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The Importance of Understanding Migratory Connectivity and Seasonal Interactions

RECENT TECHNOLOGICAL ADVANCES potentially allow researchers to follow migratory birds throughout the annual cycle, thus opening two exciting avenues for research on the ecology and evolution of migratory birds. First, researchers can examine seasonal interactions—how events or conditions in one season affect reproduction and/or behavior in another. At the population level, events on the wintering grounds may affect population dynamics on the breeding grounds, and these may be particularly important to understand in times of rapid habitat alteration and climate change. At the individual level, events on wintering grounds can affect individual breeding strategies, such as overall reproductive effort, parental care, and possibly extra-pair copulatory behavior. Second, patterns of connectivity (weak vs. strong) are likely to affect the degree to which birds are locally adapted to their wintering grounds and the rate of winter range expansion. Patterns of migratory connectivity seem less likely to affect adaptation to the breeding grounds, and it is not clear whether patterns of migratory connectivity promote or hinder the speciation process. These latter processes are more likely to be affected by natal dispersal (gene flow among breeding populations) than by migratory patterns per se. This is not to say, however, that migration is irrelevant to these processes, as natal dispersal may have a complex relationship with migration patterns, depending on how migratory behavior is transmitted from one generation to the next. On the whole, it is clear that a better understanding of migratory connectivity is needed before we can understand the forces that have shaped and continue to shape the lives of migratory birds.

INTRODUCTION

Many migratory birds spend approximately 3 months of their annual cycle on the breeding grounds, 6 months on their overwintering grounds, and 3 or more months traveling between these locations. Large-scale movements such as these—through a diverse array of habitat types and environmental conditions—create a series of complex ecological interactions that have important consequences for the biology of migratory birds. Simultaneously, these large-scale movements complicate our ability to fully understand these organisms, as it is difficult to follow them across the entire annual cycle. Despite the complexities raised by the movement of migratory individuals between summer and winter locations, recent technological advances now make it possible to detect connections between broad regions of the summer and winter ranges (e.g., Haig et al. 1997; Hobson and Wassenaar 1997; Chamberlain et al. 1997, 2000; Wennerberg 2001; Rubenstein et al. 2002; Ruegg and Smith 2002), and even greater precision appears to be within reach (Webster et al. 2002). These advances open the door for new kinds of studies and a deeper understanding of migratory birds. In this chapter we discuss two important avenues for future research on migratory birds, both of which depend on an ability to track (either directly or indirectly) individuals or populations across the annual cycle.

First, “seasonal interactions” can occur if events and conditions in one region/season affect populations and individuals in another, but these have proven difficult to study in migratory birds because of the geographical separation between summer and winter regions. For example, weather conditions and/or territory quality on the wintering grounds may affect later reproductive success on the breeding grounds (Marra et al. 1998; Sillett et al. 2000). These seasonal interactions may influence individual behavior, reproductive success, and population dynamics. Migratory birds may also face opposing conditions and selective forces on the wintering and breeding grounds, and this may affect both short-term population processes and long-term evolutionary responses.

Second, the patterns of connections among specific summer and winter populations may have important consequences for the ecology and evolution of migratory birds. For any migratory organism, breeding locations (or populations) are connected to wintering locations (populations) via the movement of individuals, and we term these connections “migratory connectivity” (Webster et al. 2002). Many different patterns of connectivity are possible (see Salomonsen 1955). For example, connectivity is strong if most individuals breeding in one area also spend the winter together at a particular location. At the opposite end of the spectrum, migratory connectivity is diffuse if a breeding population in one area is composed of individuals from a large number of separate wintering locations, and vice versa. In this latter case a breeding population is only weakly connected to any particular wintering population. Determining the strength of migratory connectivity is critical to

a thorough understanding of the ecology and evolution of such organisms as well as to the development of sound conservation strategies.

In this chapter we illustrate the consequences of both seasonal interactions and migratory connectivity for population dynamics and conservation. In particular, we emphasize the consequences for the behavior of individuals and the evolution of migratory populations.

SEASONAL INTERACTIONS, POPULATION DYNAMICS, AND INDIVIDUAL BEHAVIOR

Evidence is mounting that seasonal interactions can affect the population dynamics of migratory organisms. For example, research on waterfowl indicates that good conditions on the wintering grounds can result in better recruitment into breeding populations (Heitmeyer and Fredrickson 1981; Kaminski and Gluesing 1987; Raveling and Heitmeyer 1989). Similarly, Sillett et al. (2000) found that for the migratory Black-throated Blue Warbler (*Dendroica caerulescens*) recruitment into both wintering and breeding populations was positively correlated with fecundity the preceding summer and was also affected by the El Niño–La Niña climate cycle. Thus, winter events can affect the dynamics of breeding populations (and vice versa) when conditions on the wintering grounds affect the number of individuals that return to the summer grounds to breed.

