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Migration and parasitism: habitat use, not migration distance, influences helminth species richness in Charadriiform birds

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ABSTRACT

Aim Habitat use and migration strategies of animals are often associated with spatial variation in parasite pressure, but how they relate to one another is not well understood. Here we use a large dataset on helminth species richness of Charadriiform birds to test whether higher habitat diversity and seasonal migration increase parasite richness in avian hosts.

Location Global.

Methods We compiled a global dataset on helminth species richness, habitat use strategies (marine/freshwater/mixed wintering and osmotic generalist/specialist) and various ecological/life-history traits (migration distance, geographic range size, diet, body mass, sampling latitude) of Charadriiform birds. To test if hosts with different habitat use strategies encounter different parasite pressures, we used comparative methods that correct for shared ancestry and phylogenetic uncertainty.

Results Habitat generalists (mixed wintering habitats and osmotic generalists) harboured more parasite species than habitat specialists; marine- and freshwater-restricted hosts had similar helminth species richness. Contrary to previous results, we found no association between parasite species richness and migration distance. Overall helminth species richness also increased with diet diversity, with no effects of other ecological/life-history traits.

Main conclusions We suggest that birds exploiting diverse habitats and diets are exposed to a more diverse parasite fauna and conclude that distribution patterns and habitat use, rather than migration distance, shape parasite diversity within host populations. Overall, these results demonstrate the significant role of habitat use in explaining how migration may indirectly affect parasite richness in host populations.

Key words birds, habitat use, life history, migration, parasite species richness

INTRODUCTION

Parasites have caused selection for a wide range of defence mechanisms in hosts, including the immune system (Schmid-Hempel, 2011) and behavioural traits that reduce the likelihood of infection and/or its negative effects (Gray *et al.*, 2012). Among them, migration and other movements (e.g., habitat shifts) of animals play a pivotal role in defence against parasites. For example, in monarch butterflies (*Danaus plexippus*) parasitized by the protozoan *Ophryocystis elektroscirrha* prevalence is lower among long-distance migratory populations relative to short-distance and non-migratory populations (Altizer *et al.*, 2011). Similarly, parasite prevalence correlates negatively with migration distance in galaxiid fishes (Poulin *et al.*, 2012). Migrations can lower parasite transmission by allowing hosts to escape parasites that accumulate in the environment (‘migratory escape’) or by removing affected individuals from the population (‘migratory culling’) (Altizer *et al.*, 2011).

On the other hand, migration increases parasite transmission in some animals. Notably, migratory bird species have higher nematode species richness compared to non-migratory species (Koprivnikar & Leung, 2015). Migration links habitats with differing physical and ecological characteristics, thus exposing hosts to a higher diversity of parasites (Møller & Erritzøe, 1998; Alerstam *et al.*, 2003). Furthermore, the physiological and energetic demands of long-distance migration can suppress the immune system and thus increase susceptibility to parasites (Weber & Stilianakis, 2007; Piersma, 2011, but see Hasselquist *et al.*, 2007). This idea is supported by the positive relationship between distance flown by migratory waterfowl and their parasite species richness (Gregory, 1990; Figuerola & Green, 2000) and the fact that the longest distance flights are performed by birds using parasite-poor environments (Piersma, 2011). Although studies of different taxonomic host groups have produced inconsistent results, possibly because they used different indices of parasite pressure (from prevalence of a single versus multiple parasite species to parasite species richness at the host species level), it seems clear that migration affects the transmission of parasites within and among host species (Altizer *et al.*, 2011).

Along this line, Piersma (1997) hypothesized that the evolution of migration patterns of shorebirds (Charadrii) may be driven by spatial variation in disease risk in different wintering and breeding habitats. This hypothesis has received empirical support from studies showing that arctic-breeding bird species wintering in saline habitats have lower presence and/or diversity of blood parasites than more southerly breeding species wintering in freshwater habitats (Figuerola, 1999; Mendes *et al.*, 2005; Yohannes *et al.*, 2009; Clark *et al.*, 2016). However, whether this pattern also applies to parasites other than blood microparasites (haematozoa) remains to be tested. Further, some avian hosts are able to switch seasonally between freshwater and saline habitats, while others are restricted to either saline or freshwater habitats (Gutiérrez, 2014). A combined use of freshwater and marine habitats should increase exposure to a greater diversity of parasites because parasite faunas typically differ in marine versus freshwater habitats (Zander & Reimer, 2002).

Although the role of habitat use in driving macroparasite infection patterns in birds has not been studied to date, there have been other comparative studies on macroparasite (helminth) species richness in birds (Bush *et al.*, 1990; Gregory, 1990; Gregory *et al.*, 1991, 1996; Morand & Poulin, 2000; Koprivnikar & Leung, 2015). From these and other comparative studies on vertebrate hosts, some general patterns have emerged. For example, hosts having a broader diet show higher parasite richness than more specialised hosts (Poulin & Morand, 2004; Thieltges *et al.*, 2013). Latitudinal trends in parasite species richness have been observed among mammalian hosts, with species that spend a greater amount of time at lower latitudes exhibiting increased parasite species richness (Lindenfors *et al.*, 2007). Further, parasite species richness is often positively correlated with host geographic range in a range of animal hosts, as larger geographic ranges might offer more opportunities for host-parasite associations to become established (Poulin & Morand, 2004; Kamiya *et al.*, 2014). Finally, host body size tends to be generally positively correlated with parasite species richness across major taxonomic groups (Kamiya *et al.*, 2014).

Here, we test whether higher habitat diversity and seasonal migration increase helminth parasite richness in avian hosts. We do so using an extensive dataset of helminths in Charadriiformes (sandpipers, plovers, gulls, auks and allies) which we compiled from the published literature. Charadriiform birds represent extensive variation in host ecology, with diverse feeding habits, habitat use and migration patterns. Importantly, Charadriiform birds show strong dichotomies in habitat use strategies: Some species are strictly marine or are confined to marine habitats outside the breeding period, while others are restricted to inland freshwater habitats all-year-round or in the non-breeding season, and, finally, some species use both habitats in winter (marine versus freshwater versus mixed wintering habitat use; Piersma 1997). Moreover, Charadriiform birds include species that switch seasonally between freshwater and saline habitats and others that are restricted to either saline or freshwater habitats (osmotic generalist versus osmotic specialist habitat use; Gutiérrez 2014). Knowing that the parasite fauna differs between marine and freshwater habitats, one would expect that birds that use both marine and freshwater habitats during wintering (mixed wintering habitat use) and birds that can make use of both habitats (osmotic generalists) should have the highest parasite richness. If habitat use is the mechanism determining parasite richness in migratory birds, its effect should be independent of the actual migration distance.

Hence, in our analysis we compared parasite richness among hosts with differing habitat use and migration strategies. We also investigated the effect of other ecological drivers and host life history traits known to affect parasite richness (latitude, geographic range, diet and body mass). By investigating the role of host habitat use in determining macroparasite richness patterns in birds with differing migration strategies, our analysis contributes to understanding the mechanisms of how migration affects parasite richness in hosts.

MATERIALS AND METHODS

Parasite species richness

We carried out a search across 'all years' (1945-2014) of the *Web of Knowledge* using combinations of the following terms or truncated variants thereof: Charadriiformes, seabird, shorebird, wader, sandpiper, plover, larid, gull, tern, skua, alcid, auk, metazoan parasite, helminth, digenean, trematode, cestode, nematode, and acanthocephalan. Additionally, we searched the bibliographies of the publications found for further references. Another major body of our dataset comes from our extensive search of publications in Russian, as many extensive surveys of the helminth fauna of Charadriiformes (and other taxa) were conducted in the former Soviet Union. We compiled all data on helminth species richness in Charadriiformes—overall and relative to each helminth group: trematodes, cestodes, nematodes and acanthocephalans—in a single dataset.

Parasite species richness was obtained for each host population as the number of parasite species occurring in the sample. Hosts were examined for helminths using standard procedures, i.e. each host was necropsied, and the organs were examined for helminths using a stereoscope. Parasites were morphologically identified using microscopy techniques. For some host-parasite records, parasites were identified only to the genus-level. We included these parasites in estimates of helminth species richness provided that no other members of the genus were recorded for the host population. To avoid potential problems arising from different sampling procedures, we only included data from studies that (*i*) involved animals freshly collected in the field; (*ii*) reported the actual number of birds examined to control for uneven sampling effort; (*iii*) examined five or more host individuals per population; (*iv*) examined for helminth parasites in all visceral organs; and (*v*) reported original collecting sites. Richness measures represent parasite richness at the host-population (study) level. The complete dataset included data on helminth species richness from 68 studies representing 106 host species and 11,056 individual hosts (see Appendix S1 in Supporting Information; a list of the data sources is found in Appendix 1).

