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Population dynamics in migratory networks

Caz M. Taylor · D. Ryan Norris

Abstract Migratory animals are comprised of a complex series of interconnected breeding and nonbreeding populations. Because individuals in any given population can arrive from a variety of sites the previous season, predicting how different populations will respond to environmental change can be challenging. In this study, we develop a population model composed of a network of breeding and wintering sites to show how habitat loss affects patterns of connectivity and species abundance. When the costs of migration are evenly distributed, habitat loss at a single site can increase the degree of connectivity (mixing) within the entire network, which then acts to buffer global populations from declines. However, the degree to which populations are buffered depends on where habitat loss occurs within the network: a site that has the potential to receive individuals from multiple populations in the opposite season will lead to smaller declines than a site that is more isolated. In other cases when there are equal costs of migration to two or more sites in the opposite season, habitat loss can result in some populations becoming segregated (disconnected) from the rest of the network. The geographic structure of the network can have a significant influence on relative population sizes of sites in the same season and can also affect the overall degree of mixing in the network, even when sites are of equal intrinsic quality. When a migratory network is widely spaced and migration costs are high, an equivalent habitat loss will lead to a larger decline in global population size than will occur in a network where the overall costs of migration are low. Our model provides an important foundation to test predictions related to habitat loss in real-world migratory networks and demonstrates that migratory networks will likely produce different dynamics from traditional metapopulations. Our results provide strong evidence that estimating population connectivity is a prerequisite for successfully predicting changes in migratory populations.

Keywords Habitat loss · Costs of migration · Migratory animals · Migratory connectivity

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Introduction

Predicting the effects of environmental change on migratory animals presents a unique challenge because individuals are typically distributed over a series of complex, interconnected breeding and nonbreeding populations. Such "migratory networks" can show various degrees of connectivity between seasons. For example, networks may be mixed, whereby individuals in a given population migrate to a variety of sites in the following season, or they may be segregated, whereby individuals in different populations migrate to separate sites the following season (Webster et al. 2002). Historically, patterns of connectivity in migratory animals have been difficult to measure because of the challenge of following individuals year-round over large geographic distances—but see the examples of between-season recovery of bird bands in Alerstam (1990) and

Brewer et al. (2000). However, new techniques, such as stable isotopes and genetic markers, have provided the potential to estimate patterns of connectivity between sites that are separated by thousands of kilometers (e.g., Boulet et al. 2006; Chamberlain et al. 1997; Hobson and Wassenaar 1997). Generally, results using these techniques have demonstrated that populations of many migratory species show some degree of mixing between seasons (e.g., Boulet et al. 2006; Norris et al. 2006; Rubenstein et al. 2002). Other migratory species appear to form segregated parallel migration systems (Alerstam 1990). The implications of these different migration patterns for predicting changes in population size and conserving species are not well understood.

Martin et al. (2007) demonstrated how information on connectivity can dramatically change where, when, and how many resources should be allocated for conserving migratory species. Their model showed that failure to consider patterns of connectivity drove some breeding populations of American redstarts (*Setophaga ruticilla*) to extirpation because decisions focused on conserving wintering habitat did not consider where overwintering birds were breeding. Although this example emphasizes the importance of estimating patterns of connectivity, we still lack a predictive framework for understanding how populations within migratory networks, and the connections with that network, will respond to environmental changes, such as habitat loss or deterioration (Dolman and Sutherland 1995; Marra et al. 2006).