A timely nonavian example of a seasonal interaction at the population level is that of the monarch butterfly (*Danaus plexippus*). This species spends its summers in the northern United States and southern Canada but overwinters at a small number of locations in Mexico and along the California coastline. In January 2002, unusually cold night-time temperatures at a key wintering site in Mexico resulted in massive mortality, with an estimated 200–300 million butterflies dying in just 2 days (see [www.wwf.org.mx/news_new_monarch.php]). This massive die-off on the wintering grounds will likely result in reduced monarch populations in the eastern United States and Canada. These populations may experience higher levels of reproductive success over the next several years because of reduced density dependence. This is a good example of a seasonal effect of wintering-ground mortality on breeding-ground recruitment. Interestingly, migratory connectivity also plays a role in determining the consequences of this die-off: western populations will be relatively unaffected by the mass mortality event because populations west of the Rocky Mountains overwinter in California rather than Mexico (Hobson et al. 1999). Thus, because of the pattern of migratory connectivity in this species, winter events in Mexico affect some monarch summer populations but not others; these differences may in turn be reflected in milkweed, which is the monarch’s principal food resource.

Events or conditions in one season also can have consequences for survival and reproduction of individuals in an-

other season. Consider a male warbler that breeds in the temperate zone and overwinters in the Tropics. Research on the breeding grounds indicates that for many such species, male reproductive success depends on arrival date and condition at the time of arrival, as these could affect the quality of the territory and mate that a male obtains (e.g., Lozano et al. 1996; Hasselquist 1998). In turn, arrival date and condition likely are affected by the quality of the winter territory that a male occupies and the overall conditions, such as weather, at the wintering site. Such effects of winter weather and territory quality on reproductive success during the summer are an example of a seasonal interaction.

To date, only one study provides empirical support for the idea that seasonal interactions may affect reproductive success of individual migratory birds. Using stable-carbon isotopes, Marra et al. (1998) showed that American Redstarts (*Setophaga ruticilla*) overwintering in high-quality habitats arrived on breeding grounds earlier and in better physical condition than individuals overwintering in low-quality habitats. Because arrival date and condition often are positively correlated with reproductive success on the breeding grounds (Lozano et al. 1996; Verboven and Visser 1998; Kokko 1999), this study suggests that winter territory quality has an important effect on summer reproduction. Although seasonal interactions make intuitive sense and are likely pervasive in nature, identifying their magnitude and attributing variation of a biological event to circumstances in a previous season is difficult.

Seasonal interactions may also have subtle effects on male and female behavior. For example, extra-pair copulations (EPC) are common in many populations of migratory birds (e.g., Yezerinac et al. 1995; Perreault et al. 1997; Stutchbury et al. 1997; Webster et al. 2001), and seasonal interactions may play an important role in driving EPC rates by influencing the timing of female migration and the physical condition of females upon arrival at the breeding grounds. We propose three mechanisms by which this might happen. First, seasonal interactions likely influence the timing of arrival, which influences breeding synchrony. If breeding synchrony affects EPC rates (Stutchbury and Neudorf 1998; Chuang et al. 1999), then events on the wintering grounds and/or during migration that affect female arrival date may in turn affect EPC rates. Second, wintering and/or migratory conditions may influence extra-pair behavior of individual females by affecting the costs and benefits of EPC to those females. Specifically, females with poor winter territories may arrive on the breeding grounds late (Marra et al. 1998) and find most high-quality males already paired. These females will be forced to pair socially with low-quality males (Møller 1992) and, assuming that females engage in extra-pair matings to obtain genetic benefits (Jennions and Petrie 2000; Tregenza and Wedell 2000), they will be more likely to engage in EPC than early-arriving females (who had high-quality winter territories). Thus, conditions on the wintering ground, by influencing the timing of female arrival on the breeding grounds, can affect the benefits of EPC to individual females. Finally, females from

poor winter territories may arrive on the breeding grounds in poorer condition and obtain poorer breeding territories than females from high-quality winter territories. If females in poor condition have greater difficulty in evading the mate-guarding efforts of their mates (Gowaty 1996), EPC behavior would be affected.

Thus, there are several ways that winter ground events and their influence on the timing and condition of female arrival *could* influence reproductive behavior of individual females and males. Similarly, wintering conditions and/or time needed to migrate may affect the time and energy that an individual can devote to parental care (Myers 1981). We emphasize the speculative nature of these ideas because there is little evidence to support or negate them, in large part because it has been difficult to follow females across the annual cycle. More thorough and innovative tests of these hypotheses will be possible when researchers can follow individuals or populations across seasons.

