

# Links between worlds: unraveling migratory connectivity

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**Migration is the regular seasonal movement of animals from one place to another, often from a breeding site to a nonbreeding site and back. Because the act of migration makes it difficult to follow individuals and populations year round, our understanding of the ecology and evolution of migrating organisms, particularly birds, has been severely impeded. Exciting new advances in satellite telemetry, genetic analyses and stable isotope chemistry are now making it possible to determine the population and geographical origin of individual birds. Here, we review these new approaches and consider the relevance of understanding migratory connectivity to ecological, evolutionary and conservation issues.**

Migration – the regular seasonal movement of individuals, often from a breeding location to a nonbreeding location and back – is a common and taxonomically widespread phenomenon in nature, and is particularly common among birds. An important, but unresolved issue in the study of migratory birds is the extent to which individuals from the same breeding area migrate to the same nonbreeding area and vice versa [1]. We term these links between breeding and nonbreeding areas ‘migratory connectivity’. The concept of migratory connectivity is distinct from other concepts of connectivity in ecology (Box 1). Moreover, migratory connectivity can be weak (diffuse) or strong, depending on the degree to which individuals from different nonbreeding areas mix during the breeding season and vice versa (Box 2).

It is generally, if somewhat implicitly, recognized that migratory connectivity has important consequences for the ecology, evolution and conservation of migratory organisms. This recognition has led to massive mark–recapture efforts in which millions of birds have been ringed. In spite of such efforts, we still have a poor understanding of migratory connectivity for most bird species, and we do not know where individual birds from high latitudes spend their winter or vice versa. Do the individuals that comprise a single breeding population all migrate to the same nonbreeding location, or do they spread out over the entire nonbreeding range of the species? This lack of understanding has a simple underlying basis: the geographical areas and numbers of individuals involved are huge, but the organisms themselves are small. Thus, the probability of identifying, on the nonbreeding grounds, a bird that was ringed on the breeding grounds is very low.

This frustrating situation could soon be resolved. Exciting new advances in remote sensing, the analysis of molecular genetic markers and chemical isotopes offer a level of resolution that was not available previously. By integrating these new advances, we

might be on the brink of addressing the vexing issue of migratory connectivity and its biological consequences. Here, we describe some theoretical implications of migratory connectivity for ecology, evolution and conservation, and review recent technological advances and their application to the study of migratory birds. These techniques can be applied to the study of other migratory organisms [2], and our hope is that this review will stimulate further research on the consequences of migratory connectivity.

## Why is it important to understand migratory connectivity?

Migratory individuals spend different periods of their annual cycle in widely separated and ecologically disparate locations. It is now clear that these periods are inextricably linked [3–5], and that the biological phenomena observed are the result of a complex set of interactions occurring over this space and time continuum. To understand the biology of any animal, resident or migratory, we need to consider how events in different stages of the annual cycle interact and influence subsequent events at the level of the individual and, eventually, the population.

## Individual reproductive success and population dynamics

Fretwell [6] provided convincing theoretical arguments that the population dynamics of organisms living in seasonal environments result from interactions of events between those seasons. He argued that breeding densities are determined, in part, by winter survival, and that winter survival is related to events that occurred during the previous breeding season. The essential idea is that individuals carry over effects from one season to the next, and that these residual effects, such as physical condition or date of arrival [5], can explain important variation in reproductive success and/or annual survival. Although intuitively appealing, it has proved difficult to determine whether Fretwell's seasonal interaction arguments also pertain to migratory species, owing, in large part, to the difficulties of tracking populations or individuals between different phases of the annual cycle.

