Research article

Haematozoan parasites and migratory behaviour in waterfowl

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Abstract. Although it has been suggested that migratory species are exposed to a more diverse parasite community than sedentary species, this has not previously been demonstrated. To test this hypothesis, we analysed the diversity and prevalence of infections by haematozoan parasites reported in anseriform species (ducks, geese and swans) in relation to host migration patterns. Whilst controlling for research effort, the number of parasite species or genera reported per host was positively related to migration distance, but not to breeding latitude or size of the breeding or total annual range. In species undergoing longer distance migrations, a higher proportion of individuals were infected by haematozoa. Thus, there is indeed evidence that migratory birds are more susceptible or are exposed to a more diverse parasite fauna and higher risk of infection. This may help to explain why migratory species tend to have more exaggerated, sexually selected traits as well as larger immune system organs.

Key words: blood parasites, host range, migration, parasite diversity, risk of parasitism, waterfowl

Introduction

Parasites exert important selection pressures over their hosts, and parasites may influence the evolution of bird coloration (Hamilton and Zuk, 1982; see Møller, 1990), habitat use (Piersma, 1997), or other traits (Clayton, 1991; Sheldon and Verhulst, 1996).

Migratory animals are exposed to a more diverse environment than resident ones. Furthermore, a relapse of infections can occur during migration (Valkiunas, 1991), related to the stress experienced in this part of the avian life-cycle. Consequently, there may be an interaction between parasite loads and migration patterns even if migrants are not exposed to a more diverse parasite fauna. Some studies suggest that migratory birds suffer more infections by protozoan parasites than residents (Bennett and Fallis, 1960; Dogiel, 1964; Greiner *et al.*, 1975), but the effects of phylogeny were not controlled for in

these analyses, making them difficult to interpret. Recently, Møller and Err-itzøe (1998) reported larger size of two immune system organs in migratory bird species compared with sedentary species. These differences were suggested to be an adaptation to a higher exposure of migratory species to parasites. Nevertheless, as far as we know, to date there have been no rigorous studies testing for such relationships between bird migration and diversity of parasite fauna or infection risk.

The Anseriformes (waterfowl) provide several advantages for such a study. Their haematozoan infections are well known (see, e.g. Greiner *et al.*, 1975), they show a considerable diversity of migration patterns with phylogenetically related sedentary and long distance migrants (Madge and Burn, 1988; del Hoyo *et al.*, 1992), and a particularly complete phylogeny is available for this group (Livezey, 1997a). In this paper, we compare the haematozoan parasite faunas of migratory and sedentary waterfowl, to test the hypothesis that migratory species are exposed to more parasites. We also consider the importance of range size and other aspects of the distribution of host species on their parasite fauna.

Methods

The breeding and wintering distributions of different waterfowl species (ducks, geese and swans) were calculated from the range maps of Madge and Burn (1988). Mean breeding and wintering latitudes were calculated as the averages of the northern and southernmost points of the breeding and wintering ranges. Positive values were used for latitudes in the northern hemisphere and negative values for southern latitudes. Absolute breeding latitude was the number of degrees from the equator. Migration distance was calculated as the difference between mean breeding and wintering latitudes. Migratory behaviour varies in different parts of the range of some waterfowl species (Madge and Burn, 1988; del Hoyo *et al.*, 1992). However, we used an average migration distance for each species, since available parasitological data were heterogeneous in their origin without distinguishing between different populations of a given water-fowl species. All anseriform species with a migration distance of $<1°$ were considered to be sedentary species, and the other species were considered to be migratory. Annual range size was estimated as the number of grids occupied during the breeding and the wintering season in the WORLDMAP grid, a projection of the world divided in equal-area grid squares (Gaston and Blackburn, 1996; Williams, 1996). This is likely to underestimate real annual range for some migratory species because it may exclude staging areas used during migration that are located between breeding and wintering sites. Breeding range size was calculated in a similar way.

