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REVIEW

The role of parasites in ecology and evolution of migration and migratory connectivity

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Abstract All organisms are adapted to their native environment, posing problems in terms of fitness costs for individuals that leave this environment. Other species constitute an important coevolving component of this native environment, with more than half of all living organisms being parasites. All host species have evolved behavioral and physiological defenses against parasitism, and all higher organisms have evolved immunity that rely on exposure to novel substances derived from other organisms (antigens) for developing efficient defenses. The evolution of dispersal must have been affected by host–parasite interactions because dispersers and migrants inevitably encounter novel parasite strains to which they are not adapted. We provide an overview of bird migration and migratory connectivity viewed in the light of host–parasite interactions. Migratory birds generally show strong site fidelity to both breeding and wintering locations, as evidenced from studies of individuals, estimates of adult survival rates based on breeding or non-breeding captures, and studies of migratory connectivity. Connectivity is closely linked to development of the immune system and regression of immune defense organs. Empirical and theoretical evidence suggests that site fidelity is under stabilizing selection, and that offspring resemble their parents in terms of site fidelity. Populations may diverge in connectivity when the fitness benefits in terms of parasitism exceed the costs. Many species of birds have evolved migratory divides from glacial and post-glacial isolation that may constitute incipient speciation linked to divergence in parasite faunas and hence in local co-adaptation of hosts and parasites in the breeding and wintering quarters. Migration may play a role in speciation when interbreeding among hosts causes divergence in fitness costs and benefits of parasitism due to local adaptation in breeding and wintering areas. These ecological and evolutionary scenarios for migration and migratory connectivity provide a number of testable assumptions and predictions that can form the basis of future research.

Keywords Antigens · Dispersal · Immunity · Parasitism · Site fidelity

Introduction

Connectivity is defined as the degree of connection between subjects from two or more classes, with migratory connectivity reflecting unique populations of individuals in terms of separate spatial distribution during two or more seasons (Webster et al. 2002). Such connectivity is important for understanding the inter-connected nature of bird migration during different stages of the annual cycle. Connectivity also allows for a better understanding of interactions between environmental conditions at different stages of the annual cycle for life-history events, as well as for the evolution of the annual cycle. Finally, migratory

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connectivity has important conservation implications because efficient conservation cannot be achieved without considering the sites of significance for maintaining viable populations throughout the year.

The first extensive analysis of migratory connectivity and its ecological and evolutionary implications was made by Salomonsen (1955), who realized that bird species differ in the extent of overlap in distribution between breeding and wintering populations, and that such divergence is associated with divergent patterns of selection during breeding and wintering. Thus, some species have populations with different breeding areas, some with different winter quarters, and some differ with respect to both. Furthermore, such differences are often spatially organized due to leapfrog or cross-migration with more northern breeding populations migrating the longest distances thereby over-flying the breeding and winter ranges of resident or less migratory populations. These differences in migration are associated with populations with the longest migrations having late spring migration, small body size and the most southern winter quarters. These effects clearly had evolutionary implications for divergence among populations and species as reflected by different subspecies and species (Salomonsen 1955).

The main focus of the recent literature on migratory connectivity has been to connect breeding and wintering grounds of different species (reviews in Hobson 2008; Hobson and Wassenaar 2008). This initial research was subsequently followed by detailed studies of carry-over effects allowing for the study of the relative effects of environmental conditions during winter and breeding to be estimated, sometimes with a time delay (e.g., Marra et al. 1998; Norris et al. 2004; Sillett et al. 2002; Saino et al. 2004). Migratory connectivity can now be objectively quantified allowing for delineation of separate populations with specific degrees of connectivity between breeding and wintering areas (Ambrosini et al. 2009). Here, we will not review this extensive literature on connectivity, but rather we intend to provide a novel general framework for understanding the ecology and evolution of migration and migratory connectivity by focusing on parasites and host–parasite coevolution. While time, energy and aerodynamics have playing a fundamental role in developing models of optimal bird migration (Alerstam 1998; Lindström and Alerstam 1992; Alerstam et al. 2003), there has been little effort attempting to integrate studies of bird migration with predator–prey (e.g., Alerstam and Lindström 1990; Lindström 1990) or parasite–host interactions (Møller et al. 2004a). The reason seems to be that optimality approaches have focused narrowly on energy and aerodynamics, while disregarding all biological interactions. Here, we will try to redress this imbalance by making an exhaustive review of the role of parasites in the evolution of bird migration and migratory connectivity, because parasitism is the most neglected factor while simultaneously holding the greatest potential in generating novel hypotheses, predictions and tests.

