

Migratory connectivity

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INTRODUCTION

Migration represents one of the most complex and fascinating behaviors in nature. Simply defined, migration is the repeated movement of individuals from one region to another, and can occur over daily, seasonal, and annual time-frames. Migrations can occur over tens of thousand of kilometers, as in the case of the Arctic tern (*Sterna paradisaea*) moving essentially from pole to pole (Hatch 2002), or it can simply involve movements over distances as small as meters, as is the case of phantom midge larvae (*Chaoborus* spp.) moving from lake benthos during the day to the open water at night (Roth 1968). Migratory behavior has enormous taxonomic breadth including species of anadromous fish that leave natal rivers to spend several years at sea eventually returning to the same river to spawn and die (Hodgson and Quinn 2002), to the annual migrations of black rat snakes (*Elaphe obsoleta*) from winter hibernacula to summer breeding and foraging areas (Blouin-Demers and Weatherhead 2002), to the spectacular seasonal movements of long-distance migratory birds between temperate breeding and tropical winter environments (e.g., Keast and Morton 1980; Hagan and Johnston 1992). Movements such as these, by such taxonomically diverse groups of organisms, define migratory behavior and motivate the need to understand how these movements interact with and are modified by the physical structure of their environment.

For the majority of migratory birds, the spatial areas traveled are vast and the individuals too difficult to follow throughout the annual cycle. We know basic annual range distributions for most migratory birds but still have almost no information on where specific individuals, age classes, sex classes, or populations disperse during winter or the subsequent breeding season (Alerstam 1990). The geographic linking of individuals or populations between different stages of the annual cycle, including between breeding, migration, and winter stages, is known as *migratory connectivity* (Webster *et al.* 2002). In this chapter, using primarily migratory birds as an example, we compare and contrast migratory connectivity with other forms of ecological connectivity, consider the implications that different strengths of migratory connectivity have for population dynamics, review the latest techniques available to measure migratory connectivity, and finally consider the role of relative abundance in assigning the geographic origin of migratory animals.

MIGRATORY CONNECTIVITY

This book is a tribute to the importance of ecological connectivity, which, as defined in this volume, is the process of movement and how landscape structure can influence movement between habitats. Owing to the importance of this concept to basic ecological theory and conservation, connectivity research has a rich history in ecology (Taylor *et al.* 1993; Tischendorf and Fahrig 2000). Examples of connectivity considered in this book, and nicely summarized by Crooks and Sanjayan (Chapter 1), include hydrologic connectivity (Pringle Chapter 10), connectivity in diseases (McCallum and Dobson Chapter 19), and connectivity within marine ecosystems (DiBacco *et al.* Chapter 8; Harrison and Bjorndal Chapter 9).

These and other concepts of ecological connectivity, particular those in landscape ecology, consider how habitat and landscape structure influence the movement of organisms through space (e.g., Nebel *et al.* 2002; Sanzenbacher and Haig 2002a, 2002b; Taylor *et al.* Chapter 2). Currently, most studies of migratory connectivity are less concerned with such issues because the large spatial scales involved complicate our ability to understand how landscape and/or atmosphere might influence the movement of individuals between breeding areas and wintering areas. For most migratory animals, seasonal movement from point A to point B is a black box (see Webster *et al.* 2002; Webster and Marra 2005). For migratory birds, although the atmosphere likely plays a role in determining

movement dynamics and degree of connectivity (Marra *et al.* 2005; Gauthreaux *et al.* 2005), little is known about how atmospheric factors influence the establishment of migratory routes. Similarly, as birds migrate over land, habitat configuration and structure undoubtedly influence movement dynamics. For example, as birds migrate north in spring or south in autumn, they stop over periodically in habitat patches to replenish fat stores critical for fueling migratory journeys (Lyons and Haig 1995; Nebel *et al.* 2000). These stop over sites vary in quality and spatial array across the landscape, but the degree to which migratory movements are influenced by the structure, quality, and connectivity of the landscape is poorly known. In general, our knowledge of stop over ecology has been severely hampered by the fact that we can only study birds for short durations; they may migrate in small, undetected groups and they may only land at night to forage. Understanding how bird populations are geographically connected during migration will provide new spatial and temporal resolution that should open unique insights into migration biology and ultimately the protection of important stop over areas.

Currently, migratory connectivity de-emphasizes how landscape structure influences a population's distribution and instead focuses on retention of breeding population structure on the non-breeding grounds (and vice versa), as well as how conditions and events in non-breeding areas affect populations in breeding areas (and vice versa) (see Webster and Marra 2005). In the future, technological advances will likely improve our ability to track migratory individuals (Wikelski *et al.* 2003; Cochran and Wikelski 2005) and thereby allow researchers to directly assess factors such as the effect of landscape structure on migratory movements.

WHY STUDY MIGRATORY CONNECTIVITY?

The fact that individuals spend time each year in two or more widely separated geographic areas has obvious but poorly understood consequences for the biology and conservation of migratory animals. For example, factors and events on the non-breeding wintering grounds (e.g., climate and weather patterns, deforestation, wetland stabilization or drainage) may affect individual condition, subsequent reproductive success, and recruitment on the summer breeding grounds (Heitmeyer and Fredrickson 1981; Kaminski and Gluesing 1987; Marra *et al.* 1998; Norris *et al.* 2004). Subsequent differences in reproductive success in

summer can lead to changes in winter population size (Sillett *et al.* 2000). Likewise, events at migratory stop over sites may affect the timing of arrival and the physical condition and survival of birds onto breeding and/or wintering areas (Myers 1983; Ydenberg *et al.* 2002).