The number of blood parasites reported in each waterfowl species was taken from the host-parasite catalogues of Bennett *et al.* (1982) and Bishop and Bennett (1992). Hence, we calculated parasite diversity for each host in two ways. First, we counted the total number of species, including genus level identifications when no other species of the same genus was reported for a given host. Secondly, parasite diversity was measured as the number of genera reported in each host species. In general, migratory waterfowl have been more studied than non-migratory waterfowl (Green, 1996), hence it might be expected that more parasites have been described for the former group. Thus, to control for the effects of research effort on the number of parasites described, we calculated the number of citations of each host species in the Wildlife Worldwide database (National Information Services Corporation, Baltimore), that includes data on more than 410,000 papers published between 1935 and October 1998. The residuals of the regression of log transformed number of parasite species or genera on log transformed number of publications were used as estimates of parasite diversity (Fig. 1). We consider the alternative measure of research effort of using the number of sources cited in Bennett *et al.* (1982) and Bishop and Bennett (1992) for each host species as inappropriate, because studies that did not detect parasites were not cited in the catalogues unless no parasite species had ever been reported for that host. Our complete data-set is available from the authors on request.

Interspecific data should not be analysed with traditional statistical methods because of the lack of independence of data from related species (Harvey and Pagel, 1991). Thus, to examine the relationship between parasite diversity or
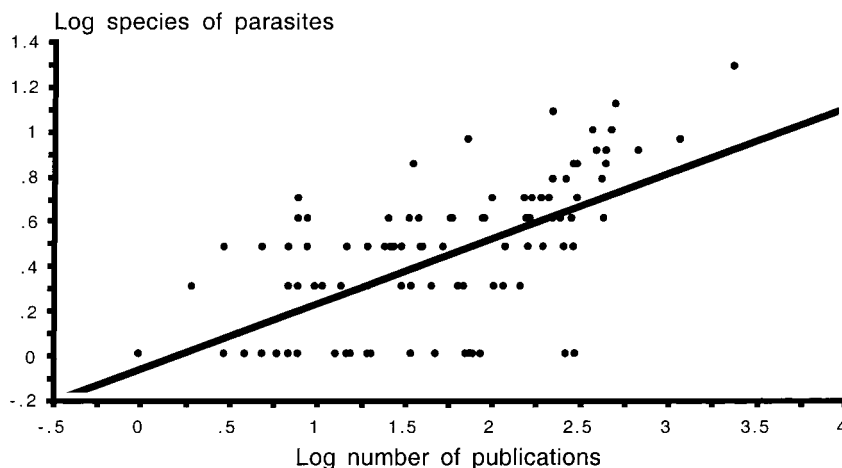

Figure 1. Relationship between the number of studies published about a host anseriform and the number of species of blood parasites reported to infect that host. $R = 0.641$, $F_{1,106} = 73.92$, $p < 0.0001$.

prevalence and different bio-geographical variables, we used independent contrasts (Felsenstein, 1985). A working phylogeny for the Anseriformes was constructed following morphological analyses (Livezey, 1986, 1991, 1995a, b, c, 1996a, b, 1997a, b; Livezey and Humphrey, 1992). Since no detailed measures of the time since divergence of different species were available, all branch lengths in the tree were set to unity (see Purvis et al., 1994). The phylogenetically independent contrasts were calculated with the CAIC programme (Purvis and Rambaut, 1995) as the differences between characters of closely related taxa, standardised by the lengths of the branches relating the taxa. The estimates of parasite diversity were transformed to the base 10 power to ensure a correct standardization of the contrasts (although analyses with untransformed data gave similar results). Multivariate regressions between contrasts were forced through the origin (Garland et al., 1992; Harvey and Pagel, 1991). The differences between migratory and non-migratory species were also examined using the Brunch procedure in the CAIC program. The relationship between migration strategy (categorical variable of two levels) and parasite diversity was examined by calculating the contrasts in function of the evolutionary changes occurring in the categorical variable (see Purvis and Rambaut, 1995). If the changes in the continuous variable are independent of changes in the categorical variable, the mean of the contrasts does not differ significantly from zero (in a t-test).