The objective of this review is to provide a theoretical framework for the study of migration, connectivity and parasitism, providing testable assumptions and predictions. The main claim is that parasites and local adaptation by hosts to the parasite community provide a uniquely strong selection pressure maintaining site fidelity to breeding areas and winter quarters, thus ensuring migratory connectivity. The structure of this review is as follows. First, we present evidence suggesting that birds generally are faithful to their breeding and wintering grounds. Second, we propose that adaptation to local parasite communities may explain why migratory birds are faithful to their breeding and wintering grounds. Third, we explore the hypothesis that parasitism may explain why migrants benefit from traveling long distances. Fourth, we propose ways in which to estimate selection on connectivity and heritability of connectivity based on the assumption that hosts are adapted to local parasite strains at their breeding and wintering grounds. Fifth, we explain why site fidelity breaks down, and why migratory divides evolve and are maintained. Finally, we explore how migration and connectivity may lead to population divergence and speciation. While many of these subjects are as yet only addressed in a cursory manner in the scientific literature, we believe that a general overview is warranted, if for no other reason than as a stimulus to future research.

Animals are faithful to their breeding and wintering grounds

Birds but also other animals are highly faithful to their breeding sites (Greenwood and Harvey 1982; Clobert et al. 2001), with reproductive failure being a major cause of breeding dispersal (Greenwood and Harvey 1982; Clobert et al. 2001). Perhaps more surprisingly, birds are highly faithful to their wintering sites, often returning year after year to the same location both during migration and in winter (reviews in Berthold 2001; Newton 2008). Traditionally, site philopatry has been explained as arising from the benefits of familiarity with feeding areas. Surprisingly, we have been unable to find a single study demonstrating such fitness advantages of familiarity in migratory birds.

If migratory connectivity is strong, and breeding and wintering sites of individuals are stable over time, we should expect apparent survival rate to be the same independent of whether estimates are based on captures during breeding or winter. Peach et al. (2001) reported annual adult survival rates of two Palearctic migrants based on captures and recaptured recaptures in the African winter quarters in Malawi. Great Reed Warblers *Acrocephalus arundinaceus* had an annual survival rate of 59%, while Garden Warblers *Sylvia borin* had an annual survival rate of 54%. These values compare well with estimates based on mark–recapture analyses from the breeding grounds of 65 and 54%, respectively (Glutz von Blotzheim and Bauer 1966–1997). Furthermore, Marsh Warblers *Acrocephalus palustris* have a survival rate of 47% in winter, and a value of 49% on the breeding grounds (Kelsey 1989; Cramp and Perrins 1977–1994). Likewise, Sillett and Holmes (2002) reported survival rates based on mark–recapture analyses of American Redstarts *Setophaga ruticilla* from the breeding grounds and the wintering grounds of 46 and 43%, respectively. Apparent adult survival estimated from winter and breeding captures was very similar and positively correlated among species. This provides evidence of strong connectivity and hence for selection against dispersal.

We can learn from the exceptions to the rule that migratory connectivity is strong. So what are these? A prime example is the Arctic Tern *Sterna paradisaea* that forages over vast regions of the Southern Ocean virtually migrating the entire winter from one site to another thus showing hardly any site fidelity (Egevang et al. 2010). Many other marine birds show similar, albeit less extreme patterns. How can such migration systems with weak connectivity be maintained? Piersma (1997) suggested that certain habitats, like coastal areas, harbor fewer parasites and vectors than freshwater wetlands, creating a parasite-poor safe haven for migratory birds. Consistent with this interpretation, Mendes et al. (2005) reported lower levels of blood parasite infections in waders living in marine than in freshwater habitats, although this conclusion awaits confirmation in phylogenetic analyses.