In this study, we develop a graph-based framework for examining population dynamics in a simple migratory network population model comprising of multiple breeding sites and multiple wintering sites. Graph-based models are already starting to provide a useful framework for metapopulation theory in which the nodes in the graph represent habitats and the links between the nodes represent the functional connections (i.e., dispersal) between habitats (Urban et al. 2009). However, new theory is needed for migratory animals since, despite some similarities between metapopulation models and migratory networks (Esler 2000), there are fundamental differences. While metapopulation models focus on dispersal and isolation between year-round (resident) populations, migratory networks are made up of sets of distinct seasonal sites with individuals regularly traveling between these sites. Habitats in a migratory network are of radically different types (i.e., winter, breeding, and migration stopover) and, to survive, individuals need to occupy each of these habitats over the course of an annual cycle. In metapopulations, individuals are not obligated to occupy multiple sites over the course of an annual cycle in order to survive. Furthermore, in a migratory network, a group of individuals using a site in one season may have originated from a number of potential

sites in the previous season and each of these sites is likely to have different population characteristics (e.g., abundance, site quality, density dependence, migration distance). Thus, the dynamics of these populations are linked in unique ways that are unlike metapopulations, and predictions generated from metapopulation models may not be directly transferable to migratory networks.

This model concept developed in this study is based on avian migration systems but may be applicable to other taxa in which seasonal migration occurs between discrete breeding and nonbreeding sites over the lifetime of an individual and populations have overlapping generations. The model is both a generalization of previous models that were used to explore habitat loss in an arbitrary network of sites (Dolman and Sutherland 1995; Sutherland and Dolman 1994) and an extension to a model of partial migration where individuals followed one of two possible strategies: to migrate or not (Taylor and Norris 2007). Our goal is to explore the effects of habitat loss on patterns of connectivity and population abundance within networks that have different geographical arrangements.

The model

Terminology

To describe a migratory network, we adopt some terminology from mathematical graph theory (Gross 1999; Urban et al. 2009). We model a migratory network as a graph where there is a collection of *nodes* (breeding, B, and wintering, W, sites that contain populations) and *edges* (migratory routes) that connect pairs of sites. We do not include migration stopover sites in this formulation but it would be a straightforward extension to the model to include a third type of site. The network can be described as *undirected* because individuals migrate both directions along an edge and *weighted* because each edge has an associated distance or cost of migration. Unlike a metapopulation, the migratory networks presented in this study are *bipartite*, meaning that the sites are divided into two disjoint sets (B and W), so an edge can only connect a B site to a W site. A network model containing migratory stopover sites would be considered *tripartite*.

To be a part of a bipartite network, a B site has to be connected to least one W site and vice versa. A graph is considered *connected* if it is possible to trace a path from any site to any other site in the graph; otherwise, the graph is *disconnected*. The *degree of connectivity* for a given site is defined as the number of edges that connect to it. Thus, a network is considered to be *mixed* when there is a high degree of connectivity at most sites and *segregated* when there are few edges or it is completely disconnected.

Model description

We assume that each individual has a genetically fixed migratory strategy in which it uses one wintering site (W) and one breeding site (B). Individuals or different migratory strategies interact with each other through density dependence at both the B and W sites. At time t, the number of individual birds (A_{ij}) that use the strategy of wintering at site i and breeding at site j is given by:

$$A_{ij}(t+1) = (c_{ij})^2 F_{ij} S_{ij} A_{ij}(t) \qquad (1)$$

where c_{ij} is the constant migration survival for an individual that migrates between nodes i and j, which is assumed to be the same in both directions, F_{ij} is the breeding success, and S_{ij} is the survival of individuals that winter at wintering site i and breed at breeding site j.

Breeding success F_{ij} depends on two factors: (1) the density-independent component (b_j), which is the intrinsic site quality or the quality of the site as density approaches zero, and (2) the density-dependent component, which depends on the intrinsic site carrying capacity (k_j) and declines with increasing abundance of individuals at site j, calculated by summing individuals migrating from all W sites that are connected to B_j. We also assume that individuals arriving from different W sites experience different strengths of competition. This is modeled by including a parameter b'_{ij}, which is the relative competition strength experienced by individuals from wintering site i at breeding at site j. Breeding success for individuals wintering at site i and breeding at site j is given by:

$$F_{ij} = b_j \exp\left(-\frac{b'_{ij}\sum_{h=1}^{N_W} A_{hj}}{k_j}\right). \qquad (2)$$