NATURAL SELECTION ACROSS THE ANNUAL CYCLE

Migration complicates selection not only because the act of migration itself selects for particular morphologies, behaviors, and physiologies, but also because migratory organisms are subject to selective pressures in different geographic locations and habitats throughout the annual cycle. For example, consider the selective pressures acting on body size in a migratory bird. Many North American migrants are sexually dimorphic in body size, with males being slightly larger than females (Dunning 1984). Most explanations regarding the evolution of sexual size dimorphism (SSD) focus on sexual selection during the breeding season (Darwin 1874; Webster 1992; Andersson 1994; Dunn et al. 2001), such as mate choice and male-male competition (Darwin 1874; Campbell 1972). However, natural selection acts year-round on individuals, and SSD is likely the result of multiple selection pressures (i.e., natural and sexual) acting differentially on males and females. For example, Darwin (1874) also proposed that sex-specific ecological adaptations could contribute to SSD (Slatkin 1984; Shine 1989; Webster 1997). Empirical evidence to support the ecological adaptation hypothesis in birds is weak and focuses primarily on sex-specific differences in bill morphology (Selander 1966, 1972; Temeles et al. 2000). In the case of a long-distance migratory bird, events and behaviors occurring during the temperate breeding, tropical winter, and migratory seasons may differ substantially from each other and, as such, may impose very different selective pressures on the sexes.

One example involves the American Redstart, which breeds in terrestrial and riparian woodlands throughout North America and winters in a variety of habitat types in the Caribbean, Central America, and northern South America (Sherry and Holmes 1997). In this species males are territorial during both summer and winter, whereas females

are territorial only during winter (Sherry and Holmes 1997). If body size plays some role in territorial defense (Marra 2000), then larger male size and SSD may result because of positive selection for size in males in both summer and winter. Selection for small body size in females also may occur during the breeding season owing to bioenergetic constraints imposed by incubation and parental care (Downhower 1976). However, a consideration of winter ecology complicates this simple interpretation. Specifically, females with territories in high-quality winter habitat (i.e., mangrove) are significantly larger than females in the poor-quality scrub habitat, whereas male body size does not vary across winter habitat types (Marra 2000). Thus, selection during the winter should favor large female size. Clearly, sexual selection during the breeding season is an incomplete explanation for SSD in this and other migratory species, and a more thorough examination of selective pressures, acting throughout the annual cycle, is needed here.

At the opposite end of the spectrum, and somewhat counterintuitively, migratory birds may actually encounter selective pressures that are more constant over the annual cycle than do nonmigratory taxa. One consequence of migratory behavior is that it allows for relatively constant ecological conditions across the annual cycle. For example, during winter, migratory organisms may be able to select and inhabit microhabitats and foraging niches that are relatively similar to their habitats and niches during the breeding season, whereas nonmigratory birds often confront dramatic seasonal differences in food and habitat. Indeed, most temperate residents switch from an insectivorous diet during the breeding season to an omnivorous or entirely granivorous diet in winter, whereas many migratory species do not. Such diet switches require morphologies suited for diverse purposes. The key point here is that a full picture of the selective forces that shape the morphology of migratory species cannot be gained without careful study of such species throughout their annual cycle. Such studies require some knowledge of migratory connectivity, because it is important to know where breeding birds spend their winters and vice versa.

MIGRATORY CONNECTIVITY AND LOCAL ADAPTATION

The above sections examined the consequences of migration and cross-seasonal effects. We now consider migratory connectivity and its effects on local adaptation (i.e., the extent to which migratory organisms can become adapted to local conditions on their breeding and wintering grounds). The relevant issues here can be seen in a simple single-locus population genetic model in which a single breeding population is connected to two different winter sites (fig. 16.1A). In this simple model we assume that this is an annual species with no overlap in generations, we ignore other possible breeding populations, and we consider a single genetic locus with two alleles (A and a). This locus affects a trait that

is under selection on the wintering grounds but not on the breeding grounds. The frequency of the A allele in wintering areas X and Y before spring migration to the breeding grounds are p_x and p_y , respectively. The proportion of individuals in the focal breeding population that migrated from wintering area Y is given by m (the remainder migrated from wintering area X). Mating on the breeding grounds is random and, as a consequence, the frequency of the A allele in winter population X after fall migration (p'_x) is a weighted mean of the frequencies in winter populations X and Y (top equation in fig. 16.1A). At the end of winter just before spring migration, the new frequency of allele A in wintering area X (p''_x) depends on the fitnesses of genotypes AA , Aa , and aa (W_{11} , W_{12} , and W_{22} , respectively) in that area (bottom equation).

This simple model has three key features. First, selection acts on this locus, favoring one allele over the other, but only during the winter (for simplicity), such that allele frequencies are affected by selection on the wintering grounds but not the breeding grounds. Second, gene exchange (reproduction) occurs only on the breeding grounds—an assumption that seems reasonable for most migratory birds. Finally, natal dispersal is limited, such that offspring tend to breed in the same general region where their parents bred. As a consequence of these last two assumptions, genetic recombination on the breeding grounds will lead to gene flow from one wintering population to another, but there will be little gene flow from one breeding population to another.