Why are animals faithful to their breeding and wintering grounds?

High levels of site fidelity in migratory birds during breeding and winter raise questions about the nature of the selective agents maintaining such fidelity. Clearly, the null expectation would be that migration as such would allow migratory species to disperse long distances at hardly any metabolic cost, simply because they have the morphology that facilitates movement (Belliure et al. 2000). Thus, there must be important selection pressures that prevent migrants from regularly moving long distances between breeding or wintering sites in subsequent years. Here, we suggest that few agents other than parasitism constitute sufficiently strong selection to maintain site fidelity. Parasites coevolve with host immunity, and local adaptation may affect interactions between hosts and parasites. Indeed, local adaptation in host–parasite interactions may help stabilize interactions and constrain dispersal of hosts (Kaltz and Shykoff 1998). Any vertebrate host species will be affected by hundreds of species of parasites, if we rely on information from human and veterinary parasitology. Although any given parasite may only show a large-scale population structure, the fact that any single host individual has to cope with the entire community of parasites that it encounters implies that hosts can only disperse with significant risks of encountering novel parasite strains. It is this mosaic of local parasite strains that we suggest severely limits the possibilities for host individuals to disperse, and only so when fitness benefits of local reproduction are jeopardized as reflected by reproductive failure (Greenwood and Harvey 1982; Clobert et al. 2001). As an adaptation to such dispersal there exists empirical evidence showing that longer dispersal distances are associated with increased investment in immunity in Great Tits *Parus major* (Snoeijs et al. 2004). Similarly, Møller et al. (2004b) showed in a comparative analysis of common European birds that there is a strong positive association between mean natal dispersal distance and cell-mediated immunity (accounting for 28% of the variance), suggesting that there are immunological costs associated with dispersal. So far, we have no information on immunity of birds and site fidelity on the wintering grounds, but we expect similar patterns as reported for the breeding areas.

A second body of information that can be used to test for benefits of site fidelity concerns the timing of immunological ontogeny. The timing of regression of immune defense organs like the bursa of Fabricius responsible for development of the B-cell repertoire and the thymus responsible for development of T-cells coincides with exposure to all sites visited during the annual cycle and the life cycle of a bird (Møller and Erritzøe 2001). While previous studies had indicated that bursal regression occurred at sexual maturity triggered by increasing levels of sex hormones, that is clearly not the case as shown by regression of the bursa in albatrosses and other long-lived species after their return to their future breeding site, but *before* having reached full sexual maturity (Møller and Erritzøe 2001). Thus, regression of these immune defense organs and the storage of immunological information as cell memory occur after staging and wintering sites have been encountered during the first year of life in short-lived species that reproduce during the first year of their life. In contrast, long-lived species do not fully regress these immune defense organs until they have visited their future breeding grounds during the last years of their pre-reproductive life. Thus, these observations suggest why breeding dispersal is generally shorter than natal dispersal, but also how exposure to parasite communities during natal dispersal and migration can be considered a means of "vaccination" against local parasites (exposure to antigens in the environment during the first annual cycle that will allow a rapid and extensive secondary immune response upon later exposure to these same antigens). Therefore, migrants are not 'tourists that travel to warm climates without vaccination', but well-prepared travelers adapted to the environmental conditions encountered in different parts of the world.

A third line of evidence consistent with parasites playing a role in local adaption is based on the link between cognitive ability and parasitism. Parasites can sharply reduce brain function and cognitive ability in birds, mammals and humans (reviews in Møller et al. 2005; Eppig et al. 2010). Given that bird migration involves a significant amount of decision-making based on assessment of environmental cues, any impaired brain function due to parasitism is likely to have negative consequences for migratory performance. Møller (2010) has recently shown that brain size predicts arrival date of Barn Swallows *Hirundo rustica* to the breeding grounds, and that brain size predicts the time it takes to capture an individual, and also the probability of recapture.