Similarly, wintering survival at site i is given by:

$$S_{ij} = d_i \exp\left(-\frac{d'_{ij}\sum_{h=1}^{N_B} A_{ih}}{k_i}\right) \qquad (3)$$

where d_i is the density-independent site quality, d'_{ij} is the relative competition strength experienced by individuals from breeding site j at wintering at site i. The survival rate (c_{ij}) is a function of the distance from i to j (D_{ij}) as shorter migrations are assumed to have higher survival rates (Table 1). In territorial animals, individuals that arrive sooner have an advantage over later arrivals as they may establish better territories (Alatalo et al. 1986; Part 2001) and experience longer breeding seasons (Slagsvold and Lifjeld 1988; Aebischer et al. 1996). We assume, therefore, that individuals from closer sites have a competitive advantage over those that have to travel further. Thus, b'_{ij} and d'_{ij} depend on the rank r_{ij} of site j with respect to distance from i (Table 1). That is, the closest breeding site to wintering site i is ranked 1, the second closest is 2, etc. The total number of birds is given by:

$$N_{\text{global}} = \sum_{i=1}^{N_W}\sum_{j=1}^{N_B} A_{ij}. \qquad (4)$$

For a given spatial arrangement of sites and associated parameters, the model can be solved algebraically resulting in multiple unstable equilibria and (usually) one stable, nontrivial equilibrium. Below, we present an analytical solution for a 1×2 network. However, for larger networks, the solutions are unwieldy and not straightforward to interpret. Thus, for networks with more than three sites in each of the seasons, we solve the model numerically, starting with a nonzero random number of individuals

Table 1 Parameter values used in population model

Parameter	Value	Description
N_B	Variable	Number of breeding sites
N_W	Variable	Number of nonbreeding (wintering) sites
D_{ij}	$\sqrt{Y^2 + X_{ij}^2}$	Distance between sites i and j. Horizontal or east–west distance, X_{ij}, is usually 1, value shown on figures for each case. North–south distance, Y, is 1 in all cases
c_{ij}	$\exp(-0.01 \times D_{ij})$	Proportion of birds migrating from site i to j that survive
d'_{ij}	$\exp(-0.02 \times (r_{ij}-1))$	Relative nonbreeding (winter) competitive ability of birds that winter at i and breed at j; r_{ji} is the rank of site j with respect to closeness of site j from site i
b'_{ij}	$\exp(-0.02 \times (r_{ij}-1))$	Relative breeding competitive ability of birds that winter at i and breed at j; r_{ij} is the rank of site i with respect to closeness of site i from site j
d_i	0.999 for all i	Site quality of nonbreeding (wintering) site i; intrinsic survival
b_j	1.4 for all j	Site quality of breeding site j; intrinsic breeding success
k_{Bj}	20,000 for all j	Carrying capacity of breeding site j
k_{Wi}	20,000 for all i	Carrying capacity of nonbreeding (wintering) site i

occupying each strategy and iterating until the number of individuals using each strategy converges within a tolerance of 10^{-6}. We tested for stability of the equilibrium by applying a perturbation to the result and reiterating the model to confirm that it reconverges to the same equilibrium.

Model analysis and results

We first examine one of the simplest possible networks with one W site and two B sites (Fig. 1). A_{11} and A_{12} are the numbers of birds at equilibrium that use breeding sites B_1 and B_2 respectively. The two breeding sites are equal in size and quality ($k_{B_1} = k_{B_2} = k_B$, $b_1 = b_2 = b$) and the relative competitive strength is given by: $\delta = \frac{d'_{12}}{d'_{11}}$.

