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**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. Here 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 the winter 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 winter 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 . Differentiation . Dispersal . Immunity . Local adaptation . Parasitism . Site fidelity . Speciation . Species richness.

58 **Introduction**

59 Connectivity is defined as the degree of connection between subjects from
60 two or more classes, with migratory connectivity reflecting unique
61 populations of individuals in terms of separate spatial distribution during
62 two or more seasons (Webster et al. 2002). Such connectivity is important
63 for understanding the inter-connected nature of bird migration during
64 different stages of the annual cycle. Connectivity also allows for a better
65 understanding of interactions between environmental conditions at
66 different stages of the annual cycle for life history events, but also for the
67 evolution of the annual cycle. Finally, migratory connectivity has important
68 conservation implications because efficient conservation cannot be
69 achieved without considering the sites of significance for maintaining
70 viable populations throughout the year.

71 The first extensive analysis of migratory connectivity and its
72 ecological and evolutionary implications was made by Finn Salomonsen
73 (1955), who realized that bird species differ in extent of overlap in
74 distribution between populations for breeding and wintering, and that such
75 divergence is associated with divergent patterns of selection during
76 breeding and winter. Thus, some species have populations with different
77 breeding areas, some with different winter quarters, and some differ with
78 respect to both. Furthermore, such differences are often spatially organized
79 due to leapfrog or cross migration with more northern breeding populations

migrating the longest distances thereby over-flying the breeding and wintering 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 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 we rather intend to provide a novel general framework for understanding 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 1991). Furthermore, marsh warblers *Acrocephalus palustris* have a survival rate of 47% in winter, and a value of 49% at the breeding grounds (Kelsey 1989; Cramp and Perrins 1984). 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 (Bellure 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

190 adaptation may affect interactions between hosts and parasites. Indeed
191 local adaptation in host-parasite interactions may help stabilize interactions
192 and constrain dispersal of hosts (Kaltz and Shykoff 1998). Any vertebrate
193 host species will be affected by hundreds of species of parasites, if we rely
194 on information from human and veterinary parasitology. Although any
195 given parasite may only show large-scale population structure, the fact that
196 any single host individual has to cope with the entire community of
197 parasites that it encounters implies that hosts only can disperse with
198 significant risks of encountering novel parasite strains. It is this mosaic of
199 local parasite strains that we suggest severely limits the possibilities for
200 host individuals to disperse, and only so when fitness benefits of local
201 reproduction are jeopardized as reflected by reproductive failure
202 (Greenwood and Harvey 1982; Clobert et al. 2001). As an adaptation to
203 such dispersal there exist empirical evidence showing that longer dispersal
204 distances are associated with increased investment in immunity in great tits
205 *Parus major* (Snøeijns et al. 2004). Similarly, Møller et al. (2004b) showed
206 in a comparative analysis of common European birds that there is a strong
207 positive association between mean natal dispersal distance and cell-
208 mediated immunity (accounting 28% of the variance), suggesting that there
209 are immunological costs associated with dispersal. So far we have no
210 information on immunity of birds and site fidelity at the wintering grounds,
211 but we expect similar patterns as reported for the breeding areas.

212 A second body of information that can be used to test for benefits of
213 site fidelity concerns the timing of immunological ontogeny. The timing of
214 regression of immune defense organs like the bursa of Fabricius
215 responsible for development of the B-cell repertoire and the thymus
216 responsible for development of T-cells coincides with exposure to all sites
217 visited during the annual cycle and the life cycle of a bird (Møller and
218 Erritzøe 2001). While previous studies had indicated that bursal regression
219 occurred at sexual maturity triggered by increasing levels of sex hormones,
220 that is clearly not the case as shown by regression of the bursa in
221 albatrosses and other long lived species after their have returned to their
222 future breeding site, but *before* having reached full sexual maturity (Møller
223 and Erritzøe 2001). Thus regression of these immune defense organs and
224 the storage of immunological information as cell memory occur after
225 staging and wintering sites have been encountered during the first year of
226 life in short-lived species that reproduce during the first year of their life.
227 In contrast, long-lived species do not fully regress these immune defense
228 organs until they have visited their future breeding grounds during the last
229 years of their pre-reproductive life. Thus, these observations suggest why
230 breeding dispersal generally is shorter than natal dispersal, but also how
231 exposure to parasite communities during natal dispersal and migration can
232 be considered a means of “vaccination” against local parasites (exposure to
233 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 to the breeding grounds, and that brain size predicts the time it takes to capture an individual, but 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 *Hirundo rustica* 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

manuscript). 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 that migratory connectivity to play a role in determining individual parasite load, thereby affecting body condition and hence migratory performance. The reason is that individuals that 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. Jan von Rönk (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 of barn 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 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 two 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 scope for high heritabilities as well.