Recently, Marra *et al.* [3] explored these ideas in migratory songbirds using stable isotopes. They showed that winter habitat quality determined both timing of spring migration and physical condition at departure, which in turn influenced arrival time and physical condition in the breeding season. These effects probably influence individual reproductive

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### Box 1. Migratory and other types of connectivity

Migratory connectivity describes the movement of individuals between summer and winter populations, including immediate stopover sites. The term 'connectivity' has also been used extensively in the field of landscape ecology, where it generally refers to the regional movement of individuals among habitat patches [a,b]. Migratory connectivity differs from landscape connectivity in both the spatial scales (the former typically involves movements over much larger distances than does the latter) and temporal scales involved (the former is, by definition, cross-seasonal, whereas the latter will often involve movement of individuals within a season).

The term 'connectivity' has also been used in the fisheries literature, where it often refers to natal dispersal from one population to another [c]. For migratory organisms, such natal dispersal would involve the movement of newborns to the wintering grounds and then back to a summer population for first breeding. As such, natal dispersal is the indirect consequence of two rounds of migratory movement.

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- c Cowen, R.K. *et al.* (2000) Connectivity of marine populations: open or closed? *Science* 287, 857–859

success, because it has been reported from studies of Nearctic and Palearctic migrants that individuals arriving early in temperate breeding areas have higher reproductive success than do those arriving later [7,8]. Other studies have shown that winter conditions are correlated with higher survival and recruitment the following summer [4,9], and one recent study has demonstrated a link between winter habitat quality, survival and reproduction on the breeding grounds [5]. Thus, important connections might exist between conditions in one season and performance in the next, but strong tests of these ideas require knowledge of connectivity between specific breeding and nonbreeding populations.

Theoretical modeling efforts have honed our thinking about year-round population dynamics and the importance of seasonal interactions [10,11]. For example, Sutherland [12] modeled total population size as the equilibrium point between density-dependent net breeding output and density-dependent winter mortality, and concluded that habitat loss would have the greatest effect in the period where density dependence is strongest. Unfortunately, parameterizing and testing this simple yet important model requires data on individuals throughout their annual cycle, which have been impossible to collect until now.

#### *Behavioral and evolutionary effects*

The previous examples illustrate how seasonal interactions can influence individual success and population dynamics, but less is known about how seasonal interactions affect other aspects of the behavioral ecology and evolution of migratory birds, such as individual breeding strategies and genetic differentiation. For example, females from poor

winter habitats might arrive at breeding grounds late to find that high-quality males are already paired. These females will probably pair with poor-quality males, and therefore might pursue extra-pair copulations [13]. Thus, winter habitat quality could affect female breeding strategies via effects on arrival date. Similarly, interseasonal effects could influence parental behavior of both sexes [14].

On an evolutionary timescale, the strength of migratory connectivity will probably affect the ability of migratory species to evolve in response to changing selective pressures, such as those that might result from climate change. Populations showing weak connectivity will probably contain substantial genetic variation for migratory behavior (e.g. direction and timing). These populations will thus be able to respond rapidly to changes in the locations of favorable breeding and wintering habitats. By contrast, populations showing strong connectivity are likely to contain little genetic variation of this sort, and their evolutionary response to large-scale climate changes could be severely hampered [15]. Although migratory direction can evolve rapidly [16], some studies suggest that there are evolutionary constraints on migratory behavior [15,17], possibly as a consequence of strong population connectivity. Such evolutionary constraints will limit the ability of a species to adapt to changing conditions, and the severity of this limitation will depend on the degree of migratory connectivity and its effects on additive genetic variation within populations.