Such effects, termed *seasonal interactions* (Fretwell 1972; Myers 1981; Webster *et al.* 2002; Webster and Marra 2005), are likely to be most pronounced at the population level with strong connectivity (i.e., if individuals breeding together in one location also winter near each other; termed *allohiemy* by Salomonsen (1955)), but may be less pronounced if there is weak connectivity (i.e., if individuals breeding in one area spread out over a large geographic range for the winter period; termed *synhiemy* by Salomonsen (1955)). For example, American redstarts (*Setophaga ruticilla*) breeding at the Hubbard Brook Experimental Forest in New Hampshire could either remain clustered in one specific region on the wintering grounds (strong connectivity) or disperse equally across their entire winter range (weak connectivity). The former scenario can have profound implications for population dynamics if, for example, breeding populations are wintering within a country undergoing rapid deforestation. Alternatively, if migratory connectivity is indeed weak and the Hubbard Brook population disperses throughout the wintering grounds, regional land-use practices on the wintering grounds will likely have less of an impact on population abundance. An important point of clarification here is that our definitions of weak versus strong migratory connectivity counter those in the traditional connectivity literature. Specifically, we predict if we find strong migratory connectivity it suggests that populations are tightly linked and have experienced minimal dispersal or mixing. Strong landscape connectivity predicts the exact opposite—high rates of movement and dispersal. Further explanations below will clarify this distinction.

The challenge in studying migratory connectivity is to understand not only the geographic connections among breeding and non-breeding populations (Webster *et al.* 2002) but also how these connections influence the ecology, evolution and conservation of migratory species (Webster and Marra in press). For example, under strong migratory connectivity, gene flow among subpopulations is limited and we expect greater levels of local adaptation and potential for speciation (Webster and Marra in press). Migratory connectivity is also critical to conservation efforts as is illustrated with migratory salmonids in which evolutionary and management units are defined by the timing and geography of migratory breeding “runs” (Waples 1991; Neville *et al.* Chapter 13).

An analogous situation exists in the management of North American waterfowl populations which, for management purposes, are defined in terms of geographic subpopulations based on similarity of migratory pathways and wintering grounds (Bellrose 1976). Understanding the connectivity of these populations (referred to as the “derivation of harvest” problem in waterfowl management – see “Statistical approaches for estimating migratory connectivity” section below) is critical in the management of all game species. As a result, considerable effort has been devoted to the assessment of migratory connectivity using band recovery data with species such as waterfowl (Munro and Kimball 1982) and mourning doves (Nichols and Tomlinson 1993).

Notable examples also exist for non-game species where the ability to link breeding and non-breeding areas has affected critical management decisions. Perhaps most dramatic was the identification of specific Swainson’s hawk (*Buteo swainsoni*) wintering sites in Argentina after the population of breeding birds in the western USA and Canada experienced a significant decline (Goldstein *et al.* 1999). Use of satellite transmitters provided locations of fields where excessive monocrotophos, an organophosphate insecticide that farmers apply to alfalfa fields for grasshopper control, was being used and ultimately where tens of thousands of Swainson’s hawks were found dead. An international agreement has now been signed and the pesticide will not be used on grasshoppers or alfalfa fields (American Bird Conservancy 1996). With the endangered piping plover (*Charadrius melodus*), over 20 years of banding data indicated birds exhibit strong fidelity to winter and breeding sites, although populations mix in winter sites (Haig *et al.* in press). This discovery has allowed managers to pay more attention toward protecting specific winter sites. A similar situation has arisen for the buff-breasted sandpiper (*Tryngites subruficollis*), where their small and declining numbers in North America have also been found wintering in specific fields in Argentina leading to further recognition of the importance of their winter sites (Lanctot *et al.* 2002). In the endangered Mariana moorhen (*Gallinula chloropus guami*), a subspecies of less than 300 birds on four islands (Takano and Haig 2004a), identification of movements between wet and dry seasons indicated inter-island movements of birds between the islands of Saipan and Tinian, but only local movements on Guam (Takano and Haig 2004b). Linking islands and identifying habitat preferences during the wet and dry seasons has provided important guidance on subspecies-wide habitat protection. Finally, the Great Basin population of the western willet (*Catoptrophorus semipalmatus*) has shown a surprisingly strong

connectivity between breeding sites in western Oregon and California to very specific sites in and around San Francisco Bay (Haig *et al.* 2002), providing further indications for the importance of conservation efforts in the San Francisco Bay to help protect this species.

As shown in the above examples, knowing the migratory connectivity for a given species can often help with vital management decisions. More generally, other factors such as habitat availability on either the wintering or breeding grounds can also strongly affect key aspects of population demographic structure, such as sex ratio dynamics (Runge and Marra 2005). We do not yet know how different strengths of migratory connectivity and population size are influenced by different amounts of habitat loss. In this next section, we develop a simple equilibrium population model to further explore this relationship.

MIGRATORY CONNECTIVITY AND POPULATION DYNAMICS

Here, we explore how habitat loss affects equilibrium population size (E) under different degrees of migratory connectivity in a species with multiple breeding and wintering (non-breeding) populations. We define three general types of connectivity: *strong connectivity*: all individuals from one breeding population migrate to a single wintering population and vice versa; *no connectivity*: individuals from all breeding populations migrate in equal proportions to all wintering populations; *moderate connectivity*: the majority of individuals from each breeding population migrate to one wintering population and a smaller number migrate to the remaining wintering populations. It is important to note that in any scenario that is not strong connectivity, populations can therefore be considered to mix between the breeding and wintering grounds. In the examples provided here, no connectivity equates with “complete mixing” and moderate connectivity equates with “partial” mixing. In all three scenarios, we investigate the effect of habitat loss (population decrease) occurring at one wintering location on (1) E at all breeding and wintering populations, and (2) change in strength of connectivity (i.e., change in number of individuals migrating between each combination of breeding and wintering populations).