Solving model Eqs. 1, 2, and 3 for this network shows that breeding site B_2 is used when the survival during migration is high enough. The total population size at equilibrium is given by:

$$N_{\text{global}} = A_{11} + A_{12} = \frac{2k_B k_{W_1}}{(k_{W_1} + k_B + k_B \delta)} \ln(b d_{W_1} c_{11} c_{12}).$$
(5)

If we simplify further and make the carrying capacities of all sites equal ($k_B = k_{W_1} = k$) and let $r=bd_1$, then the equilibrium number of birds using W_1 and B_2 is given by:

$$A_{12} = \begin{cases} 0 & c_{12} \leq \frac{1}{4} c_{11}{}^{2\delta} r^{\delta-2} \\ \frac{3}{2+\delta} \ln\left(\frac{c_{12}{}^4 r^{2-\delta}}{c_{11}{}^{2\delta}}\right) & c_{12} > \frac{1}{4} c_{11}{}^{2\delta} r^{\delta-2} \end{cases}.$$
(6)

As c_{12}, the survival of birds traveling to B_2, drops, then both A_{12} and the total population size decrease. The level of usage of B_2 depends in part on the survival cost of migration, which, in turn, we assume is negatively related to distance (Table 1). When survival drops below the threshold shown in Eq. 6, B_2 will not be used. In other words, suitable breeding habitat that is sufficiently distant from wintering sites will not be part of the network.

In this simple network, when habitat loss occurs at one breeding site, the number of birds using that site drops but the overall population decline is buffered by the existence of the other breeding site in which usage increases (Fig. 1b, c). Habitat loss at the closest breeding site, B_1, causes a larger decline in global population size than the equivalent loss at B_2 because $c_{12}<c_{11}$ and so the more distant site B_2 is a less effective population buffer than B_1. Reducing the carrying capacity of B_1 to one fifth its original value causes a 19% population loss compared to 17% when the same change is made to B_2 (Fig. 1b, c). Reducing the carrying capacity of the only winter site W_1 to one fifth of its original value causes a 73% loss in population size (result not shown).

A larger network (3×3 sites; Fig. 2) with evenly spaced sites that have equal quality (b, d) and carrying capacity (k)

Fig. 1 a The equilibrium population sizes and connectivity of a migratory network with one wintering and two breeding sites and a cost of migration that is proportional to the distance between sites. *Numbers adjacent to each site* show the population size at that site. *Width of arrows* is proportional to the fraction of the entire population that uses this route. Parameter values are as shown in Table 1. **b** The new population sizes and connectivity following 80% habitat loss at site B_1. **c** The new population sizes and connectivity following 80% habitat loss at site B_2
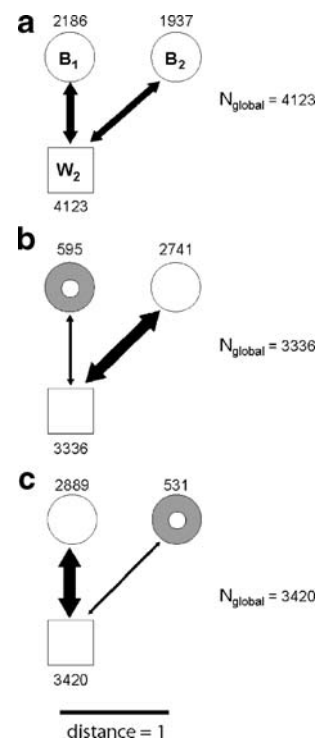
can be characterized as disconnected. That is, a given W site will only have one edge connecting it to the closest B site and vice versa (Fig. 2a). When one W site experiences habitat loss, it produces a number of interesting results (Fig. 2b, c):

1. Habitat loss increases the degree of mixing by introducing connections that did not previously exist. This occurs because habitat loss at a W site reduces k and the numbers of individuals at that site but, since b and k at the corresponding B site have not changed, there is space for additional individuals at this B site (B_1 in Fig. 2b and B_2 in Fig. 2c). This B site, therefore, becomes more "attractive" to additional individuals that overwinter at sites further away.

2. When one W site experiences habitat loss, the population size at the other W sites increases but declines at all the B sites. The decline occurs at a B site even if there was no edge initially connecting it to the W site experiencing habitat loss. The magnitude of this increase in population abundance at neighboring W sites and the magnitude of the decrease in population size at B sites are positively related to the distance from the W site affected by habitat loss.

