforward species-area relationship in this parasite genus (Poulin, 2014). Our data do not support the latitudinal gradient in *Haemoproteus* diversity within African-Palaearctic species suggested by Clark et al. (2014), but may instead represent a higher potential for sharing of *Haemoproteus* lineages in hosts occupying a large geographic range. Closely related hosts may be more likely to share *Haemoproteus* parasites (Ricklefs et al., 2004), so host species resident on both continents may be more likely to come into contact with numerous closely-related host species at various points across their range, which may lead them to harbour a greater diversity of parasites overall. It would be useful to test this in closely-related species with differing range sizes, controlling for total range size and sampling individuals from across the range. There are no consistent patterns in *Haemoproteus* vector (biting midge; Diptera: Ceratopogonidae) diversity or abundance that could currently be linked to predictions regarding parasite transmission: a comparison of biting midge diversity and abundance across three European countries found the highest diversity in Sweden, the highest species richness in the Netherlands, and the highest abundance in Italy (Möhlmann et al., 2018), although this study included all species, not just the ornithophilic species likely to be vectors of *Haemoproteus* parasites. More studies are needed on the ecology of biting midges, which may provide further insights into biogeographical patterns of *Haemoproteus* transmission.

In contrast to patterns for *Plasmodium* and *Haemoproteus*, *Leucocytozoon* diversity did not differ between host groups. Fewer studies tend to examine *Leucocytozoon* than *Haemoproteus* and *Plasmodium* (Clark et al., 2014), probably due to the nested PCR

Table 3
Summary results and full model outputs from phylogenetically-controlled mixed-effects models testing the effect of resident/migrant grouping on parasite prevalence. Results are presented from the summary of the fixed effects, providing mean, upper and lower 95% confidence internals (CI), and effective sample size. Full model results include the significance of pairwise comparisons for analyses of parasite prevalence.

Overall model	Mean	Lower CI	Upper CI	Effective sample size
Plasmodium	0.937	0.579	1.291	9176
Haemoproteus	1.580	0.948	2.256	9998
Leucocytozoon	3.232	1.471	5.157	5988
All parasite genera	Estimate	Lower 95% CI	Upper 95% CI	*P*
Intercept	−2.993	−3.772	−2.232	<0.001
A vs. E	**0.778**	**0.251**	**1.294**	**0.003**
A vs. I	*0.460*	*−0.052*	*1.000*	*0.084*
A vs. RB	0.297	−0.335	0.962	0.364
E vs. I	−0.319	−0.805	0.119	0.170
E vs. RB	**1.070**	**0.500**	**1.671**	**<0.001**
I vs. RB	**0.760**	**0.189**	**1.355**	**0.011**
Random: phylogeny	0.747	0.049	1.631	
Plasmodium				
Intercept	−2.775	−3.689	−2.006	<0.001
A vs. E	**−0.761**	**−1.367**	**−0.195**	**0.010**
A vs. I	0.486	−0.133	1.052	0.120
A vs. RB	0.345	−0.355	1.042	0.317
E vs. I	−0.278	−0.843	0.273	0.327
E vs. RB	**1.106**	**0.388**	**1.775**	**0.002**
I vs. RB	**0.827**	**0.141**	**1.537**	**0.020**
Random: phylogeny	0.743	0.004	2.043	
Haemoproteus				
Intercept	−2.761	−3.926	−1.649	<0.001
A vs. E	0.019	−0.834	0.866	0.972
A vs. I	−0.623	−1.460	0.210	0.143
A vs. RB	*0.952*	*−0.058*	*2.020*	*0.074*
E vs. I	*−0.604*	*−1.257*	*0.101*	*0.081*
E vs. RB	**0.931**	**−0.001**	**1.885**	**0.049**
I vs. RB	0.319	−0.542	1.205	0.481
Random: phylogeny	1.484	0.029	3.783	
Leucocytozoon				
Intercept	−4.061	−6.237	−1.939	0.001
A vs. E	**−1.741**	**−3.135**	**−0.346**	**0.012**
A vs. I	**2.392**	**1.025**	**2.798**	**0.002**
A vs. RB	−0.339	−2.023	1.419	0.703
E vs. I	0.643	−0.463	1.834	0.272
E vs. RB	**1.399**	**0.009**	**2.884**	**0.050**
I vs. RB	**2.044**	**0.467**	**2.592**	**0.008**
Random: phylogeny	4.396	0.003	13.100	

A, African residents; E, Eurasian resident; I, intercontinental migrants; RB, resident in both. Significant pairwise comparisons ($P < 0.05$) are highlighted in bold; marginally different comparisons ($0.05 < P < 0.1$) are in italic font.

protocols used to detect *Leucocytozoon* separately from *Plasmodium* and *Haemoproteus* (Hellgren et al., 2004; Waldenström et al., 2004), resulting in smaller sample sizes and a reduced power within our analysis to detect any trends.