Finally, parasites may play an important role in the evolution of connectivity. Large-scale geographical patterns of haemosporidians have shown weak evidence for connectivity being linked to parasitism (Fallon et al. 2006; Durrant et al. 2008; Pagenkopp et al. 2008). In sharp contrast, wintering Barn Swallows in South Africa could, with more than 80% certainty, be correctly assigned to communal rosts, showing strong evidence for connectivity (A.P. Møller and T. Szép, submitted). Therefore, blood parasites may not constitute the best markers for studies of connectivity because they are vector transmitted, and frequent horizontal transfer of blood parasites (e.g., Ricklefs and Outlaw 2010) makes this parasite taxon an unlikely candidate for showing such effects.

Migration and parasitism

If bird migration is affected by parasitism and the ability to cope with parasites, we should expect measures of migratory performance to correlate with parasitism and immunity. Indeed, studies of Barn Swallows from Denmark, Italy and Spain have shown that spring arrival date to the breeding grounds is predicted by the abundance of chewing lice, feather mites and blood parasites in males, but less so in females that compete much less for early arrival (Møller et al. 2004a). Furthermore, arrival date of males, but not females is predicted by T-cell mediated immune response (Møller et al. 2004a). This relationship was causal because experimental manipulation of the intensity of infection by hematophagous mites affected arrival date the subsequent spring (Møller et al. 2004a). Less extensive data for other species also suggest that spring migration, especially among individuals that compete for rapid migration, is predicted by parasite load (review in Møller et al. 2004a).

Furthermore, we should expect migratory connectivity to play a role in determining individual parasite load, thereby affecting body condition and hence migratory performance. The reason is that individuals the disperse and hence contribute to disrupting migratory connectivity will encounter novel parasites (or parasite strains) to which they are not adapted, thereby reducing the condition of that individual with consequences for ability to endure heavy workloads such as that characterizing long-distance migration. von Rönn (2010) has recently shown in studies of Barn Swallows that heterogeneity in stable isotopes of feathers grown in the African winter quarters is associated with greater diversity and prevalence of blood parasites including *Plasmodium*. Thus, individuals that winter in different areas and/or habitats become infected with *Plasmodium* parasites that are otherwise not encountered by the population ofBarn Swallows. These results are consistent with predictions concerning winter habitat specificity and parasite-mediated selection against dispersal during winter.

What are the fitness benefits of migration?

Migration has evolved because the associated fitness costs are more than compensated by benefits, and ancestral resident populations may initially have started to migrate as a consequence of intense intraspecific competition (Alerstam and Enckell 1979). Any migrant that moved away from environments with intense competition would be at a selective advantage, even when such migration was seasonal and only provided a fitness benefit during part of the annual cycle (Alerstam and Enckell 1979). Migratory birds have been shown to be more common than residents at higher latitudes in the northern hemisphere (MacArthur 1959; Herrera 1978). This pattern has recently been attributed to the greater benefits of reduced nest predation enjoyed by migrants at northern latitudes, a benefit that residents can only achieve through survival during a cold winter (McKinnon et al. 2010). Here, we suggest the alternative hypothesis that lower population density and less favorable conditions for development of parasites at high latitudes may reduce the fitness costs of long-distance migration. We can test these alternative explanations by quantifying the fitness consequences of predation and parasitism for migratory individuals breeding at different latitudes.