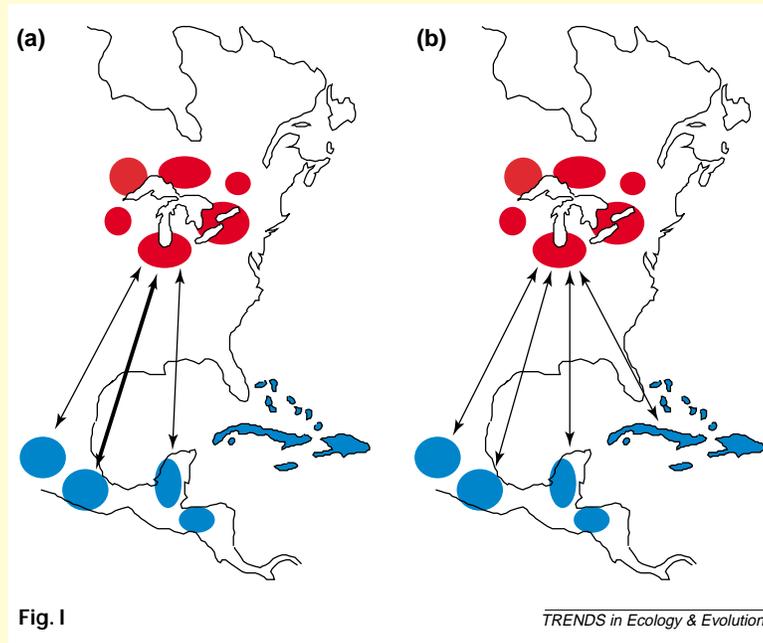
The strength of connectivity might also affect the degree to which populations of migratory birds respond to selective pressures. For example, when connectivity is weak, individuals from one breeding population migrate to a variety of winter locations, and these might vary with respect to selective pressures. Intermixing on the breeding grounds will result in gene flow among winter populations, and local adaptation to the winter conditions could be hampered. By contrast, when connectivity is strong, most individuals from one breeding population will migrate to the same winter location and will thus be subject to similar selective pressures in both seasons, potentially leading to pronounced local adaptation. Similarly, genetic and morphological divergences could develop among subregions, potentially leading to speciation. These ideas are necessarily speculative and other evolutionary hypotheses are possible. Our main point here is that tests of these hypotheses, and hence a full understanding of factors that shape migratory organisms, require knowledge of the geographical origins of migrant individuals.

#### *Conservation implications*

In addition to the ecological and evolutionary implications of migratory connectivity, there are practical reasons for determining the links between populations of migratory organisms. For example, migratory birds might transport human diseases, such as Lyme disease [18,19] and West Nile virus [20],

## Box 2. The strength of migratory connectivity

The range of a migratory species can be divided into geographically separate subranges. For many migratory species, such as the hypothetical bird whose range is shown in Fig. 1, breeding occurs in one subrange (red) but not the other (blue). Within each subrange, individuals typically are distributed among several more-or-less discrete, geographically defined populations. Populations in the breeding range are connected to those in the nonbreeding range by the migratory movement of individuals (arrows).



The strength of these connections can vary:

- Strong connectivity (Fig. 1a) occurs when most individuals from one breeding population move to the same nonbreeding location to form a nonbreeding population (thick arrow), with a relatively small proportion of individuals migrating to other winter locations (thin arrows).
- Weak (diffuse) connectivity (Fig. 1b) occurs when individuals from a single breeding population migrate to several different overwintering locations spread throughout the nonbreeding range (and vice versa). With diffuse connections such as these, a single nonbreeding population will be composed of individuals from many, widely separated breeding populations. Thus, connectivity between a nonbreeding population and any one breeding population will be weak.

These alternatives represent two ends of a continuum and, for most species, the degree of connectivity will lie between. Likewise, it is possible to have a mixture of strong and diffuse connectivity. For example, individuals from populations on one side of a geographical barrier (e.g. a mountain range) might migrate to one subset of nonbreeding populations (with weak connectivity within this subset), whereas individuals from populations on the other side of the barrier may migrate to a different subset of nonbreeding populations.

and so measurement of connectivity would yield epidemiological benefits. Similarly, understanding the factors that govern population size is fundamental to conservation and, for migratory organisms, this requires a complete understanding both of year-round geographical ranges and of specific habitat

requirements. For example, some species might be vulnerable if large portions of a breeding population migrate to a restricted wintering location or vice versa (e.g. as seen in many migratory insects, fish, reptiles and pelagic birds). Similarly, declines in breeding populations of Neotropical migratory birds have been linked to their winter habitat preferences – a pattern that is consistent with changes in forest cover in the tropics [21]. A more specific example is the endangered Kirtland's warbler *Dendroica kirtlandii*, the largely unknown winter habitat requirements of which are probably crucial to the long-term population viability of the species [22]. Without a firm understanding of the year-round geographical ranges or habitat requirements of migratory animals, it becomes difficult to develop long-term conservation plans.