The mean prevalence of *Plasmodium* lineages per host species was lowest in Eurasian residents and migratory species, intermediate in African species, and highest in species resident on both continents. Migrant species can be infected by lineages transmitted on both breeding and wintering grounds (Bensch et al., 2007), but they may miss the periods of peak transmission on both continents. *Plasmodium* prevalence on European breeding grounds tends to peak in October (Cosgrove et al., 2008), coinciding with the peak in mosquito vector abundance (Medlock and Vaux, 2015), by which time many migrant species have begun to migrate (Briedis et al., 2016). Migrant species then arrive on wintering grounds during the dry season, when transmission tends to be lower (Hernández-Lara et al., 2017), so may also escape the period of peak transmission on wintering grounds. Studies elsewhere have suggested that avian *Plasmodium* prevalence is more tightly linked with vector ecology than that of its vertebrate hosts (Ferraguti et al., 2018); indeed, *Plasmodium* parasites are more prevalent in the peripheral blood of infected birds when mosquitoes are active (Cornet et al., 2014). However, these patterns may also depend on local habitat conditions as well as specific lineage-vector and lineage-host associations (Gutiérrez-López et al., 2020). It would be informative to repeat our analyses on the subset of data for which exact location data, and thus environmental metrics such as precipitation and temperature, could be obtained.

Eurasian residents had lower *Haemoproteus* prevalence than species resident on both continents. *Haemoproteus* prevalence can also vary seasonally, although prevalence is generally higher during the breeding than the non-breeding season, as found in yellowhammers *Emberiza citrinella* (Dunn et al., 2014), and Aquatic warblers *Acrocephalus paludicola* (Neto et al., 2015). The pattern we observe is difficult to explain, although we were unable to control for seasonality in our analysis due to the difficulties of extracting sample-specific timing from the original literature, when sampling may occur over relatively long periods.

Our findings here concur with those of de Angeli Dutra et al. (2021a), who found no difference in prevalence between residents and migrants when examining *Plasmodium* and *Haemoproteus* separately (and had no equivalent category to species resident on both continents), and with Fecchio et al. (2021), who found varied associations between parasite prevalence and host ecological traits between haemosporidian genera. Unfortunately, the structure of data within the MalAvi database makes it difficult to examine overall infection prevalence by all three genera at the host level, so we restricted our analysis to individual genera, with the caveat that we may be overestimating prevalence if individuals are

co-infected by multiple common lineages of the same genus. Conversely, rare lineages are more likely to be detected in species groups where more sampling has taken place - in this case, migrant species. Since our data take the form of prevalence per lineage (rather than overall, per host), rare lineages may have strong influence in our prevalence analyses, although we control for sample size to some extent within our model structure.

Ultimately, the prevalence of haemosporidian parasites is assessed by the detection of parasite blood stages, and factors such as host immunity and seasonality may drive existing infections into remission. During periods of remission, parasites can only be found in host tissues and not in the bloodstream, reducing the apparent (detectable) parasite prevalence (Cosgrove et al., 2008). Parasite prevalence within the same population can also vary between years (Dunn et al., 2014), and ideally the inclusion of data from multiple years within the same host-parasite systems would be required to control for this variation, although these data are not currently separated into years within MalAvi (Bensch et al., 2009). Since MalAvi contains PCR data, and PCR may detect the presence of sporozoites in the blood (Valkiūnas et al., 2009), it is also possible we may be including non-patent infections or, indeed, contaminants (Bensch et al., 2021) in the dataset.

Leucocytozoon prevalence was higher in African residents and species resident on both continents than in Eurasian residents and intercontinental migrants. Previous studies in New World birds contrast in their findings, with some demonstrating that *Leucocytozoon* tends to show an inverse latitudinal gradient (Fecchio et al., 2020), and others finding no such relationship (Starkloff et al., 2020). The prevalence of *Leucocytozoon* infections may be linked to the abundance of their blackfly vectors, although remarkably little work has been conducted in this area (McCreadie and Adler, 2014; McCreadie et al., 2018).

Overall, we found no evidence for intercontinental migrant species having a higher parasite diversity and prevalence than all resident species. Instead, our results suggest that geographic range may be more important than migratory strategy in driving parasite diversity within species along the African-Palaearctic flyway, although our findings differ between the three parasite genera included in our analysis. The patterns in parasite prevalence are more difficult to explain, and may be confounded by variables not accounted for within our dataset such as genus-specific variation in vector abundance and ecology. However, our results highlight variation in patterns of broad-scale parasite distribution between the Old World and New World, suggesting that macroecological patterns should be examined at a global scale but that regional variation also needs to be taken into account.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijpara.2023.06.002.

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