In this situation the equations describing change in allele frequency are exactly the same as those describing the joint activity of selection and gene flow in sedentary populations (Hartl and Clark 1997), with the breeding grounds serving as a conduit for gene flow from one winter population to another (fig. 16.1A). Consider a situation in which one allele (a) is favored in wintering area X but the alternative allele (A) is favored in wintering area Y (fig. 16.1B). Results from this simple model demonstrate that the ability of a population to adapt to a wintering site (i.e., frequency of the favored allele) depends strongly on the level of migratory connectivity, because this affects gene flow between wintering populations. When connectivity is strong (i.e., gene flow between wintering populations is low), local adaptation occurs quickly and is nearly complete (fig. 16.1B). Conversely, when connectivity is weak (gene flow is high), local adaptation to the wintering grounds is severely restricted.

Although greatly simplified, this model illustrates that local adaptation to the wintering grounds is severely hampered by weak migratory connectivity, because under these conditions gene flow between wintering populations is high. Strong migratory connectivity, on the other hand, limits gene flow between wintering populations and allows for local adaptation to occur. This latter situation would occur because individuals overwintering in one area would also breed together. Note that the conclusions from this simple model depend critically on random mating on the breeding grounds. If individuals mate assortatively with respect to migratory behavior, then local adaptation to the wintering

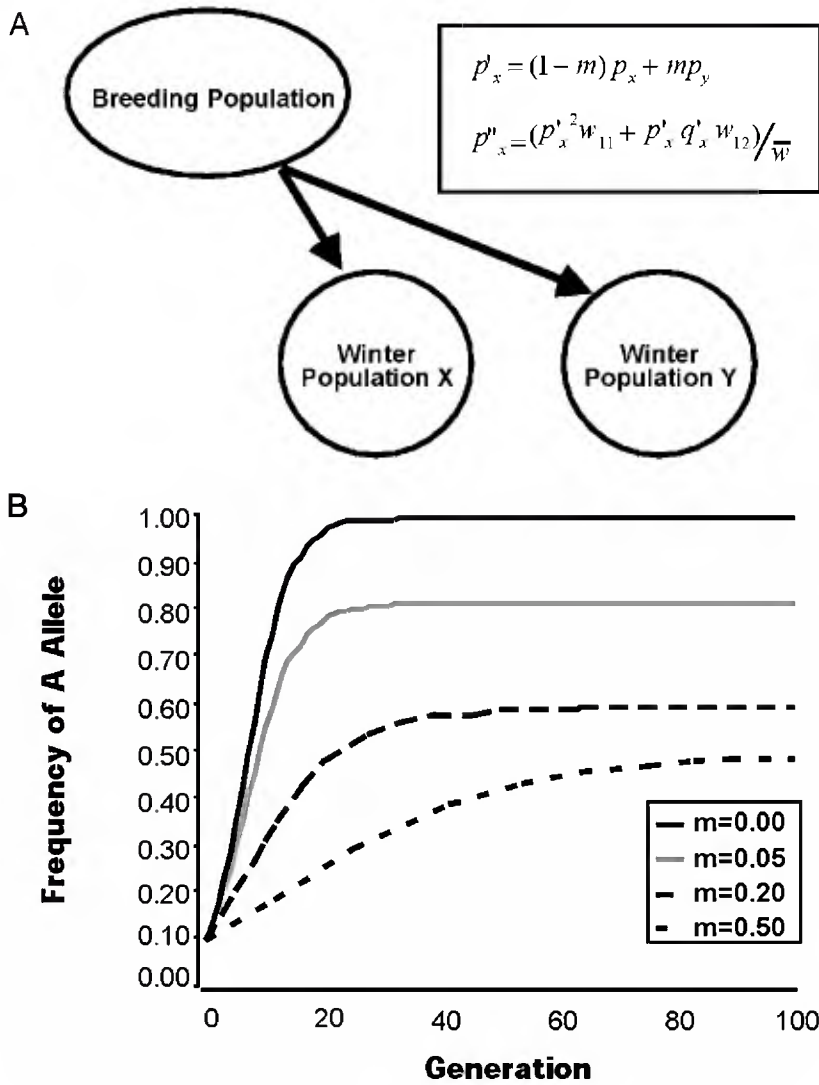


Fig. 16.1. A simple model of migration and local adaptation. Panel (A) shows that individuals from a particular breeding population can potentially migrate to two different wintering locations (X and Y). Equations in the box show the frequency of the A allele in winter population X after fall migration (p'_x) and at the end of winter just before spring migration (p''_x). Panel (B) shows the results of simulations in which natural selection favors allele A in wintering location X but allele a in wintering location Y. For these simulations there was no dominance, and fitnesses for the AA, Aa, and aa genotypes were (respectively) 0.9, 0.7, and 0.5 at wintering location X and 0.5, 0.7, and 0.9 at wintering location Y. As can be seen, the population can become well adapted to local conditions (i.e., high frequency of the A allele in wintering location X) when migratory connectivity is strong (low m , indicating low gene flow), but not when migratory connectivity is weak (high m and hence high gene flow).

grounds is enhanced. This could occur, for example, if there is pairing on the wintering grounds or during migration, or if individuals migrating from different locations arrive on the breeding grounds and form pairs at different times.