### Measuring migratory connectivity

An understanding of the implications of migratory connectivity requires detailed knowledge of where breeding birds go during the nonbreeding season and vice versa. Thus, it is necessary to determine, either directly or indirectly, the geographical origins of birds sampled at particular sites. This has proven to be a difficult task, but new technologies are now emerging that hold great promise for measuring migratory connectivity.

#### Direct methods

Morphological variation can be used to assess directly migratory connectivity whenever morphotypes are geographically segregated within either the breeding or nonbreeding range. For example, different subspecies of several migrant songbird species winter in the same area of Mexico, indicating that some mixing of populations from different areas of the breeding range occurs [23]. In general, however, many species of migratory birds lack such morphological variation, limiting the applicability of this technique.

For species that lack distinct geographical races, the most direct way to monitor movement is to mark individual birds using leg-bands or similar markers. This approach has been the central focus of a massive bird-ringing effort during the past several decades that has provided useful information on migratory connectivity for some taxa, including some shorebirds [24] and waterfowl [25]. In these cases, resighting efforts have been aided by the large number of 'observers' involved (e.g. thousands of waterfowl hunters), and by the ability of the animals to carry large, visible tags. However, two major factors severely hamper the utility of this approach for monitoring major movements of many birds. First, the probability of recapturing or resighting ringed birds is extremely low, such that marking efforts often yield little insight into the connectivity between summer and winter areas. As an example, over one million pied flycatchers *Ficedula hypoleuca* have been ringed in the UK and Sweden, yet only six have been recaptured on their African wintering grounds [26,27]. Second, traditional statistical methods for

mark and recapture analysis [28] are not designed to assess quantitatively breeding population origin or admixture. This poses a significant problem for those wishing to measure migratory connectivity.

Perhaps more than any technological development in recent years, satellite telemetry has revolutionized our understanding of avian migratory pathways, and the locations of breeding and wintering sites for some species [29,30]. With this technology, a transmitter is attached to a bird and transmits location and other information (e.g. air temperature, altitude and activity level) via the ARGOS satellite system. Depending on transmitter size, power source and programming, transmitter life can be extended to several years.

In contrast to classic radio telemetry, satellite technology allows for scale-independent tracking of individual birds anywhere in the world. Thus, it provides for determination of migratory paths and locations during the annual cycle [31–33], locations of previously unknown breeding or winter sites [34], and time spent at sites along the migratory path [35–37]. In a dramatic example of its effectiveness, biologists identified a previously unknown winter site for Swainson's hawks *Buteo swainsoni* [36] and estimated that >20 000 had died from pesticides sprayed on croplands in the pampas region of Argentina [38].

In spite of their effectiveness, satellite transmitters have several drawbacks that eliminate them from use in many avian studies. Currently, the smallest transmitters weigh 18 g, and so are only useful for birds weighing  $\geq 600$  g. Furthermore, their cost (US\$4000–6000 per transmitter, including satellite-tracking time) is much greater than that of other methods, potentially restricting sample sizes. However, use of satellite telemetry eliminates the personnel, vehicle and flying costs associated with some other methods, and so they might be cost effective when all costs are considered.

#### Genetic approaches

Several genetic techniques are now commonly used in studies of wild birds (Box 3). Most have revealed genetic variation among avian populations and, in some cases, population-specific markers. These advances circumvent the problems of direct tracking and allow indirect estimates of connectivity, because 'very few birds have bands, but all have genotypes' [39].