The basic model structure for a single breeding and wintering population follows Norris (2005), where the population size (N) at the end of the breeding season in a given year (N_{s_i}) is represented by N at

the end of the previous winter (Nw_t) times per capita breeding output during the summer (b_t):

$$Ns_t = Nw_t b_t, \quad (7.1)$$

where b_t is the linear density-dependent function:

$$b_t = b_0 - b_1 Nw_t. \quad (7.2)$$

Here, b_0 is the intercept (per capita density-dependent breeding rate as density approaches zero) and b_1 is the slope (strength of density dependence: Norris 2005). Similarly, population size at the end of the previous winter (Nw_t) is the product of N at the end of the previous summer in year $t-1$ (Ns_{t-1}) times survival rate ($1 - \text{mortality rate } [d_t]$) during the winter:

$$Nw_t = Ns_{t-1}(1 - d_t) \quad (7.3)$$

where d_t is the linear density-dependent function:

$$d_t = d_0 + d_1 Ns_{t-1} \quad (7.4)$$

and d_0 and d_1 are analogous to b_0 and b_1 in Eq. (7.2).

Model output will predict the number of individuals migrating from each of three breeding sites (s_1, s_2, s_3) to each of three wintering sites (w_1, w_2, w_3), yielding a total of nine possible combinations. We express population size in each of these combinations as the number of individuals at the end of the breeding season (prior to fall migration) at breeding location Ns_x that are migrating to wintering location w_x . For example, the number of individuals migrating from breeding location 1 (Ns_1) to wintering location w_1 at time t is expressed as $Ns_1w_{1(t)}$. Since there are two other wintering sites in the model, the remaining individuals migrating from breeding site 1 at time t are represented as $Ns_1w_{2(t)}$ and $Ns_1w_{3(t)}$.

Based on Eqs. (7.1) and (7.3), $Ns_1w_{1(t)}$, for example, can be written as:

$$Ns_1w_{1(t)} = Ns_1w_{1(t-1)}(1 - d_{(t)}^{w_1})b_{(t)}^{s_1} \quad (7.5)$$

where $d_{(t)}^{w_1}$ now takes into account individuals arriving to w_1 from all possible breeding locations:

$$d_{(t)}^{w_1} = d_0^{w_1} - d_1^{w_1}(Ns_1w_{1(t-1)} + Ns_2w_{1(t-1)} + Ns_3w_{1(t-1)}) \quad (7.6)$$

and $b_{(t)}^{s_1}$ takes into account individuals arriving to s_1 from all possible wintering locations:

$$b_{(t)}^{s_1} = b_0^{s_1} - b_1^{s_1}(Ns_1w_{1(t-1)} + Ns_1w_{2(t-1)} + Ns_1w_{3(t-1)}). \quad (7.7)$$

In other words, the per capita mortality and breeding rates of a given wintering population (d^w : Eq. 7.6) or breeding population (b^s : Eq. 7.7) are dependent upon the total number of individuals arriving into that population from the previous season. The degree of connectivity will determine the proportion of individuals coming from each of the populations the previous season. After successive iterations of the annual cycle, E is reached when

$$N_{S_x} w_{x(t)} = N_{S_x} w_{x(t-1)}. \quad (7.8)$$

For all simulations, we used previous published parameters from Eurasian Oystercatchers (*Haematopus ostralegus*), a long-distance migratory shorebird. For a population of 2000 individuals, $d_1 = 0.00011$, $b_1 = 0.00005$ (Sutherland 1996). Given values of per capita breeding and mortality at low densities for this species (Goss-Custard *et al.* 1995), Norris (2005) approximated $b_0 = 1.4$ and $d_0 = 0.001$. Using these parameters, $E = 2180$ for a given population.

The three connectivity scenarios are: (1) strong connectivity, the entire population at a breeding site ($E = 2180$) migrates to a single wintering population (Fig. 7.1A), (2) no connectivity, where exactly one-third of each breeding population ($N = 727$) migrates to one of three wintering populations (Fig. 7.1B), (3) moderate connectivity, where 90% of each breeding population ($N = 1890$) migrates to a wintering location and 10% ($N = 218$) migrate to two other wintering sites (Fig. 7.1C). For all three scenarios, we simulated 50% habitat loss at a single wintering population (w_3), where habitat loss is reflected by a change in the strength of the winter density-dependent mortality function (d_i ; in this case $d_1^{w_3}$) (Sutherland 1996; Norris 2005).

We assume that all breeding and wintering locations have equal amounts and quality of habitat and that the strength of density dependence is equal between populations. We also assume that individuals cannot change their migratory route once set by one of three connectivity scenarios, an assumption that may or may not be realistic depending on the species (see discussion below). Our aim in this exercise, however, is to examine how migratory connectivity can influence the number of individuals migrating between populations based on population dynamics alone. Other models have considered how migration routes between breeding and wintering areas may develop through evolutionary stable-strategies, assuming individuals have the ability to change migratory routes in response to habitat loss (Dolman and Sutherland 1994; Sutherland and Dolman 1994).