The strength of migratory connectivity and local winter adaptation might also affect expansion of the wintering range. Theoretical models suggest that range expansion can be impeded by gene flow from the center of the range to the periphery, although this also may depend on specific patterns of selection and gene flow (Holt and Gomulkiewicz 1997; Kirkpatrick and Barton 1997). Under conditions of weak connectivity, gene flow from the center of the wintering range to the periphery would be substantial, and hence expansion of the winter range would be hindered by movement of “maladapted” alleles from the center of the range to the periphery (see Kirkpatrick and Barton 1997). Conversely, under conditions of strong migratory connectivity, local adaptation to conditions at the periphery of the wintering range would be possible, and so expansion of the wintering range would be less constrained and range ex-

pansion would depend only on the rate at which migratory individuals can colonize new habitats.

Interestingly, these same arguments do not apply in reverse: connectivity will not affect local adaptation to the breeding grounds or expansion of the summer range because gene exchange does not occur on the wintering grounds (at least in migratory birds; this may not hold for some other migratory organisms, such as insects). The wintering grounds therefore do not act as a conduit for gene flow from one summer population to another. Instead, adaptation to the breeding grounds is affected by the degree to which offspring migrate to the same regions where they were born—that is, natal dispersal and the heritability of migratory behavior (Berthold et al. 1992; Berthold 1996; Pulido et al. 2001). Thus, local adaptation to the breeding grounds depends on the interplay between migration and natal dispersal and not on migratory connectivity per se. Similarly, expansion of the breeding range is not affected by connectivity, but it might depend on the malleability of migratory behavior (Böhning-Gaese et al. 1998; Bensch 1999).

MIGRATORY CONNECTIVITY AND SPECIATION

Let us move from connectivity and local adaptation to a brief consideration of connectivity and speciation. Some, possibly many, migratory bird species show connectivity patterns like that shown in fig. 16.2A, with a strong migratory divide across the breeding range but weak connectivity within each subrange (e.g., Bensch et al. 1999; Rubenstein et al. 2002). Patterns such as this are suggestive of increasing genetic divergence between the breeding populations on either side of the divide and also between the wintering populations that are connected to these diverging breeding populations. This increased divergence may lead ultimately to allopatric speciation, and situations such as this are likely to be fertile ground for the study of speciation in progress. However, speciation can occur even without a migratory divide (i.e., in situations of weak connectivity [fig. 16.2B]) if offspring tend to migrate to the same general breeding region as their parents. The key to speciation in migratory

species is likely the interaction between migration and natal dispersal (i.e., gene flow between breeding populations). Note that sympatric speciation could occur in migratory species if individuals mate assortatively according to migratory behavior. Again, this could occur if pairing occurs before individuals arrive on the breeding ground, or if individuals from different areas arrive at the same breeding location but at different times. As the degree of migratory connectivity is not known for most species of migratory birds, it is currently difficult to evaluate these hypothetical considerations.

MIGRATORY CONNECTIVITY, POPULATION DYNAMICS, AND CONSERVATION

Determining the magnitude of migratory connectivity is fundamental to advancing our understanding of many aspects of the conservation biology of migratory animals.