We are aware of the potential influence of host age and sex on the structure of helminth communities (Rausch, 1983; Poulin, 1996), but most parasitological surveys did not provide sufficiently detailed information to account for these two factors. We then opted to include data irrespective of host age and sex. We believe that this approach is justified because (1) although prevalence of helminth infection tend to be higher in males in some host-parasite associations (Poulin, 1996), sex-related differences in helminth species richness are unlikely (Rausch, 1983; Bush, 1990); and (2) relevant studies in our comparative analysis (Bush, 1990; Roca *et al.*, 1999; Santoro *et al.*, 2011) found a lack of consistent and statistically significant sex- and age-differences in helminth parasite species richness.

Host ecology and life history

Bird species were grouped into two types of *habitat use strategies*: First, we classified each host species as 'marine', 'freshwater' or 'mixed' according to their main non-breeding habitat occupancy (Piersma, 1997; Gutiérrez *et al.*, 2012). As some species switch seasonally between freshwater and marine habitats and others are restricted to either saline or freshwater habitats throughout the year, we further classified each species as either 'osmotic generalists' or 'osmotic specialists' (Gutiérrez, 2014). Information on host habitat and diet use was obtained from the *Handbook of the Birds of the World* (del Hoyo *et al.*, 1996) and the *Handbook of the Birds of Europe and the Middle East and North Africa* (Cramp & Simmons, 1983). Each bird species was grouped into broad categories of *diet*: (1) invertebrates, (2) fish, (3) fish and invertebrates, and (4) omnivorous (feeding on more than two diet categories). We took the *geographic coordinates* of sampling locations from the original papers. When several geographic locations were given for a sample examined as a whole, we used midpoint coordinates of the sites where the birds were collected. Birds were collected at geographical locations ranging from 46ºS to 78ºN (Fig. 1); no distinction was made between northern and southern hemispheres (96% of the bird populations were collected in the northern hemisphere).

Species' migration distances were derived using information from *Bird Life International and NatureServe* (http://www.birdlife.org/datazone). This dataset comprises distribution polygons that represent moderately coarse generalizations of species' distributions. To calculate migration distance, only polygons coded as breeding or non-breeding ("Seasonality" codes 2 and 3) were included. Then, breeding and nonbreeding latitudes were measured as the latitudes of its breeding and nonbreeding range centroids and the migration distance was estimated as the distance between their centres. Migration distance ranged from 0 km in resident species (*N*=9) to ~14,400 km (*Sterna paradisaea*), averaging 5,383 km. It is important to note that some of the species in our dataset are made up of multiple subspecies or populations with noticeably different migration pathways. Because reliable data on migratory distance at the population level were not available for most species we used species-specific data. To reduce the effects of within-species variation in migration distance, we also sorted species into three broad categories along an ordinal scale: (1) resident over whole global range, (2) population partly resident, partly migratory, and (3) fully migratory. In addition, we used species' factsheets from the *Bird Life International* website to gather data on *geographic range* for each host species (65,200-25,900,000 km^2).

Finally, we recorded *body mass* of each host species using data from Dunning (2008). When a range of body masses was given for each host species, the mid-points of these ranges were used as estimates of body masses for each host species. Body mass ranged from 21.1 g (*Calidri minuta*) to 1658.5 g (*Larus marinus*).

We excluded data from the critically endangered slender-billed curlew (*Numenius tenuirostris*) because of its tiny total population size (1-49 individuals) and distribution area (890 km^2) resulted in extreme values, even when transformed. The black-winged stilt (*Himantopus mexicanus*) was previously recognised to be a species different from *H. himantopus* but is now considered a subspecies (del Hoyo *et al.*, 2014), therefore they were treated as a single species (Appendix S1).

The spatial analyses were performed in *R* 3.0.1 (R Core Team, 2013) using the packages ‘sp’ (Pebesma & Bivand, 2005), ‘maptools’ (Bivand & Lewin-Koh, 2014), and ‘rgeos’ (Bivand & Rundel, 2013).

Statistical analyses

We used phylogenetic comparative analyses to control for the phylogenetic autocorrelation introduced by shared ancestry (Harvey & Pagel, 1991) and phylogenetic uncertainty (Huelsenbeck *et al.*, 2000). We used the most complete bird phylogeny from Jetz *et al.* (2012) (9,993 species, available at http://birdtree.org/). The tree was built using molecular data from 6,670 species, and the remaining taxa with no molecular information were added to the phylogeny based on taxonomic information and simulated branching times from a pure birth (Yule) model of diversification (Jetz *et al.*, 2012). A distribution of 10,000 trees with different topologies was obtained for the 106 species in our dataset (see Fig S2.1 for a randomly sampled phylogeny) using an online phylogeny-generating tool (http://birdtree.org). To account for phylogenetic uncertainty, we randomly sampled 100 trees from this posterior distribution of trees.

We then fitted Bayesian phylogenetic mixed models using the packages *MCMCglmm* (Hadfield & Nakagawa, 2010) and *mulTree* (Guillerme & Healy, 2014). We performed analyses on the 100 sampled phylogenetic trees, instead of using one unique consensus tree. This approach included species and study as random factors to correct for the shared ancestry and the repeated nature of data (i.e., several studies measured more than one species and/or populations). Helminth species richness per population was included as the response variable; and habitat use strategy, diet, body mass, absolute sampling latitude, geographical range and global population size as predictors. Continuous predictors were scaled and centred prior to analysis. We assumed Gaussian error distribution for all the models (Hadfield, 2010).

For all analyses, we used an uninformative prior (with variance set to 1 and belief parameter set to 0.002) for both fixed and random effects (Hadfield, 2010) and ran two chains for 555,000 iterations with a thinning value of 500 after a burn-in of 50,000, resulting in 1,000 samples. We checked for convergence between model chains using the Gelman-Rubin statistic (Gelman & Rubin, 1992). Potential scale reduction values were all less than 1.1 and the autocorrelations of posterior probabilities were all less than 0.1. Effective sample sizes for all fixed effects were all greater than 800. We considered fixed effects to be statistically significant when the probabilities in the 95% credible region did not include zero. We also calculated the deviance information criterion (DIC), a hierarchical generalization of the Akaike information criterion (Spiegelhalter *et al.*, 2002). Briefly, DIC balances model fit and parameter number simultaneously, and lower values of DIC are preferred.

We ran models for overall helminth species richness and for the four major helminth groups separately (trematodes, cestodes, nematodes and acanthocephalans) (see Table S2.1 for sample sizes). To test for the effect of habitat use strategies on helminth richness more finely, we ran separate analyses with host species classified according to their main wintering habitat use (marine, freshwater or mixed) and habitat specialization (osmotic generalists and osmotic specialists). We did not include these two factors in the same analysis in order to avoid redundant information (note that all species with a mixed wintering habitat strategy are osmotic generalists). By adopting this approach, we were able to partly account for seasonality, as ‘wintering habitat use strategy’ focuses on the wintering period only, and ‘habitat specialization’ makes no distinction across different phases of the annual cycle.

Sampling effort and parasite species richness were positively correlated (Spearman's ρ=0.336-0.539; p<0.0001 for all subsets except for that of acanthocephalans, which were infrequently recorded in birds; Figs 2 and S2.3), so we expressed helminth species richness as the residual of a (log-link) quasi-Poisson regression with parasite species richness as response variable and host sampling size (log-transformed) as explanatory variable. The use of residuals from regression as data is particularly common in controlling for confounding variables, including host sampling size in comparative studies (e.g., Morand & Harvey, 2000; Bordes *et al.*, 2011). Although this procedure has been criticized because it leads to biased parameter estimates when correlations exist between independent variables (Freckleton, 2002), host sampling size was not significantly correlated with any independent variables in our dataset (Spearman's ρ=-0.027–0.011; $p\geq$0.115).

RESULTS

The number of helminth species infecting shorebird host populations ranged from 0 to 59 and averaged 12.31±0.78 (Figs 2 and S2.2). The helminth fauna of Charadriiformes was dominated by trematodes, followed by cestodes, nematodes and acanthocephalans (Fig. 2).

(a) Wintering habitat use: marine versus freshwater versus mixed

We found overall helminth species richness not to statistically differ between host species occurring in marine and freshwater habitats outside the breeding season, but it was significantly higher in host species using both marine and freshwater ('mixed') habitats (Fig. 3a, Table 1). Moreover, birds with more diverse (omnivorous) diets harboured significantly more parasites than birds that exclusively depend on fish, invertebrates or a mix of them (Fig. 4, Table 1). Notably, migration distance and latitude had no effect on helminth species richness; however, helminth species richness tended to increase with geographic range and body mass (Table 1).