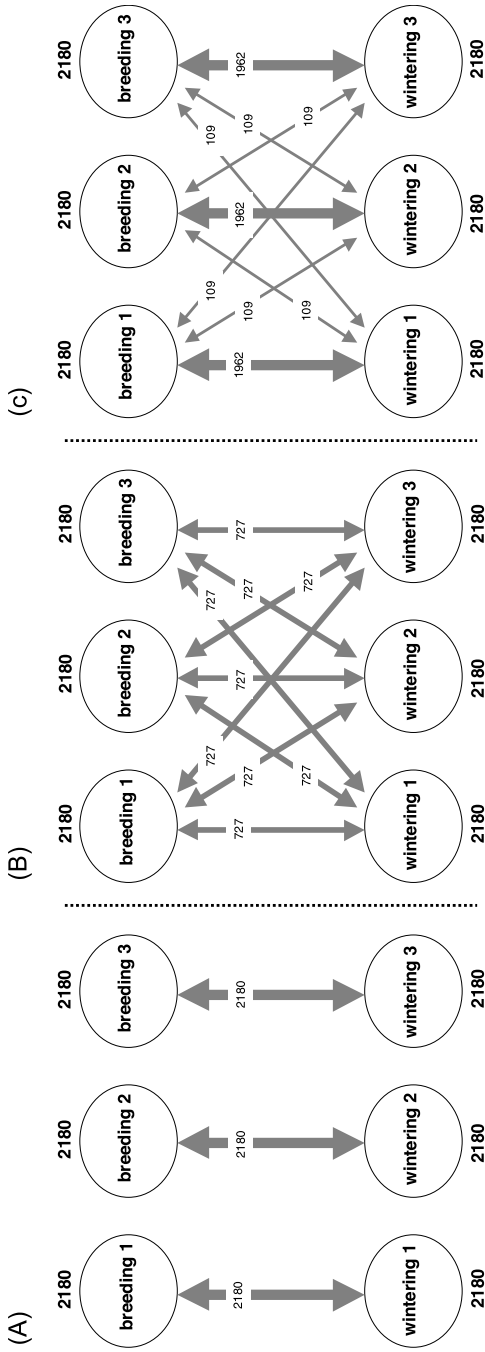


Fig. 7.1. Three connectivity scenarios where $E = 2180$ for each breeding and wintering population. (A) Strong connectivity: breeding populations migrate to a single, mutually exclusive wintering location. (B) No connectivity: an equal number of individuals from a given breeding location migrate to each wintering location. (C) Moderate connectivity: 90% of individuals from a given breeding location migrate to one wintering location and the rest migrate equally to the other two wintering locations (5% each). The numbers embedded in arrows indicate the number of individuals migrating between each of the breeding and wintering sites at equilibrium.

Model output

Under strong connectivity, 50% habitat loss at w_3 resulted in a 45% decrease in E at w_3 and s_3 (Fig. 7.2A). The smaller proportional decrease in E relative to percent habitat loss is due to a “seasonal compensation effect” of density-dependent breeding output the following season (Sutherland 1996; Norris 2005).

With no connectivity (complete mixing), 50% habitat loss at w_3 results in an equal decrease (49%) of individuals migrating from all three breeding locations to w_3 (Fig. 7.2B). Concurrently, E decreases by an equal amount (14%) at all three breeding locations. In contrast, the number of individuals migrating from all three breeding locations to the remaining wintering locations (w_1, w_2) increases by 3% (Fig. 7.2B).

When connectivity is moderate (partial mixing), the number of individuals migrating from s_3 to w_3 decreases by 43% (1890 individuals in Fig. 7.1C to 1091 individuals in Fig. 7.2C) and the number of individuals migrating from s_1 and s_2 to w_3 decreases by 86% (109 individuals in Fig. 7.1C to 15 in Fig. 7.2C). In contrast, the number of individuals migrating from s_3 to the other two wintering locations (w_1 and w_2) increases by 257% from 109 (Fig. 7.1C) to 389 (Fig. 7.2C). Overall, decreases in E at all locations are the same as the no-connectivity scenario (14% decreases at breeding locations).

By simulating habitat loss and altering population size at one wintering location, we have shown that the degree of migratory connectivity can affect population size at multiple breeding and wintering locations, as well as the number and distribution of individuals migrating between these locations. The model generates three general predictions:

- (1) When habitat is lost at one location, any level of initial mixing (i.e., moderate or no connectivity) between the breeding and wintering populations will result in synchronous population declines and a similar E among populations in the subsequent season.
- (2) If individuals mix between the breeding and wintering populations, a decline at one location will result in an increase in E of other populations in the same season.
- (3) The proportional distribution of individuals migrating between breeding and wintering populations after habitat loss is strongly affected by the initial degree of connectivity (weak vs. strong). For example, when there is no connectivity (complete mixing), the model predicts that: (A) there will be an equal decline in the number of individuals migrating from all breeding locations (s_1, s_2, s_3) to the site