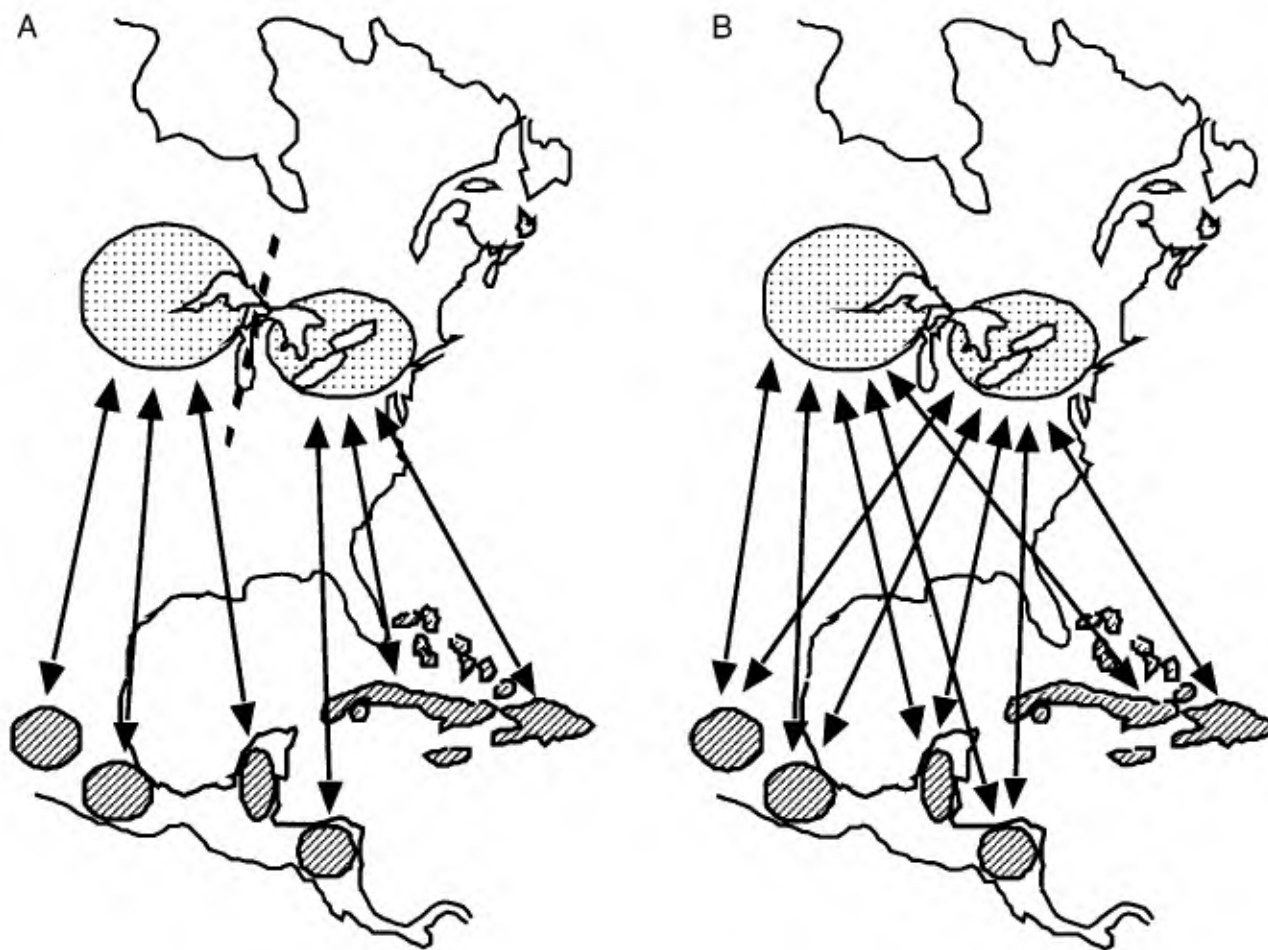


Fig. 16.2. Patterns of migratory connectivity for a hypothetical Nearctic-Neotropical migrant that breeds in eastern North America. Breeding populations are stippled, overwintering populations are cross-hatched, and arrows show migratory connections. Migratory connectivity for this species might be moderate (A), with a "migratory divide" separating western breeding populations (which overwinter in Mexico) from eastern breeding populations (which overwinter in eastern Central America and islands in the Caribbean). Alternatively, migratory connectivity may be weak (B), with both western and eastern breeding populations overwintering throughout the wintering range of the species. In this latter case birds from separate (eastern and western) breeding populations mix on the wintering grounds.

Habitat change induced by human activities, at both local and global scales, has become the primary threat for most organisms on our planet (Pimm et al. 1995; Palumbi 2001). Although both nonmigratory and migratory organisms face habitat alteration, the response of migratory organisms to anthropogenic habitat change is complicated by the geographical scale of their annual cycle. Simply put, migratory organisms must contend with human-induced habitat change on their breeding grounds, their wintering grounds, and the areas used while migrating between the two. Patterns of migratory connectivity are likely to affect the ability of migratory birds to respond to habitat alterations.

Aside from going extinct, migratory organisms may respond to anthropogenic habitat change in two general ways, both of which may be affected by migratory connectivity. First, they may accommodate the change through phenotypic plasticity or genetic adaptation. The latter can occur if habitat change is gradual rather than abrupt, as might be expected for climate change (although see Penuelas and Filella 2001; Walther et al. 2002). As an example, some migratory bird populations appear to be responding to global climate change by breeding earlier in the spring (Crick et al. 1997; McCleery and Perrins 1998; Dunn and Winkler 1999), a likely example of behavioral plasticity. As discussed above, understanding local adaptation of migratory organisms is complicated by their complex annual cycles, and it is unclear how easily migratory birds will be able to adapt to changing habitat pressures. Although adaptive responses to climate change can be rapid (Pulido et al. 2001; Warren et al. 2001), in many cases genetic adaptation will be too slow to track climate change (e.g., Etterson and Shaw 2001). This will be particularly true for migratory organisms if gene flow from peripheral populations is strong—as in the case of weak connectivity and adaptation to the wintering grounds.