When considering major helminths groups separately, we found that trematode species richness was higher in hosts using marine and mixed habitats and in hosts feeding on a mix of fish and invertebrates, and in those with omnivorous diets (Table S3.1). Trematode species richness also increased with host body mass and geographical range, but was not influenced by latitude and migration distance (Table S3.1). Likewise, nematode species richness increased with host body mass, but was not affected by any of the other predictors (Table S3.2). Cestode species richness did not differ among habitats and diets, but tended to be higher in host species with invertebrate and omnivorous diets and increased with latitude (Table S3.3). Finally, we found no relationships between acanthocephalan species richness and any of the ecological and life-history variables (Table S3.4).

(b) Osmotic habitat use: generalists versus specialists

Osmotic generalist birds harboured more parasite species than osmotic specialist birds (Fig. 3b, Table 2). Helminth parasite richness was also higher in birds with omnivorous diets (Table 1, Fig. 4). However, helminth parasite richness was not influenced by host migration distance and latitude but tended to increase with geographic range and body mass (Table 2).

When considering major helminth groups separately, osmotic habitat use strategy influenced trematode and nematode parasite species richness, with osmotic specialists harbouring fewer parasites than osmotic generalists (Tables S3.5 and S3.6). However, osmotic habitat use strategy had no strong effect on richness of cestodes and acanthocephalans (Tables 3, S3.7 and S3-8). Host species with more diverse diets (mix of fish and invertebrates and omnivorous diets) exhibited higher trematode species richness than those with more restricted diets (fish or invertebrates) (Table S3.5); however, diet did not influence nematode, cestode and acanthocephalan species richness (Tables 3 and S3.6-S3.8). Trematode species richness increased with geographic range (Tables 3 and S3.5). However, this predictor did not strongly influence the richness of the other parasite groups (Tables 3 and S3.6-S3.8). Nematode species richness decreased with migration distance (Table S3.6), and cestode species richness increased with latitude (Table S3.7). Acanthocephalan species richness was not affected by any of the ecological and life-history variables (Tables 3 and S3.8).

(c) Model fit

Models for overall helminths parasites considering either wintering habitat use or habitat strategy explained approximately the same amount of variability in data (modal DIC for overall helminth species richness=674.460 and 673.031, respectively; Table S3.9). The phylogenetic residual term was similarly high in our two principal models (model 1: 2.351; model 2: 2.422; Tables 1 and 2, respectively), indicating an important role for shared ancestry in the relationship between ecological/life history traits and helminth species richness. Models for overall helminths parasites using hosts migratory strategy as a categorical fixed factor were qualitatively similar to those using migration distance (Tables S3.10 and S3.11).

DISCUSSION

We present the first evidence that habitat generalist hosts have higher helminth species richness than habitat specialist hosts. Interestingly, we found no association between overall parasite species richness and migration distance suggesting that migration distance *per se* is not an important determinant of the richness of helminth parasites in Charadriiform birds.

The higher parasite richness in habitat generalists most likely results from general differences between marine and freshwater parasite faunas (Zander & Reimer, 2002). Birds exposed to both saltwater and freshwater habitats have the potential to pick up helminths with specific marine and freshwater transmission pathways and therefore have a richer helminth fauna than those restricted to a single habitat type. Unlike previous studies dealing with avian blood parasites (Figuerola, 1999; Mendes *et al.*, 2005; Yohannes *et al.*, 2009; Clark *et al.*, 2016), we did not find evidence for a higher helminth species richness in bird species using freshwater habitats compared to species using saltwater habitats. In fact, in the case of trematodes (the most abundant parasites; Fig. 2) parasite richness was lower in freshwater species than in marine and mixed species (Table S3.1). This difference to blood parasites is possibly due to different modes of transmission. Blood parasites (e.g., avian malaria) usually require appropriate arthropod vectors, which are expected to be more abundant in freshwater than in marine habitats (Piersma, 1997). On the other hand, trophic transmission patterns of helminth parasites to vertebrate definitive hosts in aquatic food webs seem to be similar in marine and freshwater ecosystems (Thieltges *et al.*, 2013). Indeed, a comparative study on parasite richness in neotropical fish showed that marine and freshwater fish species do not differ in macroparasite richness (Luque & Poulin, 2007), suggesting that general risks to become infected with helminths may be relatively similar in the two habitats. Hence, our results suggest that it is the diversity of habitats (and the resulting diversity of parasite transmission pathways) exploited by definitive hosts, rather than the salinity of the habitat, that determines total helminth parasite richness in birds.

In contrast to previous studies in other orders of birds (Figuerola & Green, 2000; Koprivnikar & Leung, 2015), we did not find any positive association between total parasite species richness and migration distance. These conflicting results can arise in different ways. Firstly, in the above-mentioned studies parasite diversity was measured as the number of parasite species or genera reported infecting bird species across their geographic range, whereas in this study parasite diversity was measured as the number of species in each host population; the former measure might overestimate the actual parasite pressure incurred by a bird population (Morand & Poulin, 2000), particularly in migratory species that have been more studied than non-migratory ones (Figuerola & Green, 2000). Secondly, Figuerola & Green (2000) focused on blood parasites that rely on different modes of transmission, which may produce different spatial patterns of parasitism (Piersma, 1997). Thirdly, the study by Koprivnikar & Leung (2015) on nematode species richness of migratory and resident birds did not include host traits (e.g., habitat use, diet, range size) that are shown here to account for some of the variation in parasite diversity. Further research is needed to clarify the relationship between host migration strategies and parasite diversity over a wider range of parasite and host groups to determine if patterns of covariation between parasite diversity and host migration differ among groups of parasites.

Besides habitat use strategies, the diet type of bird hosts significantly contributed to explaining overall helminth species richness, with bird species with omnivorous diets exhibiting highest parasite richness. As helminths are trophically transmitted to birds via infected prey, an increase in parasite richness with increasing exposure can be expected. Indeed, studies on parasite-inclusive food webs have shown that parasite richness in vertebrate definitive hosts increases with their diet range (Chen *et al.*, 2008; Thieltges *et al.*, 2013). Hence, our data suggest that migration distance *per se* is not an important determinant of the richness of helminth parasites in birds, but rather the exposure to different habitats during migration and to different prey types within these habitats.

In contrast to habitat use strategies and diet, the other ecological and life history traits analysed did not significantly contribute to explaining overall helminth species richness, suggesting them to be of minor importance in affecting overall parasite species richness in birds. However, the separate analyses of the four parasite groups indicated that the relative importance of these traits differed among parasite groups. For example, in trematodes, parasite richness increased with host range. In general, hosts with larger geographic ranges may occupy more habitats, leading to more opportunities for host-parasite associations to become established and thus to higher parasite species richness (Gregory, 1990; Poulin & Morand, 2004; Kamiya *et al.*, 2014). Many Charadriiformes are known to perform regular long-distance migrations, with some species flying the full distance between breeding and nonbreeding areas without stopping over and ‘refuelling’ along the way (Gill *et al.*, 2009). Such long-distance migrating birds spend a considerable amount of their time in the air where the chances of helminth infection are zero. On the other hand, most other species use multiple stopover sites along the route, where refuelling birds might pick up more parasites. This could explain why parasite species richness tended to increase with geographic range but not with migration distance.

Like host range, host body size showed a positive association with parasite species richness in trematodes and nematodes when analysed separately. This might occur because larger hosts offer more space to parasites and they may provide a greater variety of niches for parasite occupation (Kamiya *et al.*, 2014). Moreover, larger hosts consume greater quantities of food and might thus be exposed to a wider range of parasite infective stages (Kamiya *et al.*, 2014). Consistent with a recent meta-analysis on parasite richness across animal, plant and fungal hosts (Kamiya *et al.*, 2014), we found no strong evidence for an effect of latitude on helminth richness, except the positive association found for nematodes. This difference might be due to the fact that helminth parasite richness in intermediate hosts also often does not show strong latitudinal gradients (e.g., Thieltges *et al.*, 2009), leading to similar exposure of down-stream hosts at different latitudes.