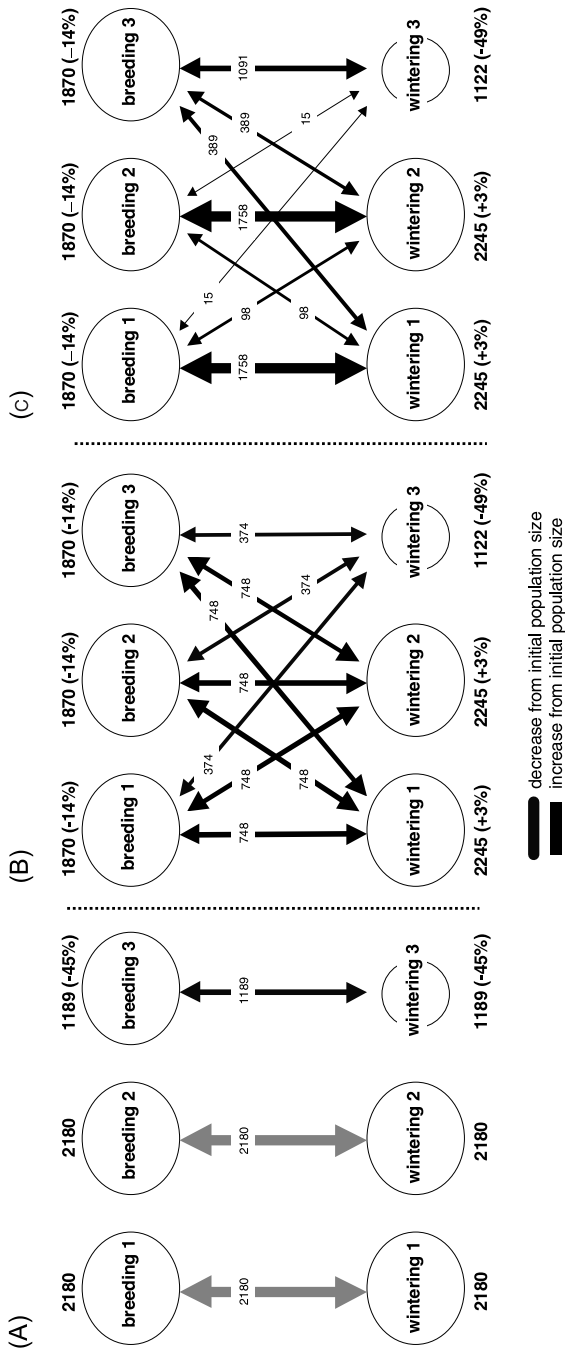


Fig. 7.2. As in Fig. 7.1 but after 50% habitat loss at wintering location 3 (ψ_3 in model). (A) Strong connectivity, (B) No connectivity, (C) Moderate connectivity. The numbers in parentheses beside E indicate the percent change in E after habitat loss. The pattern of arrows indicates an increase (black stripes) or decrease (solid black) in the number of individuals migrating from a given breeding and wintering location.

experiencing habitat loss (w_3), and (B) individuals migrating to all other wintering locations will increase. Alternatively, when populations are strongly (but not completely) connected, the model predicts that (C) small populations migrating to the site where habitat loss occurs (i.e., s_1w_3 and s_2w_3) will experience a larger proportional decrease in population size compared to large populations. This occurs because of a density-dependent feedback mechanism between breeding and wintering sites. In the model (Fig. 7.2C), the s_3w_3 group experiences a large absolute decrease in population size, thereby increasing the number of individuals migrating from s_3 to other wintering sites (s_3w_1 , s_3w_2) by over 250% (through an increase in density-dependent breeding output). The density-dependent feedback occurs as a result of increases in these s_3w_1 and s_3w_2 groups, whereby an increase in the number of individuals in the w_1 and w_2 populations in turn lowers the s_1 and s_2 populations through negative density-dependent effects on reproduction. This, combined with the habitat loss at w_3 , acts to decrease the s_1w_3 and s_2w_3 by a large amount relative to its initial size before habitat loss.

Such model predictions can be applied to data from long-term population trends of migratory species. For example, many Neotropical–Nearctic migratory birds exhibit asynchronous population trends across their breeding range (Sauer *et al.* 2004) and recent studies suggest that winter habitat may limit reproductive success on temperate breeding grounds (Marra *et al.* 1998; Norris *et al.* 2004). If a species shows strong connectivity between breeding and wintering locations, severe habitat loss at a single wintering location should only affect a single breeding location and should not affect the population size at other wintering locations. In contrast, our model predicts that species that mix between the breeding and wintering grounds should have relatively *synchronous* population trends across their breeding range or a portion of their range in which mixing occurs (prediction 1). Interestingly, if populations exhibit mixing or weak connectivity, severe habitat loss at one wintering location should *increase* population size at other wintering locations (prediction 2).

In general, our model shows how the degree of migratory connectivity can impact population dynamics. Previous studies that have modeled the effect of habitat loss in multiple breeding and wintering populations have assumed that individuals have the ability to change migratory routes and that individuals redistribute themselves according to an ideal-free distribution (i.e., equal fitness within and between wintering and/or

breeding areas: Fretwell and Lucas 1970; Dolman and Sutherland 1994; Sutherland and Dolman 1994). These assumptions may apply for some species (e.g., red-breasted goose, *Branta ruficollis*: Sutherland and Crockford 1993; light-bellied brent goose, *Branta bernicla hrota*: Clausen *et al.* 1998), however, other migratory birds have shown remarkably fixed migration patterns over time, even after major historical events (e.g., Swainson's thrush, *Catharus ustulatus*: Ruegg and Smith 2002). We do not advocate one assumption over the other but rather wish to point out that the strengths of migratory connectivity may change even if migration routes are fixed for some species. Furthermore, many species likely do not distribute themselves between spatially distinct migratory populations according to ideal-free properties. Passerines, in particular, have been shown to be highly territorial on wintering grounds (e.g., Marra *et al.* 1993; Stutchbury 1994), which can lead to significant differences in physical condition, timing of migration, and annual survival (Marra *et al.* 1998; Marra and Holmes 2001; Studds and Marra 2005).

The nature of how species are distributed within a season, as well as the degree of flexibility in changing migratory routes, will almost certainly produce different outcomes in relation to habitat loss and migratory connectivity. For example, results of this model show that when there is any degree of mixing between breeding and wintering populations, habitat loss at one wintering location will increase population size of other wintering locations through density-dependent feedback mechanisms. In contrast, models developed by Sutherland and Dolman (1994) and Dolman and Sutherland (1994) suggest that loss of habitat in one wintering area will decrease population size in other wintering areas because individuals are able to change migration routes and settle across wintering areas according to an ideal-free distribution.

One of the most basic requirements for understanding factors that influence population trends of migratory species will be acquiring detailed knowledge of population distributions during breeding and non-breeding seasons. Clearly, we will also need accurate data on dispersal, density dependence, and migratory behavior to be able to accurately predict the consequences of habitat loss across an entire network of migratory populations. Although not incorporated into this model, connectivity between migratory stopover sites and breeding and wintering areas will also likely play a key role in the dynamics of migratory populations and should be incorporated into future theoretical and empirical work.

TOOLS FOR MEASURING MIGRATORY CONNECTIVITY

We are a long way from understanding the importance of migratory connectivity for most migratory birds because of our inability to track individuals between breeding and wintering grounds. However, we are making some progress in development of tools for measuring geographic connectivity of migratory populations (Webster *et al.* 2002; Rubenstein and Hobson 2004). Below, we briefly summarize techniques currently available to measure geographic origin and also consider their latest applications to measure migratory connectivity in birds.