Second, organisms can respond to climate change by shifting their ranges to track shifts in suitable habitat (Parmesan 1996). For migratory organisms, such changes in species range will require changes in the migratory program itself (i.e., the genetic program underlying the direction, distance, and timing of migration). Some empirical evidence suggests that such changes in the migratory program can be rapid (e.g., Berthold et al. 1992), but other evidence suggests that the migratory program may constrain range shifts or expansions (Böhning-Gaese et al. 1998; Bensch 1999) as well as other aspects of breeding biology (Both and Visser 2001).

In an important contribution, Dolman and Sutherland (1994; see also Sutherland 1996) explored interactions between habitat loss, population regulation, and the evolution of migration behavior in response to gradual loss of a wintering site. Their model considered a simple migratory species (fig. 16.3[top]) in which two separate breeding populations (A and B) migrate to two geographically separate wintering sites (X and Y). Migratory behavior is genetically determined at a single locus—individuals in breeding population X with the dominant allele (genotypes AA and Aa) migrate to winter location X, whereas individuals homo-

zygous for the alternative allele (genotype aa) migrate to location Y. Initially the populations are at equilibrium and the frequency of the alternative allele in population A (p_0) is low (i.e., most individuals in population A migrate to area X). The model considers the effect of the gradual loss (i.e., complete loss over course of 100 years) of wintering location X on the size of breeding population A. This model is applicable to situations in which habitat becomes unsuitable for an organism, whether through direct habitat modification by humans or indirect habitat change via anthropogenic climate change.

A key result from Dolman and Sutherland's model is that when connectivity is strong, such that almost all individuals from breeding population A go to wintering site X, then breeding populations can be severely affected by loss of winter habitat (i.e., reduced to extremely low numbers) and likely lost (fig. 16.3[bottom]). In contrast, when connectivity is weak, such that some individuals in the breeding pop-

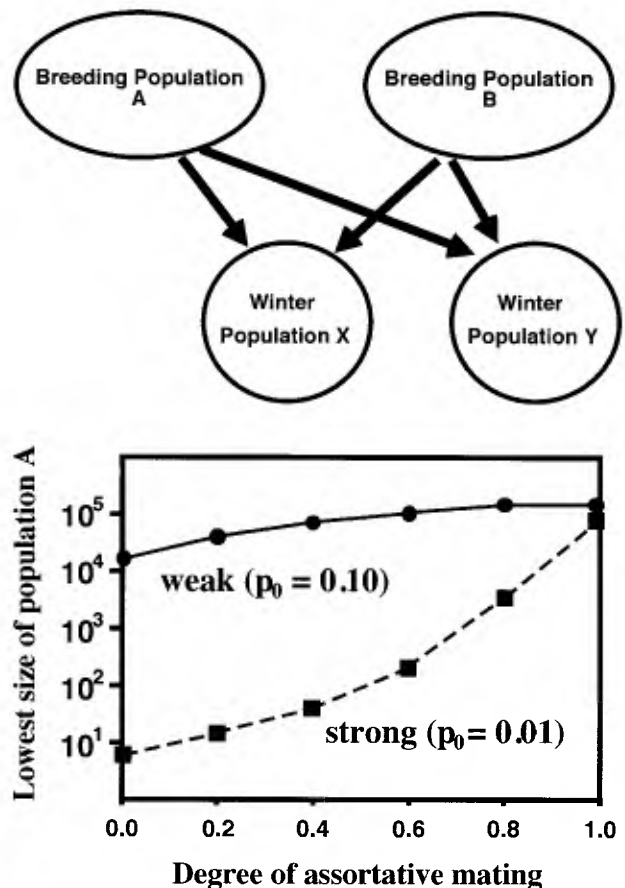


Fig. 16.3. Modeling the flexibility of migratory connectivity. The top panel shows a simple migratory species in which two separate breeding populations (A and B) migrate to two geographically separate wintering sites (X and Y). The lower panel shows the lowest size that population A reaches as a function of the degree of assortative mating (0.0 = random mating, 1.0 = completely assortative mating) and initial frequency of the alternative allele (p_0). Lines show results of simulations under conditions of strong connectivity (initial frequency of alternative migration allele $p_0 = 0.01$) and relatively weak connectivity ($p_0 = 0.10$). Bottom panel redrawn from Dolman and Sutherland (1994).