3. When heterogeneity in population abundance arises at W sites as a result of habitat loss, this also causes heterogeneity in population abundance at B sites. After habitat loss at W_1, B sites support different numbers of individuals at equilibrium from each other, despite all breeding sites being identical in all respects except in distance to W sites.
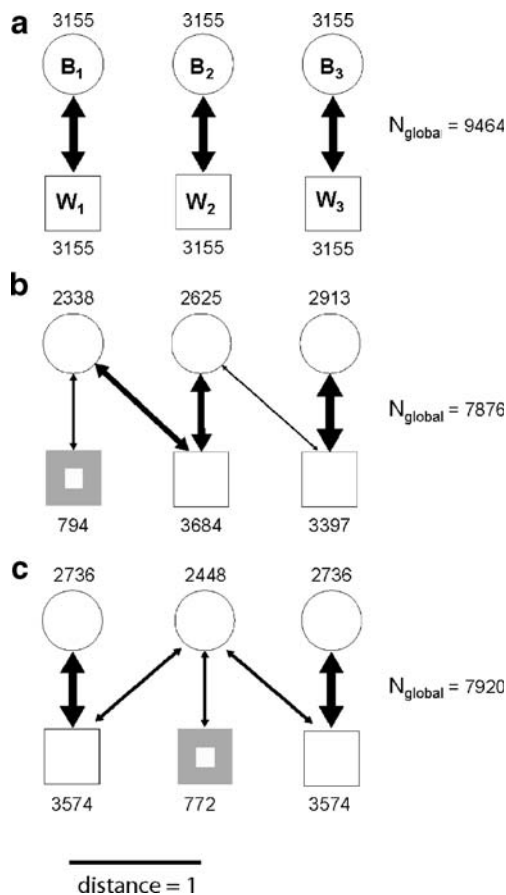
Fig. 2 a The equilibrium population sizes and connectivity of a migratory network with three evenly spaced wintering and three evenly spaced breeding sites and a cost of migration that is proportional to the distance between sites. *Numbers adjacent to each site* show the population size at that site. *Width of arrows* is proportional to the fraction of the entire population that uses this route. Horizontal distance is 1 and vertical distance is 1. Parameter values are as shown in Table 1. b The new population sizes and connectivity following 80% habitat loss at site W_1. c The new population sizes and connectivity following 80% habitat loss at site W_2

4. The position of a site where habitat is lost within a network matters to both local population size and global population size. Loss of habitat at W_2 causes a bigger drop in number of individuals at that site than an equivalent loss of habitat at W_1 but a smaller drop in global population size. This is because W_2 is buffered by two neighboring winter sites, whereas W_1 is only buffered by one neighboring site.

If sites are too distant from one another, they do not function as a network (Fig. 3). When sites are homogeneous, a widely spaced network (Fig. 3a) has the same equilibrium number as a more closely spaced set of sites (Fig. 2a). However, when habitat loss occurs in a widely spaced network, the other sites provide no buffering and the

three populations remain unconnected (compare Fig. 2c with Fig. 3b) and equivalent habitat loss results in a much larger population loss (compare N_{global} in Fig. 2c versus Fig. 3b). Figure 4 shows how the spacing of the sites affects total population size in a 3×3 network in the condition when W_2 has one fifth the carrying capacity of W_1 or W_3. When sites get sufficiently far apart, they act as separate populations and no subsequent increase in spacing affects population number.

In some networks, we find that habitat loss is capable of disconnecting part of the population from the network (Fig. 5). In Fig. 5, habitat loss at W_1 causes B_1–W_1 to be disconnected from the rest of the network. In this network, as in the 3×3 case, loss at W_1 causes a larger population decline than loss at W_2 but this is because of the disconnection that occurs. In cases where habitat loss is not sufficient to disconnect part of the network, we found that, in this arrangement of sites, population decline is the same regardless of which site is affected.