There are a few caveats to our study, notably regarding the effects of within-species variation on parasite richness. It is important to note that the ecological and life-history variables used in our study relate to the host species level, whereas parasite richness was estimated at the host population level. One potential drawback of this approach lies in the fact that bird populations of a given species may exhibit differences in migration and feeding strategies and that they do not occur across the entire species' range. Unfortunately, reliable population-based data were not available for most species in our dataset, so we used species-specific data on these variables while still correcting for problems associated with phylogenetic and regional non-independence among data. Another caveat related to our dataset is that potential effects of seasonal variation on parasite richness were not accounted for as the respective data were not available for most species. As a consequence, we cannot tease apart the respective role of different life-history events (migration versus breeding or wintering periods). Although we acknowledge that the results thus need to be interpreted with some caution, several elements suggest that our analyses did not generate spurious patterns. First, the fact that helminth richness is higher in birds with diverse feeding habits and habitat use is in line with our *a priori* prediction, regardless of the different approaches used to assess habitat use and migration strategies. Second, none of the other traits that we included in our analyses (e.g., body mass, latitude) altered our conclusions. Third, although parasite species richness can vary in space (among populations), it rarely varies in time (across seasons or generations) (Morand & Poulin, 2000; Bensch *et al.*, 2007). As such, parasite species richness is considered to be a more reliable metric of parasitic pressure than host infection prevalence or intensity (Bordes & Morand, 2009; Koprivnikar & Leung, 2015). Moreover, parasite species richness is likely to be more reflective of the long-term selection pressure posed by parasites which may influence host immune investment (Koprivnikar & Leung, 2015).

Although generalist hosts are expected to benefit from habitats that are heterogeneous in space and/or time (Devictor *et al.*, 2008), they might be more negatively affected by higher parasite diversity than specialists. Furthermore, generalist hosts could be exposed to greater physiological stresses than those confronting specialists. For example, changes in dietary salt intake associated with habitat shifts could adversely affect immune responsiveness in generalist birds (Gutiérrez *et al.*, 2013). Future studies combining indices of parasite diversity and immunocompetence will be needed to determine if immune investment differs between generalist and specialist hosts, as well as to understand the implications for their health. Globally, generalist bird species are at a much lower risk of extinction than specialists (Burin *et al.*, 2016), and in birds there is a positive relationship between increased specialization and increased risk of human-driven extinction (Sekercioglu, 2011). Thus, ongoing human-driven environmental changes are likely to distort future macroevolutionary dynamics by changing diversification rates and favouring generalist species at the expense of specialists. The evolutionary coexistence of specialists and generalists might result from trade-offs between acquiring resources (habitats or diets) and habitat and diet associated costs of becoming parasitized.

In conclusion, we found support for diverse diet and habitat use leading to increased parasitism in migratory birds. This result appears most consistent with exposure to more parasites that accumulate in different habitats and diets, and could also reflect increased susceptibility to parasitism in species that exploit more diverse habitats and associated diets. The lack of association between overall parasite species richness and host migration distance suggests that distribution patterns and habitat use, rather than migration *per se*, shape parasite diversity within host populations. Overall, these results demonstrate the significant role of habitat use as a mechanism explaining how migration affects parasite richness in host populations. Understanding the mechanisms linking migration and parasite richness has important implications since many Charadriiform birds constitute major hosts for parasites and viruses and perform regular long-distance migrations, thereby potentially distributing parasites and viruses around the world (Olsen *et al.*, 2006).

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REFERENCES

Alerstam T., Hedenström A., & Åkesson S. (2003) Long-distance migration: evolution and determinants. *Oikos*, **2103**, 247–260.

Altizer S., Bartel R., & Han B.A. (2011) Animal migration and infectious disease risk. *Science*, **331**, 296–302.

Bensch S., Waldenström J., Jonzén N., Westerdahl H., Hansson B., Sejberg D., & Hasselquist D. (2007) Temporal dynamics and diversity of avian malaria parasites in a single host species. *Journal of Animal Ecology*, **76**, 112–22.

Bivand R. & Lewin-Koh N. (2014) Tools for reading and handling spatial objects. *R package version 0.8-39.*, 79.

Bivand R. & Rundel C. (2013) rgeos: Interface to Geometry Engine - Open Source (GEOS). 61.

Bordes F., Guégan J.F., & Morand S. (2011) Microparasite species richness in rodents is higher at lower latitudes and is associated with reduced litter size. *Oikos*, **120**, 1889–1896.

Bordes F. & Morand S. (2009) Parasite diversity: An overlooked metric of parasite pressures? *Oikos*, **118**, 801–806.

Burin G., Kissling W.D., & Guimara P.R. (2016) Omnivory in birds is a macroevolutionary sink. *Nat Commun*, **7**, 11250.

Bush A.O. (1990) Helminth communities in avian hosts: determinants of pattern. *Parasite communities: patterns and processes* (ed. by G.W. Esch, A.O. Bush, and J. Aho), pp. 197–232. Chapman and Hall, London, New York.

Bush A.O., Aho J.M., & Kennedy C.R. (1990) Ecological versus phylogenetic determinants of helminth parasite community richness. *Evolutionary Ecology*, **4**, 1–20.

Chen H.W., Liu W.C., Davis A.J., Jordán F., Hwang M.J., & Shao K.T. (2008) Network position of hosts in food webs and their parasite diversity. *Oikos*, **117**, 1847–1855.

Clark N.J., Clegg S.M., & Klaassen M. (2016) Migration strategy and pathogen risk: non-breeding distribution drives malaria prevalence in migratory waders. *Oikos*, in press.

Cramp S. & Simmons K.E.L. (1983) *Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic. 3. Waders to gulls.* Oxford University Press, Oxford.

Devictor V., Julliard R., & Jiguet F. (2008) Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos*, **117**, 507–514.

Dunning J.B. (2008) *CRC handbook of avian body masses.* CRC Press, Boca Raton.

Figuerola J. (1999) Effects of salinity on rates of infestation of waterbirds by haematozoa. *Ecography*, **22**, 681–685.

Figuerola J. & Green A.J. (2000) Haematozoan parasites and migratory behaviour in waterfowl. *Evolutionary Ecology*, **14**, 143–153.

Freckleton R.P. (2002) On the misuse of residuals in ecology: Regression of residuals vs. multiple regression. *Journal of Animal Ecology*, **71**, 542–545.

Gelman A. & Rubin D.B. (1992) Inference from iterative simulation using multiple sequences. *Statistical Science*, **7**, 457–511.

Gill R.E., Tibbitts T.L., Douglas D.C., Handel C.M., Mulcahy D.M., Gottschalck J.C., Warnock N., McCaffery B.J., Battley P.F., & Piersma T. (2009) Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? *Proceedings of the Royal Society B*, **276**, 447–57.

Gray B., Jacobs A.C., Mora A.B., & Zuk M. (2012) Antiparasite behavior. *Current Biology*, **22**, R255–R257.

Gregory R.D. (1990) Parasites and host geographic range as illustrated by waterfowl. *Functional Ecology*, **4**, 645–654.

Gregory R.D., Keymer A.E., & Harvey P.H. (1991) Life history, ecology and parasite community structure in Soviet birds. *Biological Journal of the Linnean Society*, **43**, 249–262.

Gregory R.D., Keymer A.E., & Harvey P.H. (1996) Helminth parasite richness among vertebrates. *Biodiversity and Conservation*, **5**, 985–997.

Guillerme T. & Healy K. (2014) mulTree: a package for running MCMCglmm analysis on multiple trees. ZENODO. 10.5281/zenodo.12902. .

Gutiérrez J.S. (2014) Living in environments with contrasting salinities: A review of physiological and behavioural responses in waterbirds. *Ardeola*, **61**, 233–256.

Gutiérrez J.S., Abad-Gómez J.M., Villegas A., Sánchez-Guzmán J.M., & Masero J.A. (2013) Effects of salinity on the immune response of an “osmotic generalist” bird. *Oecologia*, **171**, 61–69.

Gutiérrez J.S., Dietz M.W., Masero J.A., Gill R.E., Dekinga A., Battley P.F., Sánchez-Guzmán J.M., & Piersma T. (2012) Functional ecology of saltglands in shorebirds: Flexible responses to variable environmental conditions. *Functional Ecology*, **26**, 236–244.

Hadfield J. (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software*, **33**, 1–22.

Hadfield J.D. & Nakagawa S. (2010) General quantitative genetic methods for comparative biology: Phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology*, **23**, 494–508.

Harvey P.H. & Pagel M.D. (1991) *The comparative method in evolutionary biology.* Oxford University Press, Oxford; New York.

Hasselquist D., Lindström A., Jenni-Eiermann S., Koolhaas A., & Piersma T. (2007) Long flights do not influence immune responses of a long-distance migrant bird: a wind-tunnel experiment. *Journal of Experimental Biology*, **210**, 1123–31.

del Hoyo J., Collar N.J., Christie D.A., Elliott A., & Fishpool L.D.C. (2014) *HBW and BirdLife International Illustrated Checklist of the Birds of the World.* Lynx Edicions BirdLife International,

del Hoyo J., Elliott A., & Sargatal J. (1996) *Handbook of the Birds of the World, Vol. 3. Hoatzin to Auks.* Lynx Edicions, Barcelona.