Genetic assignment of individuals is most clear cut and powerful when genetic markers are specific to particular populations or subsets of populations. In such cases, it is relatively straightforward to assign individuals sampled *en route* or in their wintering grounds back to the appropriate breeding locations. Moreover, population 'assignment tests' can be used to identify the most probable source population for individuals sampled during or after migration, even when marker differences among populations are not fixed (Box 4).

Although simple in concept and powerful in their efficacy, population-specific markers have been used

only rarely in studies of avian migration. In part, this is because many avian geneticists have been more interested in defining mating systems and phylogenetic relationships than in defining population structure. In addition, two aspects of avian biology might limit the use of genetic markers. First, because birds can fly, there can be widespread dispersal and weak genetic differentiation among populations. Second, in the northern temperate zone, lack of differentiation might reflect relatively recent postglaciation expansion of species ranges [40,41]. As a consequence of these factors, phylogeographical analyses of migratory birds have often shown differentiation between large geographical regions and little differentiation within regions [42–46]. A combination of multiple genetic markers might greatly improve the resolution of these analyses, but this will probably require a broad screening of a large number of potential markers [e.g. randomly amplified polymorphic DNA (RAPD) or arbitrary fragment length polymorphism (AFLP) bands].

An exciting and potentially powerful genetic approach to measuring connectivity is to use the genes from organisms that birds carry rather than genes from the birds themselves. For example, area-specific genetic signatures might be traceable from avian parasites. Because vector-borne parasites can be transmitted only in the area where they coexist with the host, they could provide information about the winter or summer location of a bird at a finer scale than its own genotype will allow. The possibility of parasites providing such information has been suggested for willow warblers *Phylloscopus trochilus* studied on migration in Finland [47]. Such an approach would be even more powerful if parasite lineages, rather than morphological species, could be identified. It is now possible to amplify (and sequence) DNA of blood parasites from avian blood samples. Avian malaria of the genera *Plasmodium* and *Haemoproteus* show high sequence diversity at their cytochrome *b* gene within species of migratory birds [48], and several lineages of *Trypanosoma* have been detected in ribosomal RNA genes amplified from avian blood samples [49].

#### Biogeochemical approaches

Ratios of stable isotopes of naturally occurring elements [e.g. carbon (C), hydrogen (H), nitrogen (N) and strontium (Sr)] vary across the landscape, often in systematic ways and often at continental scales. For example, for C,  $\delta^{13}\text{C}$  (a standardized measure of the  $^{13}\text{C}:^{12}\text{C}$  ratio) is determined by the relative frequency of C3 and C4 plants at a particular locality, and this ratio varies geographically with the occurrence of these two types of plant [50]. Similarly, the H isotopic ratio ( $\delta\text{D}$ , a measure of  $^2\text{H}:^1\text{H}$ ) in precipitation varies systematically with latitude in North America [51], and Sr ratios ( $\delta^{87}\text{Sr}$ ) are associated with the type of local bedrock [52].

Isotopic ratios in the local environment are incorporated into plants during nutrient uptake and

### Box 3. Useful genetic markers

- Mitochondrial DNA (mtDNA) haplotypes have been the workhorse of avian phylogeographical and population analyses for years. Genetic differentiation and population-specific markers are likely to arise in mtDNA relatively quickly, because the effective population size for mtDNA is smaller than that for nuclear markers. Fixed or nearly fixed mtDNA differences have been found in several avian species at continent-wide scales, particularly among subspecies. Although these markers are not necessarily population-specific, regional and subspecific markers are extremely helpful in tracking movements. For example, mtDNA haplotypes have made it possible to determine the population origins and migration routes used by migrating dunlin *Calidris alpina* [a]. Within regions, however, haplotypes are often shared between populations, sometimes with a clinal change in frequency across the breeding range [a,b].
- Microsatellites have become the nuclear marker of choice for answering questions at the level of individuals and populations, mainly because of their pronounced polymorphism. However, microsatellites appear to be relatively rare in the avian genome [c], often require considerable development time, and can often show weak population differentiation [d,e]. It is therefore unsurprising that there are few published studies using microsatellites to examine population differentiation of migratory bird populations. Nevertheless, microsatellites might prove useful for assignment tests (Box 4), particularly if a large number are used or they are combined with other markers.
- Dominant nuclear markers, such as randomly amplified polymorphic DNA (RAPD) [f] or arbitrary fragment length polymorphisms (AFLP) [g], provide a useful alternative to microsatellites. These methods target arbitrary DNA fragments and require relatively little adjustment to new study species. By varying the primers used, these methods offer an almost infinite number of potential markers. Only two studies of