ulation migrate to winter site Y, then the effect of loss of a wintering site on the focal breeding population is greatly reduced, the reason being that birds in the breeding population quickly evolve to migrate to alternative wintering sites. The critical point here is that when connectivity is weak, substantial genetic variation for migratory behavior exists within a breeding population, thus allowing for rapid evolutionary responses of the migratory program. Note that a little bit of connectivity goes a long way: Dolman and Sutherland (1994) found that the focal breeding population is little affected by loss of a wintering site when the initial frequency of the "alternative" migration allele was only $p_0 = 0.10$ (fig. 16.3[bottom]), even though under this situation only 1% of the initial population migrates to area Y (assuming random mating). Thus, some populations may be able to evolve new patterns of migratory connectivity in response to habitat loss and climate change, except in cases where connectivity is very strong (i.e., situations in which virtually no individuals migrate to alternative sites). This conclusion, of course, relies on the assumption that some of the wintering locations used by a breeding population are less severely affected by human activities. Also important to consider is the effect of assortative mating on the example shown in fig. 16.3[bottom]. When individuals mate assortatively according to migratory behavior, new patterns of migratory connectivity will evolve more rapidly and the breeding population is unlikely to be reduced to very low numbers.

Finally, patterns of migratory connectivity also have implications for conservation and management plans (see Esler 2000 for discussion). For example, when connectivity is strong it may be possible to manage or maintain particular breeding or winter populations by protecting critical breeding sites. An excellent example of where such an approach has worked is management of the Kirtland's Warbler by protecting the remaining coniferous breeding habitat. Interestingly, little is known of the winter ecology of this species. In contrast, in cases where migratory connectivity is weak, protection efforts will be more challenging and must include larger geographic areas for the protection of a species.

FUTURE DIRECTIONS

In this chapter we have discussed the importance of understanding migratory connectivity and seasonal interactions. We have argued that such seasonal interactions are likely to be common and to have important consequences at the level of both the population and the individual. At the population level, events on the wintering grounds may affect population dynamics on the breeding grounds (e.g., Sillett et al. 2000), and these may be particularly important to understand in times of rapid habitat alteration and climate change (Saether et al. 2000). At the individual level, events on the wintering ground can potentially affect individual breeding strategies, such as overall reproductive effort

(Marra et al. 1998), parental care (Myers 1981), and possibly extra-pair copulatory behavior. Other areas of research, such as an examination of selective pressures and habitat choice throughout the annual cycle, similarly require a better understanding of migratory connectivity.

We have also argued that patterns of connectivity (weak vs. strong) are likely to affect the degree to which birds are locally adapted to their wintering grounds and the rate of winter range expansion. In contrast, patterns of migratory connectivity seem unlikely to affect adaptation to the breeding grounds, and it is not clear that patterns of migratory connectivity promote or hinder speciation. These latter processes are more likely to be affected by natal dispersal (gene flow between breeding populations) than by migratory patterns per se. This is not to say, however, that migration is irrelevant to these processes, as natal dispersal may have a complex relationship with migration patterns depending on how migratory behavior is transmitted from one generation to the next. On the whole, it is clear that a better understanding of migratory connectivity is needed before we understand the forces that have shaped and continue to shape the lives of migratory birds.

Our review has revealed several important avenues for future research. First, recent studies have suggested that events in one season can affect populations in another (e.g., Marra et al. 1998; Sillett et al. 2000; Gill et al. 2001), but in most cases we can only guess at the mechanisms underlying these seasonal interactions. Research in this area has been hampered by the logistic difficulties of tracking individuals across seasons. Thanks to recent technological advances (Webster et al. 2002), we will soon be able to follow individuals, or at least populations, throughout the annual cycle.

Second, the potential effects of winter conditions and events on breeding-season behavior have received little empirical or theoretical attention. Most of the work on extra-pair copulations, for example, has focused on potential genetic benefits of EPC to females, but far less attention has been paid to extrinsic factors that might affect a female's propensity to seek EPC (Griffith et al. 2002). Winter conditions, such as the quality of a female's winter territory, may play a significant role here by affecting the timing of arrival on the breeding grounds and/or the female's condition during breeding. Similarly, winter conditions may also affect individual parental care and other breeding-season behaviors, and thereby provide a link to population dynamics as described above. These possibilities remain unexplored. We must also gain a better understanding of how the breeding season influences events during fall migration and the subsequent winter period.

Finally, seasonal interactions are likely to influence the evolution of migratory organisms and vice versa. Theoretical genetic models suggest that migratory connectivity should affect local adaptation and range expansion, but empirical data from migratory birds are lacking. Böhning-Gaese et al. (1998) and Bensch (1999) have examined the possibility that migratory behavior itself affects range size, but these analyses are preliminary and more detailed exam-

ination is necessary. In particular, the interplay between migration and local adaptation requires examination in the same way that the relationship between gene flow and local adaptation has been explored for nonmigratory populations (Dias and Blondel 1996; Smith et al. 1997; Blondel et al. 1999). In summary, understanding the population connectivity of migratory animals, and ultimately how the periods of the annual cycle interact, will undoubtedly provide unexpected advances in our knowledge of the basic ecology and evolution of these organisms.

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