Huelsenbeck J.P., Rannala B., & Masly J.P. (2000) Accommodating phylogenetic uncertainty in evolutionary studies. *Science*, **288**, 2349–2350.

Jetz W., Thomas G.H.H., Joy J.B.B., Hartmann K., & Mooers A.O.O. (2012) The global diversity of birds in space and time. *Nature*, **491**, 444–448.

Kamiya T., O'Dwyer K., Nakagawa S., & Poulin R. (2014) What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. *Biological Reviews*, **89**, 123–134.

Koprivnikar J. & Leung T.L.F. (2015) Flying with diverse passengers: greater richness of parasitic nematodes in migratory birds. *Oikos*, **124**, 399–405.

Lindenfors P., Nunn C.L., Jones K.E., Cunningham A.A., Sechrest W., & Gittleman J.L. (2007) Parasite species richness in carnivores: Effects of host body mass, latitude, geographical range and population density. *Global Ecology and Biogeography*, **16**, 496–509.

Luque J.L. & Poulin R. (2007) Metazoan parasite species richness in Neotropical fishes: hotspots and the geography of biodiversity. *Parasitology*, **134**, 865–878.

Mendes L., Piersma T., Lecoq M., Spaans B., & Ricklefs R.E. (2005) Disease-limited distributions ? Contrasts in the prevalence of avian malaria in shorebird species using marine and freshwater habitats. *Oikos*, **2**, 396–404.

Møller A.P. & Erritzøe J. (1998) Host immune defence and migration in birds. *Evolutionary Ecology*, **12**, 945–953.

Morand S. & Harvey P.H. (2000) Mammalian metabolism, longevity and parasite species richness. *Proceedings of the Royal Society B*, **267**, 1999–2003.

Morand S. & Poulin R. (2000) Nematode parasite species richness and the evolution of spleen size in birds. *Canadian Journal of Zoology*, **78**, 1356–1360.

Olsen B., Munster V., Wallensten A., & Waldenstrom J. (2006) Global patterns of influenza A virus in wild birds. *Science*, **312**, 384–388.

Pebesma E.J. & Bivand R.S. (2005) Classes and methods for spatial data in R. *R News*, **5**, 9–13.

Piersma T. (1997) Do global patterns of habitat use and migration strategics co-evolve with relative investments in immunocompetence due to spatial variation in parasite pressure? *Oikos*, **80**, 623–631.

Piersma T. (2011) Why marathon migrants get away with high metabolic ceilings: towards an ecology of physiological restraint. *Journal of Experimental Biology*,

214, 295–302.

Poulin R. (1996) Sexual inequalities in helminth infections : a cost of being a male? *The American Naturalist*, **147**, 287–295.

Poulin R., Closs G.P., Lill A.W.T., Hicks A.S., Herrmann K.K., & Kelly D.W. (2012) Migration as an escape from parasitism in New Zealand galaxiid fishes. *Oecologia*, **169**, 955–963.

Poulin R. & Morand S. (2004) *Parasite biodiversity.* Smithsonian Institution Press, Washington.

R Core Team (2013) *R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.*

Rausch R.L. (1983) The biology of avian parasites: Helminths. *Avian Biology* (ed. by D.S. Farner, J.R. King, and K.C. Parkes), pp. 367–442. Academic Press, New York.

Roca V., Lafuente M., & Carbonell E. (1999) Helminth Communities in Audouin's gulls, *Larus audouinii* from Chafarinas Islands (Western Mediterranean). *Journal of Parasitology*, **85**, 984–986.

Santoro M., Mattiucci S., Kinsella J.M., Aznar F.J., Giordano D., Castagna F., Pellegrino F., & Nascetti G. (2011) Helminth community structure of the Mediterranean gull (*Ichthyaetus melanocephalus*) in Southern Italy. *Journal of Parasitology*, **97**, 364–366.

Schmid-Hempel P. (2011) *Evolutionary parasitology: The integrated study of infections, immunology, ecology and genetics.* Oxford University Press, Oxford.

Sekercioglu C.H. (2011) Functional extinctions of bird pollinators cause plant declines. *Science*, **331**, 1019–1020.

Spiegelhalter D.J., Best N.G., Carlin B.P., & Van Der Linde A. (2002) Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society*, **64**, 583–639.

Thieltges D.W., Amundsen P.A., Hechinger R.F., Johnson P.T.J., Lafferty K.D., Mouritsen K.N., Preston D.L., Reise K., Zander C.D., & Poulin R. (2013) Parasites as prey in aquatic food webs: Implications for predator infection and parasite transmission. *Oikos*, **122**, 1473–1482.

Thieltges D.W., Ferguson M.A.D., Jones C.S., Noble L.R., & Poulin R. (2009) Biogeographical patterns of marine larval trematode parasites in two intermediate snail hosts in Europe. *Journal of Biogeography*, **36**, 1493–1501.

Weber T.P. & Stilianakis N.I. (2007) Ecologic immunology of avian influenza (H5N1) in migratory birds. *Emerging Infectious Diseases*, **13**, 1139–1143.

Yohannes E., Križanauskienė A., Valcu M., Bensch S., & Kempenaers B. (2009) Prevalence of malaria and related haemosporidian parasites in two shorebird species with different winter habitat distribution. *Journal of Ornithology*, **150**, 287–291.

Zander C.D. & Reimer L.W. (2002) Parasitism at the ecosystem level in the Baltic Sea. *Parasitology*, **124 Suppl**, S119–S135.

BIOSKETCH

Jorge S. Gutiérrez’s main research interest is the ecophysiology of migratory animals. He is also interested in the evolutionary ecology of host-parasite interactions, typically testing hypotheses at the macro-evolutionary scale.

Author contributions: JSG, DWT and TP conceived the study. JSG led the literature review, data analysis and writing, with important inputs to data analysis from ER, and to writing from DWT and TP.

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APPENDIX 1. Data sources

Alekseev V.M. & Smetanina Z.B. (1968) Nematodes from fish-eating birds of the Rimsko-Korsakov islands. *Helminths of animals of the Pacific Ocean* pp. 97–104. Izdatel'stvo Nauka, Moscow.

Álvarez M.F., Cordeiro J.A., Leiro J.M., & Sanmartín M.L. (2006) Influence of host age and sex on the helminth fauna of the yellow-legged gull (*Larus michahellis*) in Galicia (northwestern Spain). *Journal of Parasitology*, **92**, 454–458.

Bakke T.A. (1985) Studies of the helminth fauna of Norway: the common gull, *Larus canus* L., as final host for Cestoda (Platyhelminthes). *Fauna Norvegica, Series A*, **6**, 42–54.

Bakke T.A. & Barus V. (1975) The common gull, *Larus Canus* L., as final host for Nematoda: Qualitative data on species of Ascaridoidea (Railliet and Henry, 1915). *Norwegian Journal of Zoology*, **23**, 183–191.

Bakke T.A. & Barus V. (1976) Studies of the helminth fauna of Norway XXXVII: the common gull, *Larus canus* L., as final host for Nematoda. II. Qualitative and quantitative data on species of Acuariidae, Capillariidae, Strongyloididae, Syngamidae and Tetrameridae; with notes on host–parasite relationship. *Norwegian Journal of Zoology*, **24**, 7–31.

Belogurov O., Leonov V., & Zueva L. (1968) Gel'mintofauna ryboiadnykh ptits (chaek i chistikov) poberezh'ia okhotskogo moria. *Gel'minty zhivotnykh tikhogo okeana* (ed. by K. Skryabin and Y. Mamaev), pp. 105–124. Izdatl'stvo Akademii Nauk SSSR, Moskva.

Bosch M., Torres J., & Figuerola J. (2000) A helminth community in breeding Yellow-legged gulls (*Larus cachinnans*): pattern of association and its effect on host fitness. *Canadian Journal of Zoology*, **78**, 777–786.

Buck O.D., Cooper C.L., & Crites J.L. (1976) Helminth parasites of Herring gull, *Larus argentatus*, from Bass Island of western Lake Eire. *Proceedings of the Helminthological Society of Washington*, **43**, 233–234.

Bush A.O. (1990) Helminth communities in avian hosts: determinants of pattern. *Parasite communities: patterns and processes* (ed. by G.W. Esch, A.O. Bush, and J. Aho), pp. 197–232. Chapman and Hall, London, New York.