Haematozoa prevalence shows high geographical (Bennett et al., 1995; Merilä et al., 1995) and seasonal (Allander and Sundberg, 1997) variability, and its use in comparative analyses has been questioned (Clayton, 1991; Weatherhead et al., 1991). In the case of waterfowl, we found separate estimates of haematozoa prevalences for five different host species (sources: Worms and Cook, 1966; Greiner et al., 1975; Peirce, 1981; Bennett et al., 1991). The reliability of prevalence estimates derived from these data was very low (intra-class correlation = 0.16) and not statistically significant ($F_{4,8} = 1.51$, $p = 0.29$). For this reason, we could not include this variable in the regression models used in the above analyses. To test if blood parasites infect a larger proportion of individuals in migratory species, we compared data from pairs of phylogenetically related taxa differing in the extent of any migrations. Only species with more than 20 individuals sampled in each locality were included, so as to reduce the effect of sampling error, seasonality and other temporal or spatial variation on prevalence estimates (see Gregory and Blackburn, 1991). Pairs were constructed using data reported in the same study to control for the heterogeneity in prevalence reported in different studies. Two species (mallard, *Anas platyrhynchos* and black duck, *A. rubripes*) were included in two separate comparisons, but the data came from different studies of distinct populations in each case, and each comparison was with a different species. The black duck was the less migratory species in one of the comparisons, and the more

migratory in the other, due to the characteristics of the other species paired with it. Prevalences were compared with a one-tailed Wilcoxon signed-rank test, because we were testing a directional hypothesis (that migrants have higher prevalences).

Results

Increases in the migration distance of waterfowl species were positively related to increases in parasite diversity, estimated as species-publications residuals (Table 1, Fig. 2) or as genera-publications residuals (Table 2). None of the other variables characterising breeding and non-breeding distribution were significantly correlated with the diversity of parasite faunas reported in each host.

No effect of migration *per se* was detected when migration strategy was considered merely as a variable of two categories. In this analysis, mean contrasts in residual numbers of parasite species did not differ significantly from zero (mean $\pm$ SD: 0.132 ± 0.482, $t_{21} = 1.288$, $p = 0.212$). Likewise, there was no effect of migration *per se* on changes in residual number of parasite genera (0.048 ± 0.440, $t_{21} = 0.517$, $p = 0.610$).

The percentage of individual birds infected by haematozoa was higher among waterfowl species migrating longer distances ($27.2\% \pm 31.8$) than in paired species migrating shorter distances ($19.2\% \pm 27.9$, Wilcoxon signed-rank test $= 9.50$, $n = 7$, $p = 0.031$, Table 3).

Discussion

The analyses of haematozoa diversity in waterfowl suggest that migratory species were affected by a more diverse parasite fauna than non-migratory species. This was not related to a difference *per se* between migratory and sedentary species, but rather parasite diversity was directly proportional to the

Table 1. Results of multiple regression through the origin testing the relationship for waterfowl between different ecological variables and the number of haematozoa species reported in a host, estimated as the residuals from a regression of log number of parasite species on log number of scientific publications about the host species (fit of the model: $F_{5,96} = 3.01$, $p = 0.01$).

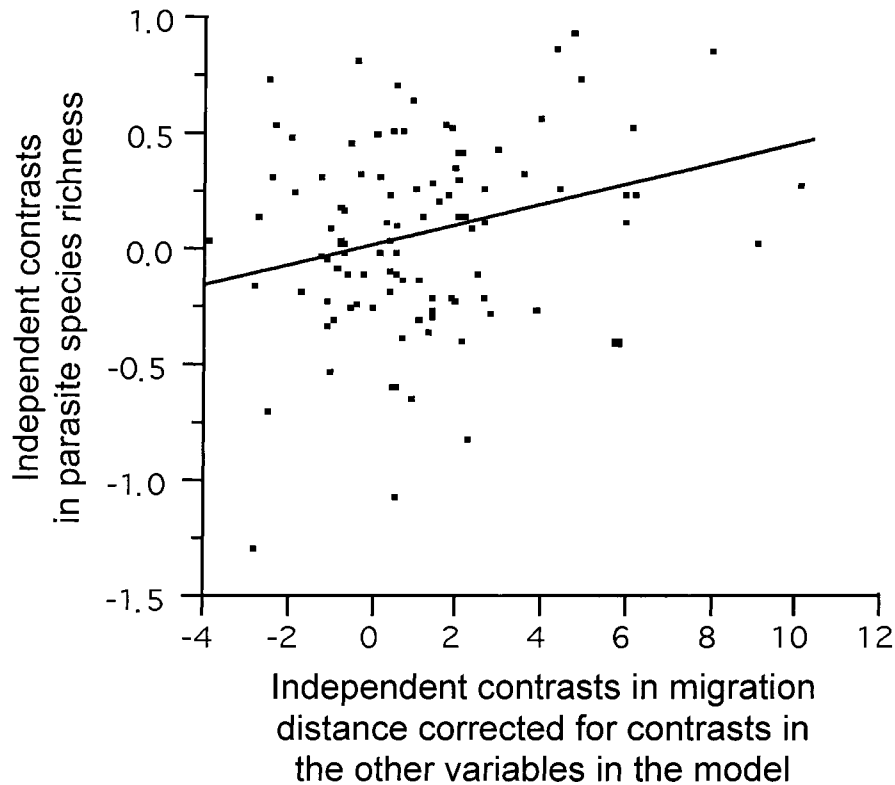| Variable	Estimate	SE	$F_{1,96}$	p
Breeding latitude	−0.0019	0.0038	0.235	0.629
Absolute breeding latitude	−0.0065	0.0080	0.645	0.424
Migration distance	0.0435	0.0141	9.488	0.003
Breeding range	0.0026	0.0129	0.040	0.843
Annual range	−0.0002	0.0090	0.001	0.979