migratory birds have used RAPD, but results were promising. In the first [f], several populations of each of six species of shorebirds were examined for the presence and/or absence of population markers generated by screening 40–68 RAPD primers. Informative markers were found for all species, including population exclusive markers for two species. In the second study [h], RAPD markers differentiated woodcocks *Scolopax rusticola* sampled in Sweden from those sampled in Turkey, and woodcocks from Italy showed affinity to both locations. The few studies that have used AFLP uncovered weak but significant population differentiation [i,j], but no population-specific markers.

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then passed through local food chains [53,54]. Thus, the isotopic composition of animal tissues at higher trophic levels reflects that of the local environment where those tissues were grown. The resulting geographical variation in stable isotope ratios in animal tissues then provides the basis for determining the geographical origins of migratory populations across seasons and space. Therefore, in contrast to genetic markers, isotopic markers are independent of genetic (e.g. meiosis) and population (e.g. natal dispersal) processes, and have great potential for identifying the source area from which an individual might have come.

The use of isotopes to determine migratory connectivity require: (1) geographical structure of isotopic ratio distributions; (2) knowledge about where animals incorporate isotopes into tissues and their turnover times; and (3) tissue samples from individuals at different parts of their annual cycle. In the past decade, this technique has been used to identify movements of populations in a wide range of animals [2], including birds [51,52,55–57]. To date, these studies have provided information on

movement patterns only at large scales. For example, Chamberlain *et al.* [52], using both  $\delta^{13}\text{C}$  and  $\delta\text{D}$ , showed that breeding populations of black-throated blue warblers *Dendroica caerulescens* could be divided into three major regions, and that variances in isotope ratios from local winter sites were larger than those in summer, which would be expected if individuals from different breeding localities mixed in winter habitats. Similarly,  $\delta\text{D}$  signatures for five species of Neotropical migrants sampled at a single locality in Guatemala represented individuals from throughout the breeding range of each species [51]. By contrast,  $\delta\text{D}$  signatures in feathers of loggerhead shrikes *Lanius ludovicianus* indicated that birds from the same breeding areas tended to winter together [58]. Similarly, populations of willow warblers wintering in different parts of Africa (where they molt) have distinctly different  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures, and these differences could be used to identify breeding locations across Scandinavia [59].

These studies represent the first attempts at measuring population connectivity in migratory birds

#### Box 4. Population assignment tests and connectivity

Recently developed tests that use genetic information to assign individuals to specific populations [a–c] hold great promise for studies of population connectivity. For these tests, one calculates the probability that an individual's genotype might exist in a particular population. Thus, if one knows the frequencies of various genetic markers in several potential source populations (e.g. breeding locations), and samples birds during or after migration, it is possible to calculate the probability that an individual originated from each of the potential source populations. The confidence of population assignment will depend on genetic differentiation among source populations and also the number of markers used.

The effects of genetic differentiation on population assignment are illustrated in Fig. 1, which details the results of simple computer simulations. The Figure shows the log-likelihood [c] that an individual originated from breeding population A plotted against the log likelihood that it originated from population B (individuals that originated from A are shown with red symbols, those originating from B with blue symbols). Figure 1a depicts the situation in which five microsatellite loci are used to assign individuals back to breeding populations that are well differentiated ( $F_{st} = 0.14$ ). In such cases, individuals can be assigned to particular breeding populations with high confidence (99.9% of individuals assigned to correct population in 100 trials, 100 individuals per trial). By contrast, when breeding population differentiation is weak (Fig. 1b,  $F_{st} = 0.04$ , five loci used), it is more difficult to assign individuals with high confidence to either source population (90.2% of individuals correctly assigned). Population assignment tests are not specific to the type of marker used, and therefore can combine data from multiple genetic marker types.