For decades, devices such as aluminum leg bands, collars, or ear tags have been used to trace movements of individually marked animals. Such methods require recapturing or resighting the same individual. Return rates of marked individuals, such as birds marked with aluminum bands, thus far suggests that these methods do not hold much hope for understanding connectivity of migratory bird populations. Monitoring marked waterfowl and shorebirds may be the exceptions to this problem (Alerstam 1990; Bairlein 2001). Satellite telemetry also offers some promise for understanding migratory connectivity, at least for large mammals such as bowhead whales (*Balaena mysticetus*; Heide-Jorgensen *et al.* 2003), sea turtles (Craig *et al.* 2004; Harrison and Bjorndal Chapter 9), and larger migratory birds such as raptors (C. L. McIntyre, pers. comm.), geese (e.g., Green *et al.* 2002; Fox *et al.* 2003), storks (Berthold *et al.* 2001), and seabirds (e.g., Hatch *et al.* 2000). However, the prohibitive costs of satellite transmitters have yet to produce a study with large enough sample sizes to assess the range-wide connectivity of any migratory species.

In many ways, molecular genetic approaches have revolutionized our ability to examine migratory connectivity (see also Frankham Chapter. 4; Neville *et al.* Chapter. 13). The classic genetic approach to measuring the movement of individuals among geographically separated populations is to infer gene flow from measures of population structure such as Wright's F_{ST} (Wright 1978), which is a measure of variance in allele frequencies among populations. Recent advances in molecular genetic techniques have offered significant advances on two fronts. First, new classes of molecular markers have been developed, such as microsatellites (Jarne and Lagoda 1996) and amplified fragment length polymorphisms (Mueller and Wolfenbarger 1999), which reveal substantial genetic variation within and across populations. As a consequence of the often substantial variation revealed, these markers can be highly sensitive

indicators of genetic differentiation among populations. Second, sophisticated analytical techniques have been developed, such as population assignment tests (Smouse *et al.* 1986) that potentially allow individuals to be assigned to specific populations (Haig *et al.* 1997; Webster *et al.* 2002; Cegelski *et al.* 2003).

Although molecular approaches have the potential to uncover patterns of migratory connectivity, it is currently unclear how useful they will prove in many avian systems. The ease with which birds disperse provides for potentially high levels of gene flow. Thus, developing population-specific markers is difficult when there is little difference among populations. Not surprisingly, studies examining variation at mitochondrial markers have typically uncovered only weak geographic patterns (but see Wenink and Baker 1996; Wennerberg 2001), such as weak east–west genetic variation in North America (e.g., Milot *et al.* 2000; Gorman 2001; Lovette *et al.* 2004). As a consequence, mitochondrial (and other) markers by themselves may be most useful in determining only broad geographic patterns of connectivity (e.g., Kimura *et al.* 2002). However, molecular markers may be combined with other types of markers to increase the precision and resolution of connectivity studies (Clegg *et al.* 2003). It is important to note that a lack of genetic differentiation in mitochondrial DNA could be due not just to gene flow but to historical demographic events such as rapid population expansions, which erase phylogeographic structure. Therefore, the absence of differentiation does not necessarily preclude the existence of connectivity between winter and summer populations.

Stable isotope compositions of animal tissues can also be used to track migratory patterns. Isotope approaches have been applied to migratory animals including birds (Chamberlain *et al.* 1997, 2000; Hobson and Wassenaar 1997; Marra *et al.* 1998, Kelly *et al.* 2002; Rubenstein *et al.* 2002), butterflies (monarch butterflies: Wassenaar and Hobson 1998), fish (salmon: Kennedy *et al.* 1998; Harrington *et al.* 1998), and mammals (African elephants: van der Merwe *et al.* 1990; Vogel *et al.* 1990; Koch *et al.* 1995). The method is based on the fact that natural variations in the stable isotope ratios in animal tissues (bones, muscle, blood, egg shells, feathers, etc.) are incorporated from local climatic conditions, soil type, vegetation, and diet (Mizutani and Wada 1989; Schaffner and Swart 1991; Hobson and Clark 1992). For example, stable isotope ratios of carbon ($\delta^{13}\text{C}$: Korner *et al.* 1991; Van Klinken *et al.* 1994) and hydrogen (δD : Epstein *et al.* 1976, Estep and Dabrowski 1980) in plants and animals vary systematically with latitude and climatic conditions, and strontium

isotope ratios ($\delta^{87}\text{Sr}$) in animal tissues vary as a function of bedrock type (Kennedy *et al.* 1998).

By integrating three isotopes, Chamberlain *et al.* (1997) were able to show that δD and $\delta^{13}\text{C}$ values of feathers and $\delta^{87}\text{Sr}$ values in bones of black-throated blue warblers (*Dendroica caerulescens*) varied systematically across their north temperate breeding grounds. Feathers were used because their stable isotopic composition reflects that of the foods eaten during their period of growth (Mizutani *et al.* 1990, 1992; Hobson and Clark 1992) and these ratios remain inert after the feather is grown. Since black-throated blue warblers molt only once per year, between July and September on or near their breeding area (Holmes 1994), the isotopic composition of their feathers reflects that of the food chain at their breeding locality (Chamberlain *et al.* 1997). Studies have also been conducted to assess the utility of using these isotope patterns for identifying the breeding origins of individual birds wintering in the Greater Antilles (Chamberlain *et al.* 1997; Rubenstein *et al.* 2002). These results suggest weak connectivity of individuals between the breeding and wintering grounds, although a greater proportion of individuals wintering in the western Caribbean islands were from northern breeding grounds, whereas those wintering further east were from southern breeding populations.