There are latitudinal gradients in parasites with lower diversity at higher latitudes (Rohde 1992; Guégan et al. 2001; Guernier et al. 2004). Furthermore, parasite virulence decreases with increasing latitude both in humans and in birds (Guernier et al. 2004; Møller et al. 2009). Indeed, Møller et al. (2009) showed that this latitudinal decline in parasite-induced mortality was independent of parasite taxon and of a range of different ecological factors that have been hypothesized or shown to affect the evolution of parasite virulence. There is also evidence for cell-mediated immunity of birds being stronger in temperate than in subtropical populations of the same species, with the difference in immunity being positively related to the difference in population density (Møller et al. 2006). Transmission of parasites is usually density-dependent (Combes 2001), and population density generally decreases at high latitudes (MacArthur 1972), thereby reducing the risk of transmission of parasites. Lower temperatures at high latitudes may delay or prevent development of parasites and vectors, allowing migrants a parasite-free or parasite-poor zone during reproduction when reproductive immuno-suppression may otherwise cause significant parasite-mediated mortality (Folstad and Karter 1992). Indeed, breeding at high latitudes may also constitute an alternative explanation for why waders wintering in marine habitats have few parasites (Piersma 1997; Mendes et al. 2005) because such species breed at high latitudes.

Selection for site fidelity to breeding and wintering grounds

The basic idea in this review is that migratory connectivity is a phenotypic trait with a genetic basis that can be subject to selection and hence evolve. Thus, interspecific variation in connectivity can be considered to have evolved in response to interactions among individuals belonging to different populations. Although selection on migratory connectivity has not yet been estimated, we believe that such analyses are feasible. Because each new generation of birds contains mutants and phenotypically deprived individuals with inferior migratory performance, we should a priori expect a small fraction of juveniles with an inferior migratory program and low migratory connectivity each generation. Although such individuals may sometimes encounter novel environments with an elevated probability of survival, allowing for colonization of novel environments, most often such deviant phenotypes will be selected against because they have reduced probability of survival relating to lack of local adaptation to the local parasite fauna. Thus, we should expect strong selection against deviant wintering grounds and connectivity each generation. A measure reflecting the winter location of migrants that molt during winter is the trace element and stable isotope profiles of feathers (Hobson 2008). In other words, if there is selection for site fidelity during winter, we should expect that the variance in trace element or stable isotope profile of feathers grown in the winter quarters to decrease strongly between yearlings and 2-year-old individuals, and less so in older age classes, and these selection pressures should be directly related to parasite-mediated natural selection during winter.

If trace element or isotope profile reflects the location during molt in winter, and if offspring winter in the same place as their parents, then we should expect heritability of trace element and isotope profiles. Because dispersal during winter should change the isotope and trace element profile of an individual from one year to the next, we should expect parasite load to change in parallel. Furthermore, if parasite load is partly determined by winter dispersal, and if both parasite load and isotope and trace element profile are consistent between generations, we should expect positive genetic correlations between parasite load and isotope and trace element profile. We have no data to test these predictions, although feathers collected from parents and offspring would allow such an empirical test. However, repeatability of trace element and stable isotope profiles among years provides an upper limit to heritability. Such repeatability estimates for trace element and stable isotope profiles were high in two different species (Hjernquist et al. 2009; Szép et al. 2003, 2009), suggesting that there is also scope for high heritabilities.

Evolution of migratory polymorphism and population differentiation

Many bird species have migratory divides with one part of the entire population migrating in one direction and another part in another direction, usually with separate winter quarters for populations on each side of the migratory divide. For example, many migrants have such divides at the Ural Mountains. Genetic differentiation of many animals in Central Europe reflects Ice Age refugia in the Iberian Peninsula and the Balkans (Hewitt 1996). Hence, the location of migratory divides in Europe is non-randomly distributed with disproportionately many species having such divides located in Central Europe, reflecting secondary colonization following the retreat of the ice following the last glaciations.