Few studies of migratory birds have employed assignment tests, probably because it requires extensive genetic data. Haig *et al.* [d] successfully applied this approach (with randomly amplified polymorphic DNA) to identify the breeding population of shorebirds captured on migration. However, in a study of a hybrid zone between two species of chiffchaffs *Phylloscopus collybita* and *P. brehmii* showing almost fixed differences in mtDNA, four microsatellites (mean  $F_{st} = 0.05$ ) were insufficient to discriminate between hybrids and pure genotypes [e]. In recent microsatellite studies of fish [f,g] and rodents [h], the population origin of single individuals was successfully determined using an assignment approach, providing hope for the utility of this approach in future studies of migratory birds.

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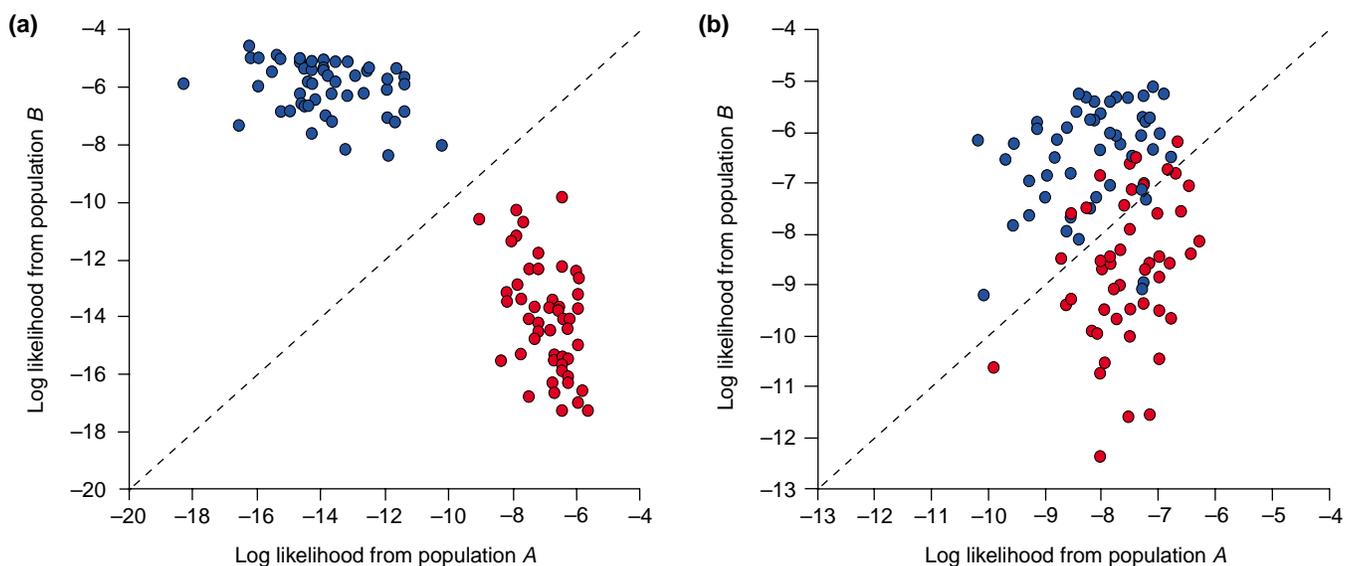


Fig. 1

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using isotopes. Future studies need more intensive winter ground sampling with larger sample sizes and also consideration of differences in sex, age and patterns of habitat occupancy. More information is also needed on the processes that affect isotopic ratios, because these processes might either sharpen or obscure

geographical signatures. For example, water stress and xeric conditions can enrich both  $^{13}\text{C}$  and  $^{15}\text{N}$  ratios, which might help identify the habitat origin of particular individuals, or might add noise to the over-all geographical pattern of these isotopes. Finally, although most isotope studies of migratory connectivity [2] have

utilized  $\delta\text{D}$ ,  $\delta^{13}\text{C}$  and  $\delta^{87}\text{Sr}$ , other isotopes could be explored, including oxygen, sulfur and lead. Indeed, the simultaneous use of multiple isotopes is likely to provide precise estimates of geographical origins [2,52].