Only one study to date has examined the connectivity of a migratory passerine bird across its entire wintering and breeding range. Combining stable-hydrogen isotopes analyzed from tail feathers and band recovery data, D.R. Norris *et al.* (unpublished data) found that American redstarts displayed high levels of regional connectivity between their temperate breeding and tropical wintering grounds. Individuals wintering in Mexico primarily bred in western Canada and the northwestern USA, individuals wintering in Central America bred in the mid-western range, whereas most individuals wintering in the Caribbean bred in the eastern USA and Canada. The latter group showed a unique pattern of chain migration, where northern wintering populations bred at the most northern sites.

Studies to date all indicate that the isotopic composition of bird tissues has great potential for identifying regional and even more localized populations of migratory species. By combining the use of isotopic tracers with molecular genetic approaches, and with other population markers (i.e., parasites, microbial communities, trace elements), we should be able to estimate with even greater precision the connectivity between breeding and wintering populations of migratory birds. Having

individual and population markers such as the ones we have described above to assign geographic origin will only solve part of the migratory connectivity riddle. Also required are robust statistical approaches that incorporate relative abundance when assigning the breeding ground origin for birds on wintering areas (Royle and Rubenstein 2005). Below, we describe the problem and a statistical method for addressing this critical issue.

Statistical approaches for estimating migratory connectivity

A natural way to characterize migratory connectivity between breeding and wintering populations is by defining a set of transition probabilities that describe where birds from each breeding population winter. That is, how breeding birds from any particular population distribute themselves across their wintering range. Formally, let $\psi_{ws} = \Pr(zw|s)$ be the probability that a bird from breeding population s winters in region w . We note that these probabilities completely determine where birds winter *given* a particular origin. However, a central question in many studies of migratory connectivity is the “inverse problem”: given a sample of birds obtained at some wintering location, from which breeding population did they originate? In probability terms, this is a question about the conditional probability $\gamma_{sw} = \Pr(s|zw)$, the “origin probabilities,” or the probability that a bird wintering in region w originates from breeding population s . Estimating these conditional probabilities is central to the classical “derivation of harvest” problem in waterfowl management and an analogous problem exists in the management of migratory fish populations. In general, knowledge of ψ_{ws} is insufficient for obtaining estimates of the conditional probabilities γ_{sw} and vice versa.

The relationship between these two sets of conditional probabilities is embodied in Bayes’ Rule, which states that

$$\Pr(s|zw) = \frac{\Pr(zw|s) \Pr(s)}{\Pr(zw)}. \quad (7.9)$$

Note that this expression involves the marginal probability $\Pr(s)$. This can be thought of as the fraction of the population that originates from s , i.e., it is proportional to the population size of breeding population s . For example, Fig. 7.3 illustrates the relative abundance map of the American redstart (computed from Breeding Bird Survey data) over its breeding range, which can (when suitably scaled) be regarded as an estimate of the probability that a randomly selected bird from the population at large originates from any particular local population.

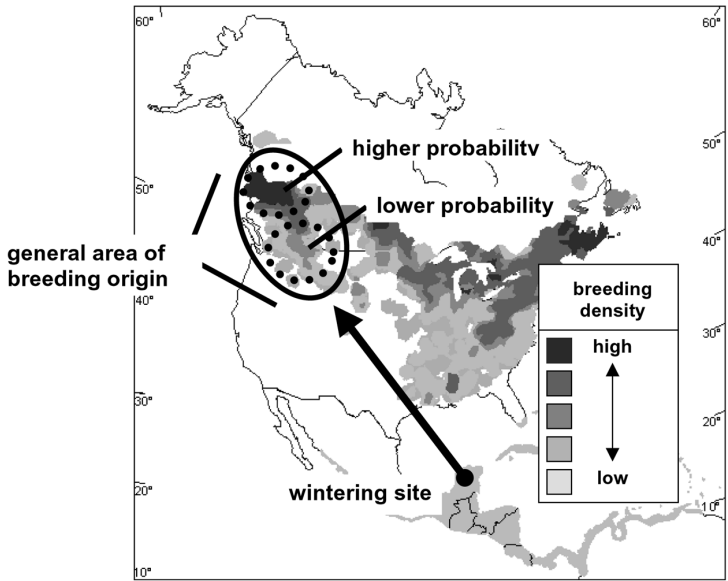


Fig. 7.3. The “probability of origin” problem in estimating migratory connectivity. A marker (for example, stable isotopes) indicates that an individual sampled at a tropical wintering site bred the previous year within the region in North America indicated by the ellipse. Within this region, there are variable breeding densities, implying that the individual had a higher probability of breeding in the area of high density rather than the area of low density. In this way, the breeding origin of individuals (i.e., migratory connectivity) can be expressed as a set of transition probabilities (in addition to using extrinsic or intrinsic markers).

In the denominator, $\text{Pr}(w)$ describes the distribution among different wintering populations, and it can be obtained by summation of the numerator of Eq. (7.9) over all possible breeding populations (thus, only knowledge of the distribution of the breeding population is necessary). This expression makes clear that one cannot answer the inverse problem without knowledge of population size, at least relatively, among the potential breeding populations.

It is sometimes possible to estimate the transition probabilities directly, for example by using band recovery data. If R_1 birds are banded in s_1 and a random sample of birds is selected from populations w_1 and w_2 yielding frequencies r_{11} and r_{21} then estimates of ψ are obtained as the proportions r_{i1}/R_1 . Then, in order to obtain estimates of the origin probabilities for any fixed wintering population, it is necessary to, in

effect, “weight” these transition probabilities by the size of each breeding population according to Eq. (7.9).