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; Prochazka et al. 2010), suggesting that populations on either side of the divide have been isolated for so 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 origin. 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 mal-adaptive 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 *Sylvia atricapilla* (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

431 to local conditions both during breeding and winter than species without
432 migratory divides, because gene flow will tend to break down local
433 adaptations, and such adaptations could be maintained through
434 reproductive isolation across divides. We could also expect that partially
435 genetically isolated populations across divides can better buffer overall
436 population size than a single population subject to unique environmental
437 perturbations in its entire winter range. A potential unique measure of such
438 adaptation is whether species with migratory divides are better able to track
439 changes in environmental conditions than species without divides. We
440 classified bird species as having migratory divides or not using maps in
441 Zink and Bairlein (1987-1995), Cramp and Perrins (1977-1994) and Glutz
442 von Blotzheim and Bauer (1966-1997) as sources. Thus, if two or more
443 populations migrated in different directions, having a clear geographic
444 divide in migratory direction, we classified the species as having a
445 migratory divide. We fully realize that some species may be misclassified
446 as not having migratory divides because of missing information, although
447 that should make our analyses conservative. Although such bias should be
448 more common in rare species with restricted ranges, we found no
449 significant difference in global breeding range size or population size in the
450 Western Palearctic, after controlling for body mass. Consistent with our
451 prediction, population trends across Europe based on the European bird
452 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: $F = 4.40$, d.f. = 1, 89, $r^2 = 0.05$, $P = 0.039$, slope (SE) = 0.0068 (0.0032); BirdLife International: $F = 3.54$, d.f. = 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.

FIG. 1 ABOUT HERE

Migration and speciation

If populations diverge in migration patterns and migratory connectivity across a migratory divide, this could result in 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 sub-species 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. 1999; Belliure et al. 2001), 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

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

518 To advance this field further we suggest three explicit tests that
519 may help resolve the open question about the evolution of bird migration:
520 (1) Transitions in migratory status. Numerous populations of birds have
521 lost migratory habits partially or completely during the last century alone
522 (Berthold 2001). Has these transitions in migratory behavior resulted in
523 correlated responses in terms of energetics, susceptibility to predation and
524 anti-predator behavior, or parasite load and anti-parasite defenses relative
525 to the ancestral migratory populations? (2) Seasonal variation in migratory
526 preparedness. Migrants are adapted to migration only during part of the
527 year, possibly because such adaptations to migration are costly to maintain
528 year-round. Thus, we believe that a test of whether migrants show a greater
529 extent of seasonality in their energetics, susceptibility to predation and
530 anti-predator behavior, or parasite load and anti-parasite defenses than
531 resident populations of the same species, or resident sister taxa living at the
532 same latitude would constitute a strong test. (3) Quantitative genetics of
533 migration syndromes. Migration has a quantitative genetic basis, and a test
534 of the relative importance of the underlying factors associated with the
535 evolution of migration could be based on a quantification of the magnitude
536 of genetic correlations between migration and energetics, susceptibility to
537 predation and anti-predator behavior, or parasite load and anti-parasite
538 defenses, with this analysis being replicated a reasonable number of times
539 to allow for a rigorous test.

540

541 **Discussion**

542 We have reviewed evidence relating to the hypothesis that host-parasite
543 interactions and local adaptation in host-parasite interactions may provide a
544 general explanation for the evolution of migratory connectivity. While the
545 study of host-parasite interactions has played a minor role in ornithology,
546 recent studies of humans suggest that the main cause of mortality is
547 infectious disease (Guernier et al. 2004), and humans have adapted in terms
548 of life history to such spatial patterns of disease prevalence (Guégan et al.
549 2001). A recent study of asexually reproducing bdelloid rotifers escaping
550 the particular threat of virulent parasites to asexual species through
551 migration constitutes an important ‘exception that proves the rule’ (Wilson
552 and Sherman 2010). We believe that host-parasite interactions have played
553 an equally important role in the evolution of life history and migration of
554 other organisms including birds. Hence, we cannot fully understand the
555 evolution of migration and migratory connectivity unless viewed in the
556 light of host-parasite interactions.

557 A very large number of studies of bird-parasite interactions is based
558 on hemosporidians. We can trace this preponderance of studies of blood
559 parasites to W. D. Hamilton, who pioneered the role of blood parasites in
560 sexual selection, the maintenance of sex and the maintenance of genetic
561 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 system 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 constitute 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 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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807

808 **Legend to figure**

809

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

813

814 Fig. 1

815

816