Figure 2. Relationship of the independent contrast of parasite species diversity to the independent contrast in migration distance after controlling for the contrasts in the other variables included in the multiple regression analysis. $R = 0.290$, $F_{1,100} = 9.34$, $p = 0.003$.

distance between breeding and wintering areas. Species migrating over larger distances also seem to present a higher prevalence of infection by haematozoa.

These results support Møller and Erritzøe's (1998) hypothesis that migratory species are more exposed to parasites, and this could explain the more devel-

Table 2. Results of multiple regression through the origin testing the relationship for waterfowl between different ecological variables and the number of genera reported in a host, estimated as the residuals from a regression of log number of parasite genera on log number of publications about the host (fit of the model: $F_{5,96} = 2.57$, $p = 0.03$).

Variable	Estimate	SE	$F_{1,96}$	p
Breeding latitude	−0.0005	0.0035	0.017	0.898
Absolute breeding latitude	−0.0090	0.0073	1.506	0.223
Migration distance	0.0393	0.0129	9.276	0.003
Breeding range	0.0056	0.0117	0.225	0.636
Annual range	−0.0036	0.0082	0.196	0.659

Table 3. Comparison of the prevalence of infection by haematozoa with migration distance in waterfowl species. The classification of a species as more or less migratory is relative and based on the distance migrated by each of the species forming the pair

More migratory	Infected (%)	Examined	Less migratory	Infected (%)	Examined	Source
Anas crecca	86.30	73	*A. rubripes*	79.32	382	Bennett *et al.*, 1991
A. clypeata	0.00	26	*A. platyrhynchos*	0.00	37	Worms and Cook, 1966
Anser caerulescens	3.47	577	*Branta canadiensis*	6.45	1148	Greiner *et al.*, 1975
Anas americana	20.07	279	*A. strepera*	8.51	47	Greiner *et al.*, 1975
A. discors	7.34	1607	*A. cyanoptera*	1.41	71	Greiner *et al.*, 1975
A. rubripes	54.44	2658	*A. platyrhynchos*	27.04	1901	Greiner *et al.*, 1975
Aythya collaris	18.59	199	*Ay. americana*	12.00	50	Greiner *et al.*, 1975

oped bursa of Fabricius and spleen (two immune defence organs) in migratory bird species. The relationship between migratory strategy and parasite diversity and prevalence could potentially arise in several different ways. Highly infectious diseases may be more common in the tropics, at least in humans (Ewald, 1994), and we may therefore expect a higher risk of parasitism in species living in the tropics. This cannot be the explanation for the patterns reported in this paper, because waterfowl living in tropical areas tend to be non-migratory (see del Hoyo *et al.*, 1992; Green, 1996) and we found no effect of breeding latitude on parasite diversity. Likewise, although migratory species tend to breed at more northern latitudes than sedentary species, the lack of a relationship between parasite richness and breeding latitude suggests that the higher prevalence and parasite diversity in migratory species are not due to an exposure to a more diverse or abundant community of vectors in their breeding grounds.