Illustration

Suppose a population exists as two geographically defined breeding populations ($s = 1, 2$) and that there are two wintering areas for the species within which these populations mix. Suppose further that, through intensive banding, the transition probabilities are known to be $\psi_{11} = 0.1$, $\psi_{21} = 0.9$ for breeding population 1 and $\psi_{12} = 0.9$, $\psi_{22} = 0.1$ for breeding population 2. Thus, most (90%) of population 1 birds winter at $w = 2$ and most (90%) of population 2 birds winter at $w = 1$. We would seem to know a lot about this system in the sense that we know the proportion of birds from each breeding population that winter in each of the two wintering populations. However, it is sometimes important (such as in harvest management of North American waterfowl) to estimate the mixture of individuals in some wintering area from the two populations. It is tempting to look at the estimated transition probabilities and declare that birds in $w = 2$ are primarily birds from population 1, and this might conceivably effect management activities directed at this species (e.g., where management objectives or actions for the two breeding populations can be made independently). Put another way, suppose one has a bird in hand, captured at $w = 2$, then one might be tempted to say that that bird most likely originated from population 1. In fact, we really know nothing quantitative about the mix of birds that occurs in the mixed population at $w = 2$. To establish this, suppose that the breeding population sizes are, respectively, $N_1 = 100$ and $N_2 = 1000$. Given the transition probabilities specified previously we expect, on average, 90 birds from population 1 (0.9×100) and 100 birds from population 2 (0.1×1000) in the mixed population at $w = 2$. That is the population of birds at $w = 2$ is made up primarily of birds from population 2. Thus, assessment of origin (the “inverse problem”) depends not just on the transition probabilities, but also on the relative size of the two breeding populations.

In many situations it is not possible to measure or estimate transition probabilities directly, but rather an extraneous trait (e.g., an allele or isotope signature) associated with each of the breeding populations is measured. Denote this trait by y , and let $f(y|s)$ denote the probability distribution of this trait for breeding population s . Then y is measured on a sample of individuals in some mixed population (the wintering population, w), yielding $f(y|w)$: the probability distribution for this trait

in the wintering population. If we wish to make an inference about the origin of the individuals in the mixed wintering population, this again is a question about the conditional probabilities $\Pr(s|w)$, the probability that a bird wintering in region w originates from breeding population s . To obtain estimates of these conditional probabilities, we note that $f(y|w)$ can be expressed as a mixture of probability distributions according to:

$$f(y|w) = \sum_s f(y|s)\gamma_{sw}. \tag{7.10}$$

Recall that γ_{sw} is the probability that a bird from breeding population s makes a transition to wintering population w . Thus, having obtained estimates of $f(y|s)$ from sampling the breeding populations, one can obtain estimates of the probabilities γ_{sw} simply by rearranging Eq. (7.10) and solving for the unknown values of γ_{sw} . Now, consider estimating the transition probabilities from each breeding population, ψ_{ws} . Applying Bayes' Rule as before we have:

$$\psi_{ws} = \frac{\gamma_{sw} \Pr(w)}{\Pr(s)}. \tag{7.11}$$

We see that it is not possible to obtain estimates of $\psi_{ws} = \Pr(w|s)$ unless information about abundance is available, or at least the relative distribution of individuals among the various populations (e.g., Fig. 7.3).

Illustration

Consider two distinct breeding populations composed of 1000 and 100 individuals, and assume that there exists a discrete marker (e.g., an allele) taking on values 1, 2, and 3. Suppose that the frequency of individuals in each population having each value of $y = (1, 2, 3)$ are (800, 150, 50) for population 1, comprising of 1000 individuals, and (20, 50, 30) for population 2, comprising of 100 individuals. We suppose these two breeding populations migrate to some location (w) with probabilities $\psi_1 = 0.1$ and $\psi_2 = 0.5$, yielding a mixed population with frequency distribution (90, 40, 20). These are computed as, for example, $0.1 \times 800 + 0.5 \times 20 = 90$. In practice, the transition probabilities are unknown and in many problems, neither will be the breeding or wintering population sizes. Rather, the observed data are the allele frequencies in a sample of the mixed population. In this case, the probability distribution of y in the mixed population w is: $f(y = 1|w) = 90/150$, $f(y = 2|w) = 40/150$, and $f(y = 3|w) = 20/150$. To obtain estimates of the conditional probabilities $\gamma_{sw} = \Pr(s|w)$, we substitute these observed quantities into Eq. (7.10) and

solve, obtaining $\gamma_1 = 2/3$ and $\gamma_2 = 1/3$. That is, $2/3$ of the individuals in this mixed population originate from population 1. To obtain estimates of transition probabilities it is necessary to consider population sizes (Eq. (7.11)), specifically, the relative sizes of the breeding population and also the relative size of the particular mixed (wintering) population in question. Finally, note that the problem of assessing connectivity using isotope markers is analogous to the example considered here, except in this case the “marker” is a continuous trait, defined by the isotope signature measured in bird tissue.

CONCLUSIONS

Phases of the annual cycle, including breeding, migration, and overwintering, for any migratory animal are inextricably linked yet these connections are poorly understood for most species. Events occurring during winter undoubtedly impact events during migration and the subsequent breeding period. Such *seasonal interactions* can have profound implications for the ecology, evolution, and population dynamics of animals that exhibit migratory behavior (Marra *et al.* 1998; Gill *et al.* 2001; Norris *et al.* 2004; Runge and Marra 2005; Webster and Marra 2005). Unfortunately, for species such as migratory birds, understanding seasonal interactions remain elusive because of the difficulties associated with following the same individuals and/or populations between specific summer, migratory stopover and winter habitats. Such *migratory connectivity* represents a critical area in need of further research and development. However, we are making progress. Technological advances in individual identification and development of genetic and stable isotope signatures to track populations are offering exciting promise to what is a giant gap in our understanding of migratory animals. This, along with more detailed modeling and statistical efforts, are needed to determine how focal breeding populations are affected by large- and small-scale events affecting various wintering populations and vice versa. It will only be through these highly multi disciplinary approaches that we will be able to come to terms with the connectivity of migratory populations and develop effective conservation strategies.

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