Discussion

Our model provides unique insights into the population dynamics of migratory networks and has a number of
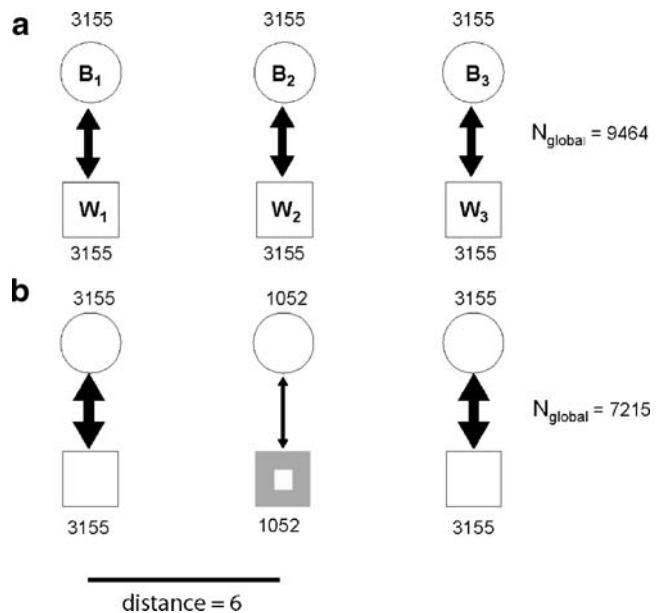
Fig. 3 a The equilibrium population sizes and connectivity of a migratory network with three evenly spaced wintering and three evenly spaced breeding sites and a cost of migration that is proportional to the distance between sites. Horizontal distance is 6 and vertical distance is 1. *Numbers adjacent to each site* show the population size at that site. *Width of arrows* is proportional to the fraction of the entire population that uses this route. Parameter values are as shown in Table 1. b The new population sizes and connectivity following 80% habitat loss at site W_2
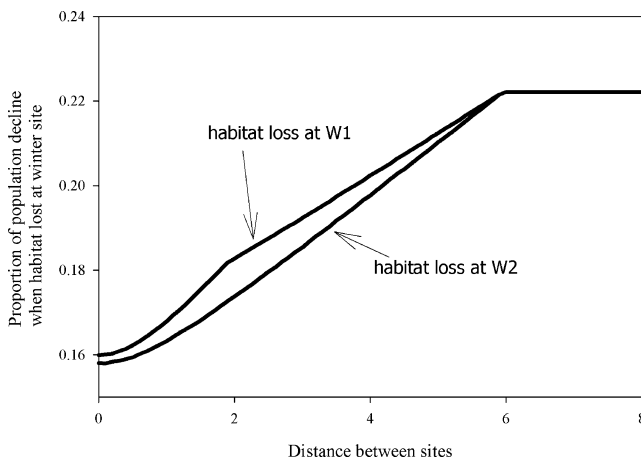
Fig. 4 Proportional decline of population size after an 80% habitat loss at a wintering site in a network arrangement like those shown in Figs. 2 and 3 versus increasing horizontal distance between sites

important implications for understanding how both patterns of connectivity and population abundance respond to habitat loss.
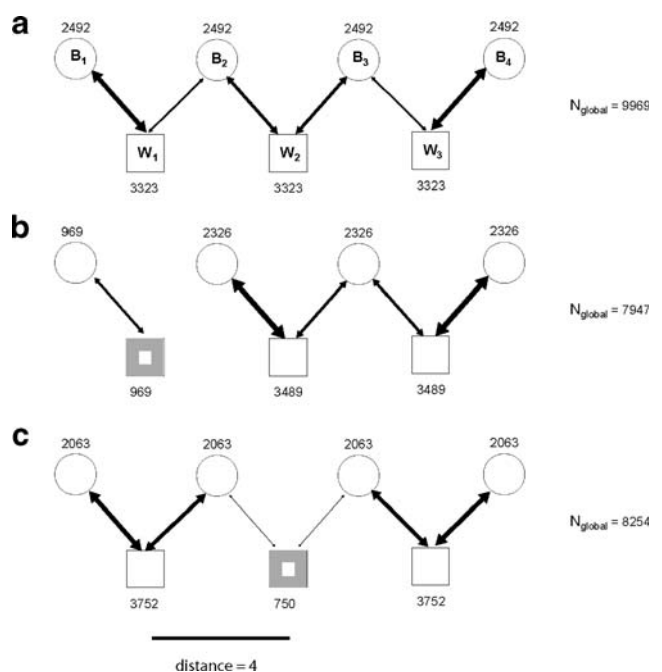
Conservation of migratory networks