### Conclusions and future prospects

Technological advances in measuring migratory populations hold much promise for the future study of migratory connectivity, but each has limitations. Satellite telemetry directly determines individual movements, and therefore should yield the greatest level of precision. Unfortunately, this method is suitable only for larger species, and the high cost of transmitters will limit sample sizes even for these. Genetic and isotopic markers do not require that individual birds are tracked, but inferences are indirect and depend on differentiation among populations and/or localities. The resolution of genetic markers will be set by population processes, such as dispersal, and by historical factors, such as range expansion. By contrast, the utility of isotopic markers will be determined by the amount of variation in isotopic ratios among geographical localities, by the processes that affect isotopic ratios within a locality, and by where animals incorporate these isotopic signals into body tissues.

In some cases, genetic and isotopic markers will provide resolution at a gross (regional) scale rather than at a fine (population) scale. However, combining multiple markers will vastly improve our ability to

track migratory movements at multiple scales. For example, in North America, deuterium appears to be most useful in separating northern from southern breeding populations [51,52,58], whereas mitochondrial markers mainly separate eastern from western populations [60]. Thus, by combining deuterium and mitochondrial markers, the breeding origins of North American migratory birds can be categorized into four separate regions. Additional genetic and/or isotopic markers will probably increase this resolution.

Understanding the factors operating on migratory individuals throughout the annual cycle is crucial to the production of robust models that can predict ecological responses to changes in habitat quantity and quality at diverse locations and throughout the year. Incorporating individual and population-level effects that might interact between seasons will produce more robust models of population dynamics and will provide vital information on where and when population limitation occurs. Changes in both breeding and winter habitats for many of these migratory species are occurring at an increasingly alarming pace and knowledge of migratory connectivity is crucial to preventing their decline and extinction. The technological advances that we have reviewed here should help provide vital information about such connectivity among populations of migratory birds and other animals.

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# Selection at the level of the community: the importance of spatial structure

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**To ask whether natural selection occurs at the level of the community is to consider whether communities represent a major transition in evolution – can particular community configurations evolve and maintain their integrity in the face of disruption arising from the self-interest of component individuals? This requires heritable variation among subcommunities in a landscape, and that alternative subcommunities maintain a degree of individuality in both time and space. Recently developed models show that spatial self-structuring in multispecies systems can meet both criteria and provide a rich substrate for community-level selection and a major transition in evolution.**

The long-running controversies about whether selection at several different levels of biological organization is possible, and whether it can be important, are in large part resolved. The theory of multilevel selection is well established [1–4]. Although genes or, using the lexicon of Dawkins [5], replicators are the units of selection, replicators reside within circumscribed vehicles on which selection acts directly [2]. Vehicles are entities that represent different levels of biological organization, such as genomes, cells, individual organisms and

populations. What remains controversial is the identity of levels of organization above the level of individual organisms on which selection can act, and the circumstances in which selection at levels above the individual are necessary to explain the evolution of particular traits at lower levels [2–4].

## The question and context

One of the grand unifying themes [6] in biology is how selection among selfish entities within one level of biological organization is prevented from overriding a common interest in the INTEGRITY (see Glossary) of a higher level of organization. There is a sound theoretical case that resolution of this problem has realized the major transitions in evolution that give rise to new, higher levels of biological organization: for example, evolution of cells from symbiotic protocells, of individual organisms from cells, and of societies from collectives of individuals [2,3]. Selection can act at higher levels when the variance in a trait among