There is evidence for genetic differentiation of populations of birds across migratory divides (Chamberlain et al. 2000; Procházka et al. 2010), suggesting that populations on either side of the divide have been isolated for such a long time that they have become partially isolated. We should also expect partial reproductive isolation across migratory divides, as described recently for the Blackcap *Sylvia atricapilla* (Rolshausen et al. 2009). Finally, we should expect significant differences in the parasite fauna across the migratory divide because populations on either side will differentially pick up novel parasites of different geographic origins. Three studies of haemosporidians have shown very little evidence consistent with this last prediction (Bensch and Åkesson 2003; Durrant et al. 2007; Svensson et al. 2007), although frequent horizontal transfer in blood parasites (e.g., Ricklefs and Outlaw 2010) make this parasite taxon an unlikely candidate for showing any such effects.

When does site fidelity break down?

Many species migrate very long distances that exceed the shortest distance between breeding areas and possible wintering areas (Sutherland 1998). This observation is usually interpreted as evidence for lack of optimality, and that constraints may somehow explain apparent maladaptive behavior. An alternative interpretation based on host–parasite interactions and local adaptation is that birds only change their migratory behavior with difficulty because of adaptation to local parasite faunas. Eventually, some individuals and later entire populations may change their migratory direction and distance, showing that selection for such change is intense, and that micro-evolution causes rapid changes. We suggest that such changes will proceed more readily when there are no or only very few closely related species co-occurring at the breeding and the novel wintering grounds because there are fewer risks of acquisition of parasites from conspecifics and from closely related hosts.

How are migratory divides maintained? Divides can only be maintained if populations are partially reproductively isolation across migratory divides, as described for the Blackcap (Rolshausen et al. 2009). Thus, mating across a migratory divide should cause breakdown of local adaptation to parasite communities on either side of the divide at the breeding and the wintering grounds. Therefore, any individual that manages to cross the migratory divide during breeding or winter should be at a selective disadvantage.

Finally, we might expect that migratory divides have population consequences if different populations track resources in different parts of the winter quarters, and if different populations of hosts are adapted to different parasites. Species with migratory divides should be better adapted to local conditions both during breeding and winter than species without migratory divides, because gene flow will tend to break down local adaptations, and such adaptations could be maintained through reproductive isolation across divides. We could also expect that partially genetically isolated populations across divides can better buffer overall population size than a single population subject to unique environmental perturbations in its entire winter range. A potential unique measure of such adaptation is whether species with migratory divides are better able to track changes in environmental conditions than species without divides. We classified bird species as having migratory divides or not, using maps in Zink and Bairlein (1987–1995), Cramp and Perrins (1977–1994) and Glutz von Blotzheim and Bauer (1966–1997) as sources. Thus, if two or more populations migrated in different directions, having a clear geographic divide in migratory direction, we classified the species as having a migratory divide. We fully realize that some species may be misclassified as not having migratory divides because of missing information, although that should make our analyses conservative. Although such a bias should be more common in rare species with restricted ranges, we found no significant difference in global breeding range size or population size in the western Palearctic, after controlling for body mass. Consistent with our prediction, population trends across Europe based on the European bird census program (Voříšek 2008) and qualitative trends in population size across Europe assessed by BirdLife International (2004) differed between species with and without migratory divides [Fig. 1; European bird census: $F = 4.40$, $df = 1, 89$, $r^2 = 0.05$, $P = 0.039$, slope (SE) = 0.0068 (0.0032); BirdLife International: $F = 3.54$, $df = 1, 214$, $r^2 = 0.011$, $P = 0.05$, slope (SE) = 0.256 (0.136)]. Both analyses showed that species with migratory divides had increasing mean population trends, while species without such divides did not.

Migration and speciation

If populations diverge in migration patterns and migratory connectivity across a migratory divide, this could result in