We demonstrate that even though an evenly spaced migratory network may be initially disconnected (Fig. 2a), the degree of connectivity between breeding and wintering sites can increase after habitat loss (Fig. 2b, c). More specifically, the site that experiences the increase in connectivity is the one that was initially strongly connected to the site that experienced habitat loss. The migratory network buffers the population somewhat from declines although the effect may not be very large. A network that remained disconnected suffers an additional 6% decline in population size following an 80% habitat loss at W_2 (Figs. 2 and 3).

However, in real migratory systems, an increase in connectivity may be less likely than a decrease in connectivity. Species that have been segregated for some time may have evolved into distinct subspecies or races and, therefore, may not reintegrate. For instance, the different races of Dunlin (*Calidris aplina*) have an evenly distributed network with circumpolar breeding sites and a matching series of temperate-tropical coastal wintering sites across the Americas, Africa, and Asia (Alerstam 1990). Based on evidence from morphological and genetic markers (Alerstam 1990; Wennerberg 2001), these different races have a strongly connected parallel migration system in which most individuals from a given breeding area migrate to the closest wintering site.

An irregularly spaced or heterogeneous network of sites results in a mixed population. Since real-world systems are

likely to be heterogeneous, we should expect that most species will show some degree of mixing between seasons. Results from band recoveries, stable isotopes, and genetic markers suggest that this is indeed the case (e.g., Boulet et al. 2006; Kelly et al. 2005; Norris et al. 2006; Rubenstein et al. 2002).

Our model shows that how patterns of connectivity change in response to habitat loss depends, in part, on the spatial arrangement of the sites (populations) over the landscape. Habitat loss may decrease connectivity and can lead to complete segregation in parts of the network. When habitat is lost at a site that is strongly connected to a distant peripheral site, the pair of sites can become disconnected from the rest of the network (Fig. 5b). Isolation could leave these sites more vulnerable to stochastic environmental fluctuations and local extirpation if they are unable to be rescued by individuals originating from other areas. Thus, it will be important to identify the provenance of individuals from peripheral sites and focus on conserving those habitats. For example, using stable hydrogen isotopes, Hobson et al. (2004) identified two previously unknown

Fig. 5 a The equilibrium population sizes and connectivity of a migratory network with three evenly spaced wintering and four evenly spaced breeding sites and a cost of migration that is proportional to the distance between sites. Horizontal distance between *B* sites and between *W* sites is 4 and vertical distance is 1. *Numbers adjacent to each site* show the population size at that site. *Width of arrows* is proportional to the fraction of the entire population that uses this route. Parameter values are as shown in Table 1. **b** The new population sizes and connectivity following 80% habitat loss at site W_1. **c** The new population sizes and connectivity following 80% habitat loss at site W_2

northern breeding populations of the endangered Bicknell's thrush (*Catharus bicknelli*) that wintered in the Dominican Republic. We suggest that conservation efforts should not only be directed towards these peripheral breeding sites but also the site(s) at which these individuals winter. Failure to do the latter could lead to their isolation from the rest of the migratory network.