Bykhovskaya-Pavlovskaya I.E. (1953) Trematode fauna of birds of western Siberia and their dynamics. *Parazitol. Sborn. Akad. Nauk, SSSR*, **15**, 5–116.

Bykhovskaya-Pavlovskaya I.E. (1962) *Trematodes of birds in the fauna of the USSR. Ecological and geographical review.* Izdalestvo Akademii Nauk SSSR, Moskva-Leningrad.

Canaris A.G. & Kinsella J.M. (1998) Helminth parasite communities in four species of shorebirds (Charadriidae) on King Island, Tasmania. *Papers and Proceedings of the Royal Society of Tasmania*, **132**, 49–57.

Canaris A.G. & Kinsella J.M. (2001) Helminth parasites in six species of shorebirds (Charadrii) from the coast of Belize. *Memorias do Instituto Oswaldo Cruz*, **96**, 827–830.

Canaris A.G. & Kinsella J.M. (2007) Helminth communities of three sympatric species of shorebirds (Charadrii) from four summer seasons at Bristol Bay, Alaska. *Journal of Parasitology*, **93**, 485–490.

Canaris A.G., Kinsella J.M., & Braby R. (2003) Helminth parasite communities in two species of shorebirds (Charadrii) from Namibia. *Comparative Parasitology*, **70**, 155–161.

Canaris A.G., Kinsella J.M., & Didyk A.S. (2009) Helminth parasites of spotted sandpipers, *Actitis macularius* (Charadriiformes), from Belize, Texas, and Montana. *Journal of Parasitology*, **95**, 1542–1544.

Canaris A.G., Kinsella J.M., & Didyk A.S. (2012) Helminth parasites of the western willet, *Tringa semipalmata inornata*, from montana and Texas with a checklist of helminth parasites. *Journal of Parasitology*, **98**, 216–221.

Canaris A.G. & Munir N.T. (1991) Helminth parasites of the western sandpiper, *Calidris mauri* (Aves), from El Paso and Hudspeth counties, Texas. *Journal of Parasitology*, **77**, 787–789.

Ching H.L. (1990) Some helminth parasites of dunlin (*Calidris alpina*) and western willet (*Catoptrophorus semipalmatus inornatus*) from California. *Journal of the Helminthological Society of Washington*, **57**, 44–50.

Didyk A.S., Canaris A.G., & Kinsella J.M. (2007a) Intestinal helminths of the spotted sandpiper, *Actitis macularius* (L.), during fall migration in New Brunswick, Canada, with a checklist of helminths reported from this host. *Comparative Parasitology*, **74**, 359–363.

Didyk A.S., Kinsella J.M., & Canaris A.G. (2007b) Intestinal helminths of fall-migrating Ruddy Turnstones, *Arenaria interpres* (L.), from New Brunswick, Canada, with a checklist of helminths reported from this host. *Comparative Parasitology*, **74**, 364–371.

Dronen N.O. & Badley J.E. (1979) Helminths of shorebirds from the Texas Gulfcoast. I. Digenetic trematodes from the long-billed curlew, *Numenius americanus*. *Journal of Parasitology*, **65**, 645–649.

Dronen N.O., Wardle W.J., & Bhuthimethee M. (2002) Helminthic Parasites from Willets, *Catoptrophorus semipalmatus* (Charadriiformes: Scolopacidae), from Texas, U.S.A., with descriptions of *Kowalewskiella catoptrophori* sp. n. and *Kowalewskiella macrospina* sp. n. (Cestoda: Dilepididae). *Comparative Parasitology*, **69**, 43–50.

Enz J.J. & Canaris a G. (2008) Metazoan parasites of lesser yellowlegs, *Tringa flavipes* (Charadriiformes) from southwestern United States and Alaska with a checklist of parasites reported from this host. *Journal of Parasitology*, **94**, 548–551.

Forrester D.J. & Spalding M.G. (2003) *Parasites and diseases of wild birds in Florida.* University Press of Florida, Gainesville, Florida.

Fredensborg B.L., Latham A.D.M., & Poulin R. (2004) New records of gastrointestinal helminths from the red-billed gull (*Larus novaehollandiae scopulinus*). *New Zealand Journal of Zoology*, **31**, 75–80.

Garcia C.A. & Canaris A.G. (1987) Metazoan parasites of *Recurvirostra americana* Gmelin (Aves), from southwestern Texas and Monte Vista National Wildlife Refuge, Colorado, with a checklist of helminth parasites hosted by this species in

North America. *Southwestern Naturalist*, **32**, 85–91.

Hair J.D. & Holmes J.C. (1970) Helminths of Bonaparte's gulls, *Larus philadelphia*, from Cooking Lake, Alberta. *Canadian Journal of Zoology*, **48**, 1129–1131.

Hinojos J.G., Campbell B.K., & Canaris A.G. (1993) Helminth parasites of the American avocet *Recurvirostra americana* (Aves), from the Salt Lake basin, Utah. *Journal of Parasitology*, **79**, 114–116.

Hinojos J.G. & Canaris A.G. (1988) Metazoan parasites of *Himantopus mexicanus* Muller (Aves) from southwestern Texas, with a checklist of helminth parasites from North America. *Journal of Parasitology*, **74**, 326–331.

Kalantan A.M., Arfin M., & Mosjen A.A.A. (2000) Digenetic trematodes of *Larus genei* (Lariformes: Laridae) caught from Al-Rames. *Pakistan Journal of Biologicat Sciencas*, **3**, 1708–1711.

Keppner E.J. (1973) Some internal parasites of the California gull *Larus californicus* Lawrence, in Wyoming. *Transactions of the American Microscopical Society*, 288–291.

Kinsella J.M. (1972) Helminth parasites of the black skimmer, *Rynchops nigra*, from Lake Okeechobee, Florida. *Journal of Parasitology*, **58**, 780–780.

Kinsella J.M., Didyk A.S., & Canaris A.G. (2007) Helminths of Hudsonian godwits, *Limosa haemastica*, from Alaska and Manitoba. *Journal of Parasitology*, **93**, 716–717.

Kinsella J.M., Didyk A.S., & Canaris A.G. (2008) Helminth parasites of Dowitchers, Limnodromus griseus from Alaska, and Limnodromus scolopaceus from Montana, U.S.A. *Comparative Parasitology*, **75**, 329–332.

Kostadinova A. (1995) Parasitologie: Trematodes of birds of the family Ardeidae from the Bulgarian Black Sea coast. *Dokladi na Bulgarskata Akademia na Naukite*, **48**, 89–92.

Kuklin V.V., Galaktionov K.V., Galkin A.K., & Marasaev S.F. (2004) A comparative analysis of the helminth fauna of kittiwake *Rissa tridactyla* (Linnaeus, 1758) and glaucous gull *Larus hyperboreus* Gunnerus, 1767 from different parts of the Barents Sea. *Parazitologiia*, **39**, 544–558.

Kuklina M., Kuklin V., & Ezhov A. (2009) Influence of helminth infestation on the digestive activity of kittiwakes (*Rissa tridactyla*) from different age groups. *Doklady Biological Sciences*, **425**, 154–156.

Kurashvili B. (1957) *Gel'minty okhotnich'e-promyslovykh ptits Gruzii v faunisticheskom i ekologicheskom osveshchenii.* Izdatel'stvo Akademii Nauk SSSR, Moscow.

Labriola J.B. & Suriano D.M. (2001) Community structure of parasitic helminths of birds of the genus Larus from Mar del Plata, Argentina. *Vie et Milieu*, **51**, 67–76.

Lafuente M., Roca V., & Carbonell E. (1998) Trematodes of Audouin's gull, *Larus audouinii* (Aves, Laridae), from Chafarinas Islands (W. Mediterranean). *Miscellania Zoologica*, **21**, 105–112.

Lafuente M., Roca V., & Carbonell E. (1999) Cestodos y Nematodos de la gaviota de Audouin, *Larus audouinii* Payraudeau, 1826 (Aves, Laridae) en las Islas Chafarinas (Mediterráneo sudoccidental). *Boletín de la Real Sociedad Española de Historia Natural. Sección Biológica*, **95**, 1.

Leyva T., Canaris A.G., & Bristol J.R. (1980) Helminths and ectoparasites of the common snipe (*Capella gallinago* L.) from Southwest Texas and Monte Vista National Wildlife Refuge, Colorado. *Journal of Wildlife Diseases*, **16**, 549–557.

Muzaffar S.B. (2009) Helminths of murres (Alcidae: *Uria* spp.): Markers of ecological change in the marine environment. *Journal of Wildlife Diseases*, **45**, 672–683.