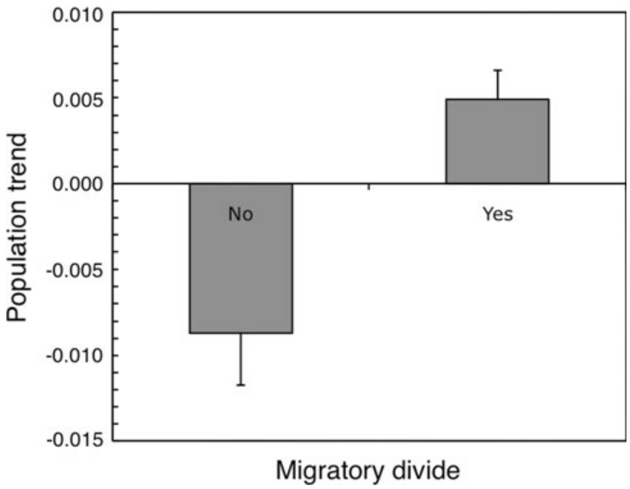

Fig. 1 Mean (SE) population trends for European breeding birds with and without migratory divides, based on population trends from the European bird census program (Voříšek 2008)

incipient speciation. While several species show divergence at the sub species level across migratory divides, as initially described by Salomonsen (1955), the extent to which subspecies have evolved as a consequence of bird migration and partial separation of populations in the winter quarters will depend on dispersal and the relative importance of selection in the breeding and the winter range (Lack 1944; Salomonsen 1955). Dispersal is responsible for the mixing of populations, with a single migrant per generation being sufficient to prevent genetic differentiation (e.g., Morjan and Rieseberg 2004). Migratory birds have longer dispersal distances than residents (Paradis et al. 1998; Belliure et al. 2000), making it less likely that migrants establish genetically isolated populations (Rensch 1933; Mayr 1942). Therefore, we might expect fewer opportunities for isolation of marginal populations in migrants than in residents for a sufficiently long time to allow population genetic differentiation. Indeed, there is a significant negative relationship between subspecies richness and migration distance among birds from the western Palearctic, after accounting for body size and breeding range size (Phillimore et al. 2006). Thus, subspecies richness is highest in residents, with intermediate levels for short-distance migrants, and the lowest levels for long-distance migrants.

We hypothesize that speciation and ultimately species richness will increase as a function of parasitism through effects on migratory connectivity. The critical test would assess whether parasite-mediated connectivity as described here preceded formation of subspecies and species. If parasites played a negligible role, we should expect isolation in allopatry (which is the predominant mode of speciation in birds; Mayr 1942) independent of parasite-mediated connectivity to account for such divergence.

Time, energy, predation and other alternative hypotheses

There are at least three explanations for the evolution and the maintenance of bird migration: energetics, predators and parasites. The evolution of migration from an ancestral state of residency may subsequently have allowed migrants to exploit seasonal environments that only provide an adequate food supply during part of the year. While time, energy and aerodynamics have played a fundamental role in developing models of optimal bird migration (Alerstam 1998; Lindström and Alerstam 1992; Alerstam et al. 2003), predator–prey (e.g., Alerstam and Lindström 1990; Lindström 1990) or parasite–host interactions (Møller et al. 2004a) may also play significant roles. There has been little effort attempting to integrate studies of bird migration, and to the best of our knowledge there are no tests attempting to distinguish among these different hypotheses. Such tests are further complicated by the fact that predation differentially affects parasitized and sick individuals (review in Møller 2008), and that parasites have negative effects on cognitive abilities and hence decision making (reviews in Møller et al. 2005; Eppig et al. 2010). Occam's razor states that simple explanations are more likely than more complex ones. However, we should not forget that, if many different phenomena can be explained by a single factor, this explanation seems more likely than having to infer many different factors. We strongly believe that the time has come to devise tests that help discriminate among alternative hypotheses for bird migration. The present review constitutes such a first step.

To advance this field further, we suggest three explicit tests that may help resolve the open question about the evolution of bird migration.