The hypothesis that host range determines parasite diversity predicts a direct relationship between the size of the host's range and the diversity of the parasite fauna (Price *et al.*, 1988; Gregory, 1990). We did not find evidence for a relationship between parasite diversity and the size of the host's annual range, as opposed to the pattern reported for helminth parasites and host breeding range in waterfowl (Gregory, 1990). Further research is needed to clarify the relationship between host range size and parasite diversity over a wider range of parasite and host groups to determine if patterns of covariation between parasite diversity and host range differ for different groups of parasites. In addition, the measurement of animal range size has a number of important problems (Gaston, 1994) that may potentially have obscured a real effect of host range in our analyses.

Exposure to parasite vectors is considered an important factor explaining differences in infection rates between habitats or even species (Clayton, 1991; Sol *et al.*, 2000). Haematozoa are transmitted by blood-sucking insects (Atkinson and van Riper III, 1991), and variation in the abundance of these vectors have been considered the most likely explanation for the absence of blood parasites in birds living in some localities (see, e.g. Warner, 1968; van Riper III *et al.*, 1986), or for habitat related differences in the prevalence of blood parasites (Bennett *et al.*, 1995; Figuerola, 1999). This could also explain the higher prevalence in migratory waterfowl species, which tend to use a greater diversity of habitats during the course of the annual cycle, and may be infected even during short stopovers in habitats with high vector abundance. However, it remains possible that the patterns reported could be merely the result of differences in the susceptibility to parasites. Under this hypothesis, migratory birds experience an increased stress during migratory flight that could increase their susceptibility to parasites when arriving at stopover or wintering sites.

Migratory bird species are more brightly coloured than non-migratory species (Fitzpatrick, 1994), and the evolution of bright male colouration is correlated with increases in migration distance in the waterfowl, even when controlling for phylogenetic effects (J. Figuerola and A.J. Green, unpublished data). Thus, the relationship we have recorded between migration and exposure to parasites suggests that bright plumage may have evolved as a sexually selected indicator of migration ability (as suggested by Fitzpatrick, 1994), or may function as an indicator of parasite resistance or overall health (as suggested by Hamilton and Zuk, 1982). These two mechanisms are not mutually exclusive and can be viewed as special cases of conditional handicap models (Iwasa *et al.*, 1991). Our results suggest that 'good migration' and 'resistance to parasites' mechanisms may in fact interact due to the relationship between migration distance and exposure to parasites.

The Hamilton and Zuk (1982) mechanism relies on cyclic coevolution between heritable host resistance and parasite variability to maintain genetic variation for 'good genes'. Zuk (1991) suggested that migratory species should be less brightly coloured than resident species because this cyclic host–parasite coevolution should proceed best in bird populations in year round contact with the same parasites. However, such a prediction is based on several assumptions that may be violated. Firstly, exposure to parasites or to the effects of parasites could be higher in migratory species (this study; Valkiunas, 1991). Secondly, the assumption that coevolution between parasite virulence and host resistance is weakened by migration in birds may be erroneous, given that the immune systems of migratory birds are more developed (Møller and Erritzøe, 1998), and that parasite generation time is likely to affect the potential for the rapid evolution of host–parasite coevolution cycles (Balmford and Read, 1991).

It has previously been suggested that the evolution of bright plumage in migratory waterfowl is associated with their tendency to have short-term pair bonds, which in turn increases sexual selection (Sorenson, 1991; Batt *et al.*, 1992; see also Figuerola and Green, 2000). Thus, the relative importance of migratory behaviour, mating patterns and parasites in the evolution of plumage coloration in birds is currently unclear. Although the number of hypotheses proposing an effect of parasites on distinct aspects of host ecology and life-history is constantly increasing, we still lack basic comparative analyses identifying the environmental and ecological factors that determine parasite distribution. Consequently, most of the hypotheses rely on a variable number of untested assumptions that need to be confirmed before testing predictions arising from the hypothesis itself. In this study, using the Anseriformes, we present the strongest evidence yet that migratory species are exposed to a higher risk of parasitism and/or are more susceptible to a more diverse parasite fauna, and that parasite diversity increases with the distance between breeding and wintering areas.

Acknowledgements

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