Pod'iapol'skaia V.P., Spasskii A.A., & Ryzhikov K. Rabota 265-i soiuznoi gel'mintologicheskoi expeditsii 1947 g. na reke Pechore (Komi ASSR). *Tr. Gel'mintol. Lab. Akad. Nauk SSSR*, **5**, 232–251.

Ryzhikov K. (1951) Rabota 268-i soiuznoi gel'mintologicheskoi ekspeditsii 1948 g. v zapadnoi Gruzii. *Gel'minthol. Lab. Akad. Nauk SSSR*, **5**, 252–260.

Ryzhikov K. & Sudarikov V. (1951) Ravota 272-i soiuznoi gel'mintogicheskio ekspeditsii 1949 g. v raione ozera Baikal. *Tr. Gel'mintol. Lab. Akad. Nauk SSSR*, **5**, 270–292.

Ryzhikov K.M., Kadenatsii A.N., Akhmerov A.K., & Kontrimavichus V.L. (1962) Rabota Amurskoi gel'mintologicheskoi ekspetitsii (314 SGE) v 1960 g. *Tr. Gel'mintol. Lab. Akad. Nauk SSSR*, **12**, 120–138.

Santoro M., Mattiucci S., Kinsella J.M., Aznar F.J., Giordano D., Castagna F., Pellegrino F., & Nascetti G. (2011) Helminth community structure of the Mediterranean gull (*Ichthyaetus melanocephalus*) in Southern Italy. *Journal of Parasitology*, **97**, 364–366.

Schmidt G.D. & Frantz D.W. (1972) Helminth parasites of Wilson's phalarope, *Steganopus tricolor*, Vieillot, 1819, in Montana and Colorado. *Proceedings of the Helminthological Society of Washington*, **39**, 269.

Secord M.L. & Canaris A.G. (1993) The metazoan parasite community of migrating greater yellowlegs, *Tringa melanoleuca*, from the Rio Grande Valley, Texas and New Mexico. *Journal of Parasitology*, **79**, 690–694.

Shigin A.A. (1961) Gel’mintofauna chaikovykh ptits Rybinskogo vodokharnilishcha. *Tr. Darvinskogo Gos. Zapov.*, **7**, 309–362.

Smogorzhevskaia L. (1976) *Gel’minty vodoplavaiushchikh i bolotnykh ptits fauny Ukrainy.* Naukova Dumka, Kiev.

Spasskii A.A., Bogoiavlenskii I., Kontrimavichus V.L., & Paramonov B.B. (1963) Rabota Kamchatskoi gel’mintologicheskoi ekspeditsii (317-ia SGE) v 1961 g. *Tr. Gel’mintol. Lab. Akad. Nauk SSSR*, **13**, 369–381.

Spasskii A.A. & Sonin M. (1961) Rabota Kamchatskoi gel’mintologicheskoi ekspeditsii (317 SGE) v 1959 g. *Tr. Gel’mintol. Lab. Akad. Nauk SSSR*, **11**, 414–431.

Spasskii A., Ivashkin V., Bogoiavlenskii I., & Sonin M. (1958) Rabota 306-i soiuznoi gel’mintologicheskoi ekspeditsii 1956-1957 gg. v Tuvinskoi avtonomoi oblasti. *Rab. Exp. Gel’mintol. Lab* pp. 73–103.

Sulgostowska T. (1960a) Extra-intestinal trematodes in birds of the mesotrophic lakes: Goldapiwo and Mamry Pólnocne. *Acta Parasitologica Polonica*, **8**, 471–492.

Sulgostowska T. (1960b) Intestinal trematodes of birds of mesotrophic lakes: Goldapiwo and Mamry Polnocne. *Acta Parasitol. Polonica*, **8**, 85–114.

Tallman E.J., Corkum K.C., & Tallman D.A. (1985) The trematode fauna of two intercontinental migrants: *Tringa solitaria* and *Calidris melanotos* (Aves: Charadriiformes). *American Midland Naturalist*, 374–383.

Threlfall W. (1968) Studies on the helminth parasites of the American herring gull (*Larus argentatus* Pont.) in Newfoundland. *Canadian Journal of Zoology*, **46**, 1119–1126.

Threlfall W. (1971) Helminth parasites of alcids in the northwestern North Atlantic. *Canadian Journal of Zoology*, **49**, 461–466.

Tsimbaliuk A.K. & Belogurov O.I. (1964) O faune nematod ryboiadnykh ptits ostovov beringova moria. *Biologicheskie Nauki*, **4**, 7–11.

Vaidova S. (1978) *Gel'minty ptits Azerbaidzhan.* Akad. Nauk Azerbaidzh, SSR. Elm, Baku.

Williams I.C. & Harris M.P. (1965) The infection of the gulls *Larus argentatus* Pont., *L. fuscus* L. and *L. marinus* L. with Cestoda on the coast of Wales. *Journal of Parasitology*, **55**, 237–256.

Yanez D.M. & Canaris A.G. (1988) Metazoan parasite community composition and structure of migrating Wilson's phalarope, *Steganopus tricolor* Viellot, 1819 (Aves), from El Paso County, Texas. *Journal of Parasitology*, 754–762.

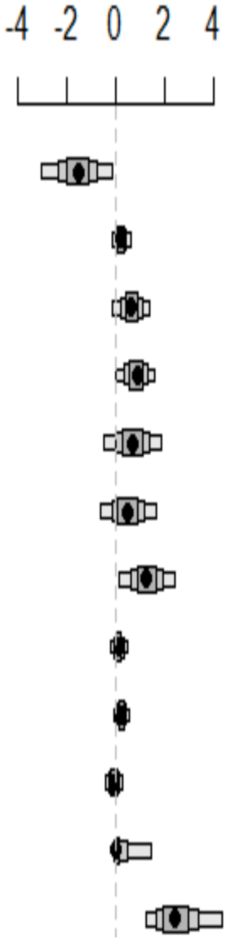
Additional Supporting Information may be found in the online version of this article:

Appendix S1. Dataset.

Appendix S2. Additional results.

Appendix S3. Group-specific parasite models.

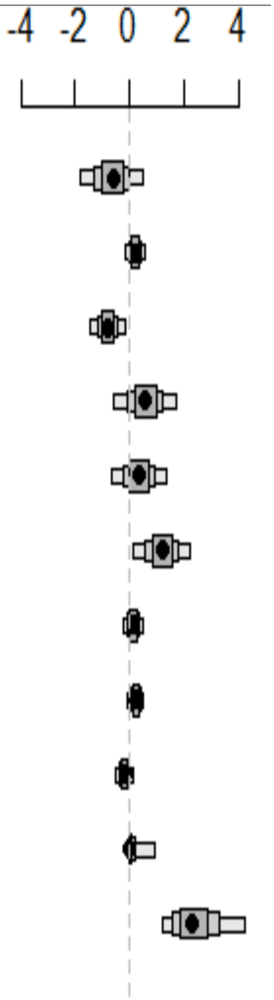
Table 1. Model explaining overall helminth species richness in Charadriiform birds by the effects of wintering habitat use strategy and additional ecological and life history traits as well as latitude of sampling location. The model was run with 100 different phylogenies (see text for details). Boxplots show the credibility intervals (CI=95, 90 and 50 %) and the mode of the central tendency of the posterior distribution. Significant predictors (i.e. their 95% CIs did not overlap with zero) are in bold.

		Estimate (β)	lower CI	upper CI	Posterior distribution
Overall helminth species richness					
Fixed terms					
Intercept		**-1.580**	**-3.034**	**-0.154**	
Mass		0.197	-0.184	0.576	
Wintering habitat[a]	-Marine	0.643	-0.123	1.398	
	-Mixed	**0.811**	**0.004**	**1.604**	
Diet[b]	-Fish-invertebrate	0.688	-0.487	1.854	
	-Invertebrate	0.475	-0.655	1.669	
	-Omnivorous	**1.286**	**0.136**	**2.406**	
Latitude		0.103	-0.255	0.462	
Geographic range		0.210	-0.105	0.531	
Migration distance		-0.074	-0.399	0.259	
Phylogenetic variance		0.003	1.434	1.485	
Residual variance		2.422	1.238	4.363	

[a] Reference category is 'freshwater habitat'

[b] Reference category is 'fish diet'

Table 2. Model explaining overall helminth species richness in shorebirds by the effects of osmotic habitat use strategy and additional ecological and life history traits as well as latitude of sampling location. The model was run with 100 different phylogenies (see text for details). Boxplots explained same as given in table 1. Significant predictors (i.e. their 95% CIs did not overlap with zero) are in bold.