1. Transitions in migratory status. Numerous populations of birds have lost migratory habits partially or completely during the last century alone (Berthold 2001). Have these transitions in migratory behavior resulted in correlated responses in terms of energetics, susceptibility to predation and anti-predator behavior, or parasite load and anti-parasite defenses relative to the ancestral migratory populations?
2. Seasonal variation in migratory preparedness. Migrants are adapted to migration only during part of the year, possibly because such adaptations to migration are costly to maintain year-round. Thus, we believe that a test of whether migrants show a greater extent of seasonality in their energetics, susceptibility to predation and anti-predator behavior, or parasite load and anti-parasite defenses than resident populations of the same species, or resident sister taxa living at the same latitude would constitute a strong test.
3. Quantitative genetics of migration syndromes. Migration has a quantitative genetic basis, and a test of the relative importance of the underlying factors associated with the evolution of migration could be based on a quantification of the magnitude of genetic correlations between migration and energetics, susceptibility to predation and anti-predator behavior, or parasite load and anti-parasite defenses, with this analysis being replicated a reasonable number of times to allow for a rigorous test.

Discussion

We have reviewed evidence relating to the hypothesis that host–parasite interactions and local adaptation in host–parasite interactions may provide a general explanation for the evolution of migratory connectivity. While the study of host–parasite interactions has played a minor role in ornithology, recent studies of humans suggest that the main cause of mortality is infectious disease (Guernier et al. 2004), and that humans have adapted in terms of life-history to such spatial patterns of disease prevalence (Guégan et al. 2001). A recent study of asexually reproducing bdelloid rotifers escaping the particular threat of virulent parasites to asexual species through migration constitutes an important 'exception that proves the rule' (Wilson and Sherman 2010). We believe that host–parasite interactions have played an equally important role in the evolution of life history and migration of other organisms including birds. Hence, we cannot fully understand the evolution of migration and migratory connectivity unless viewed in the light of host–parasite interactions.

A very large number of studies of bird–parasite interactions are based on hemosporidians. We can trace this preponderance of studies of blood parasites to W.D. Hamilton, who pioneered the role of blood parasites in sexual selection, the maintenance of sex and the maintenance of genetic diversity in hosts and parasites (e.g., Hamilton and Zuk 1982). His contributions have greatly benefited the field, but also disproportionately focused studies of bird–parasite interactions on blood parasites. This has its disadvantages. Blood parasites are peculiar among parasites in being vector-borne and frequently horizontally transmitted even among distantly related host taxa, thereby eliminating the possibility for tight coevolution. We should not expect as tight coevolution in host–parasite systems that rely on both parasites and vectors for transmission rather than parasites alone, because 'erroneous' decision-making may happen in both parties involved. Thus, it is hardly surprising that studies of connectivity and genetic population structure of blood parasites across migratory divides of hosts show weak effects. Parasites that are not vector-transmitted, and that also constitutes the majority of all parasites (Combes 2001), show much greater evidence of co-adaptation, and studies of the role of parasites in the evolution of bird migration would benefit from a broadening of the taxonomic parasite perspective.

While we have attempted to provide a general framework for understanding the evolution of bird migration and migratory connectivity based on host–parasite interactions, obviously many open questions remain. We have to move away from demonstrating connectivity to investigating the basis for phenotypic differences in connectivity among individuals, the extent to which this is heritable, the factors associated with phenotypic plasticity in connectivity, and the patterns of selection affecting connectivity including age-specific patterns of connectivity. Most importantly, we need to design tests that allow discrimination among the underlying selective factors such as familiarity with resources, parasites and predators. Such studies will require detailed information about migratory connectivity of individuals throughout their lives. So far, only a single study has ever investigated phenotypic plasticity in migration (Balbontín et al. 2009). While recent progress in the ability to track migratory animals including birds throughout their annual cycle has caused enthusiasm, such technological progress will only prove useful if combined with careful analyses of pertinent ecological and evolutionary questions. In fact, very few scientists study migrants, very few of these estimate fitness components, and even fewer of these collect information about migration and migratory connectivity of individuals across generations and information about the underlying mechanisms.

In conclusion, we have proposed that host–parasite interactions may constitute a key to understanding ecology and evolution of migration and migratory connectivity, and tests of competing hypotheses may further our understanding of this most fascinating phenomenon. Greater focus on understanding these aspects of migration may be relevant for basic research, but also for the study of emerging diseases and conservation.

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