		Estimate (β)	lower CI	upper CI	Posterior distribution
Overall helminth species richness					
Fixed terms					
Intercept		-0.623	-1.780	0.490	
Mass		0.218	-0.151	0.587	
Habitat strategy[a]	**Specialists**	**-0.808**	**-1.443**	**-0.161**	
Diet[b]	Fish-invertebrates	0.564	-0.577	1.708	
	Invertebrates	0.339	-0.678	1.384	
	Omnivorous	**1.199**	**0.137**	**2.239**	
Latitude		0.140	-0.217	0.498	
Geographic range		0.221	-0.078	0.520	
Migration distance		-0.172	-0.496	0.159	
Phylogenetic variance		0.005	0.928	0.999	
Residual variance		2.352	1.166	4.179	

[a] Reference category is ‘habitat generalists’

[b] Reference category is ‘fish diet’

Table 3. Summary of the effects of several predictors on the species richness for the four major helminth groups separately. To test for the effects of habitat use models included a) hosts' main wintering habitat (i.e. marine, freshwater or mixed); and b) hosts' osmotic habitat use (i.e. osmotic generalists and osmotic specialists). Asterisks denote significant effects (95% CIs did not overlap with zero); and NS = non-significant. For details of parameter statistics see Appendix S4.

	Habitat use	**Mass**	**Diet**	**Latitude**	**Geographic range**	**Migration distance**
a) Wintering habitat use						
Trematode species richness	***	***	***	NS	***	NS
Nematode species richness	NS	***	NS	NS	NS	NS
Cestode species richness	NS	NS	NS	***	NS	NS
Acanthocephalan species richness	NS	NS	NS	NS	NS	NS
b) Osmotic habitat use						
Trematode species richness	***	***	***	NS	***	NS
Nematode species richness	***	***	NS	NS	NS	***
Cestode species richness	NS	NS	NS	***	NS	NS
Acanthocephalan species richness	NS	NS	NS	NS	NS	NS

FIGURE LEGENDS

Fig. 1. Map showing sampling locations of bird populations covered in this study (for details, see Appendix S1 in Supporting Information). The sizes of the points are scaled relative to sample size (i.e., number of birds examined), and the more intense colour in some points is due to overlapping (i.e., two or more populations have been sampled at the same location).

Fig. 2. Mean number of helminth parasites species (overall and relative to each helminth group; mean ± SE) per the host population.

Fig. 3. Overall helminth species richness (corrected for sampling effort) of hosts populations occurring in freshwater (N=81), marine (N=129) and mixed habitats (N=95) outside the breeding season (a) and osmotic specialist hosts (N=208) versus osmotic generalist hosts (N=97) (b). Box-and-whisker plots give medians (horizontal line within plot), interquartile ranges (box), and ranges (bars).

Fig. 4. Overall helminth species richness (corrected for sampling effort) of hosts populations feeding on fish (N=32), invertebrates (N=186), fish-invertebrates (N=38) and omnivorous diets (N=49). Box-and-whisker plots give medians (horizontal line within plot), interquartile ranges (box), and ranges (bars).

Fig. 1

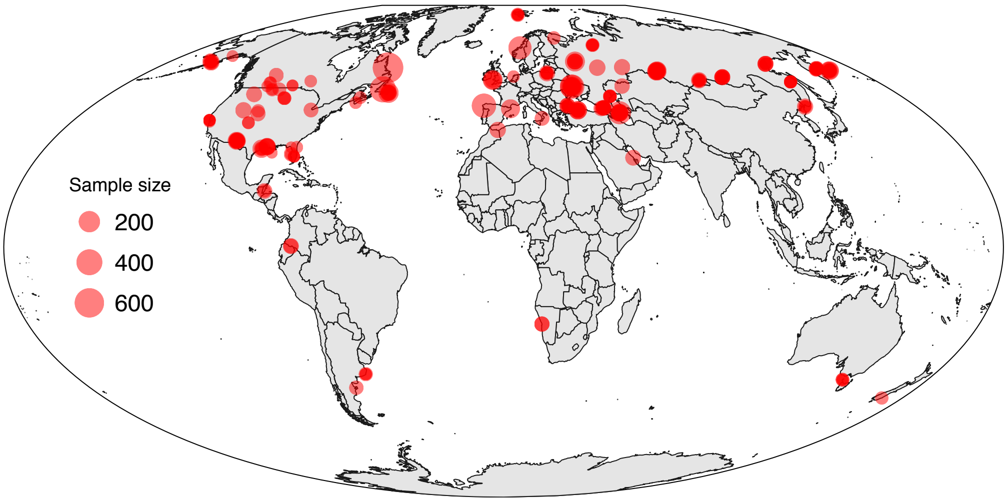


Fig. 2

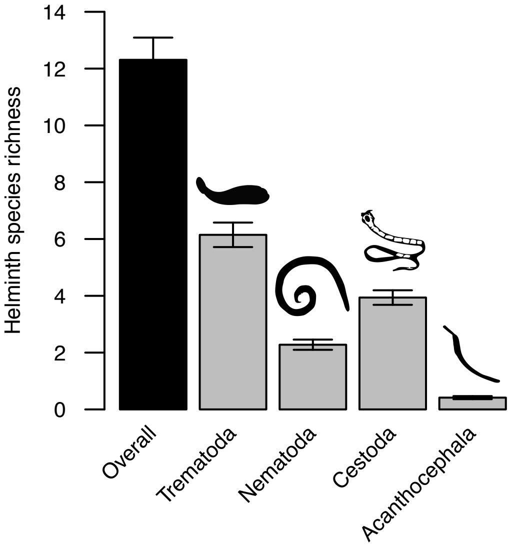

Helminth species richness
0
2
4
6
8
10
12
14
Overall
Trematoda
Nematoda
Cestoda
Acanthocephala

Fig. 3

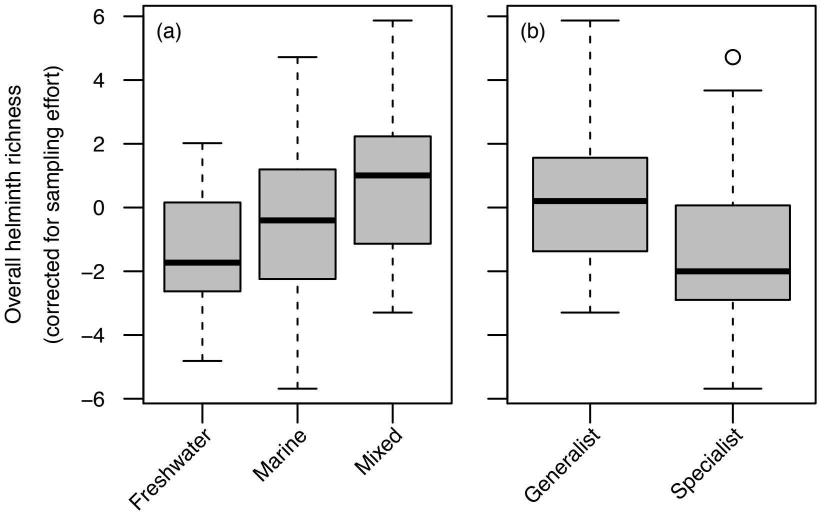
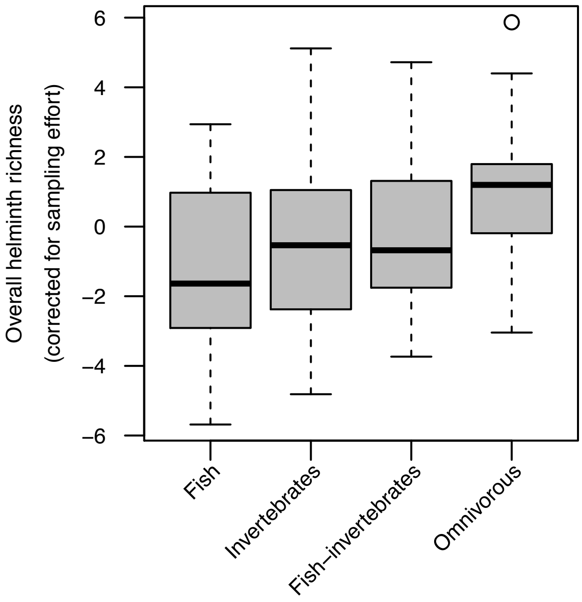

Overall helminth richness
(corrected for sampling effort)
6
4
2
0
−2
−4
−6
(a)
Freshwater
Marine
Mixed
(b)
Generalist
Specialist

Fig. 4


Overall helminth richness
(corrected for sampling effort)
6
4
2
0
−2
−4
−6
Fish
Invertebrates
Fish–invertebrates
Omnivorous