We demonstrate that connections to peripheral sites within a migratory network can be maintained, even if the cost of migrating to those sites is high, because the individuals migrating to peripheral sites experience reduced competition. If this advantage outweighs the higher mortality costs associated with reaching these sites, then the connection will be maintained. For example, several passerines such as yellow warblers (*Dendroica petechia*; Boulet et al. 2006) and tree swallows (*Tachycineta bicolor*; Ardia 2005) have extreme northern breeding populations in Alaska and the Northwest Territories that migrate to similar wintering latitudes as more southern breeding populations. The Pacific black brant (*Branta bernicla nigricans*) have what could be considered several core breeding sites in eastern Siberia and Alaska and extreme peripheral populations that breed as far east as the eastern edge of Victoria Island in the Canadian Arctic (Cramp and Simmons 1977). All of these breeding populations winter along the coast of California and northern Mexico so eastern breeding populations migrate along the Arctic coast to Alaska before turning south for the Pacific coast (Alerstam 1990).

We found that habitat loss at one site can cause a decrease in population size at multiple sites in the opposite season, even when those sites are not initially connected to the site that experienced the habitat loss. This suggests that it will be challenging to accurately identify the causes of decline within migratory networks because the changes in population size at any given site may be due to events that occur at any number of sites in the opposite season, regardless of whether they are connected to that site or not. Also other (including larger-scale) explanations are, of course, possible for observed declines (Holmes and Sherry 2001; Jones et al. 2003; Jones et al. 2007). However, if population decline at multiple sites is caused by habitat loss at a single site in the opposite season, our model does predict that the relative decrease in population size is negatively related to the migration distance of each site to the site experiencing habitat loss (Dolman and Sutherland 1995; Sutherland and Dolman 1994), a prediction that could be tested in real-world systems. For any migratory network, predicting changes in population size of a given site will require information on where individuals are spending the rest of the season and the dynamics of each of those sites.

Population response to habitat loss depends on the position of the site where habitat is lost within the migratory network. For example, in an evenly spaced network, the decline in population size is slightly greater when habitat is lost at a site on the outside of the network compared to a site in the middle. This is because outer sites have fewer connections to sites in the opposite season and are, therefore, less buffered. We suggest that these sites with a lower degree of connectivity might be considered more valuable and that conservation efforts should take into account the relative position of sites within the network.

The differential costs of migration in a network influence equilibrium population size, even when sites within a network have equal quality and carrying capacity. In an irregularly spaced network with equal intrinsic site quality, our model predicts lower population sizes in peripheral breeding sites because of the higher costs of migration to the peripheral site. Thus, we suggest that it may not be possible to equate intrinsic site quality with the relative size of a population in a migratory network (Van Horne 1983; Winker et al. 1995).

Generalizations and assumptions

We have created a simple model to explore population dynamics in migratory networks in which we make the most conservative assumptions. All sites are assumed to be equal in size, quality, and spacing, and the density-dependent processes operate in the same way at wintering sites as they do at breeding sites. The cases shown have only small numbers of breeding and wintering sites, but our results also hold when more sites are added to the network. The equivalence of the forms of density-dependent fecundity (Eq. 2) versus survival (Eq. 3) means that our predictions are the same regardless of whether winter or breeding habitat is lost.

We assume that the migration strategy (choice of wintering and breeding site) is inherited and that either parents assortatively mate or, if parents with two different strategies mate, then half their offspring (on average) follow each strategy. It has been demonstrated that there is a strong genetic component to most, if not all, traits associated with migration (Berthold 1998; Berthold and Pulido 1994; Pulido 2007; Pulido et al. 1996). This assumption should, therefore, hold for many species, particularly if the migratory network is described at sufficiently large scale (i.e., a "site" is a large geographic region). Moreover, the predictions of this model are the same even if we include weaker inheritance of migration strategy (i.e., where some offspring are randomly assigned a strategy but most still inherit their strategy from their parents). Weaker inheritance merely causes an increase in stochasticity and our results then become probabilistic. However, if inheritance is very weak, then the stochasticity can overwhelm the results.

Our model forms a framework for making general predictions and also for the development of more specific models. We recognize that even obtaining the most basic parameters for a model such as this will be very challenging for many real-world systems. Other biological phenomena, such as carry-over effects where the quality of the site in one season affects individual success in the following season (Norris and Taylor 2006), might also have important ramifications in both general models and specific systems.

Conclusion

We demonstrate that it is not possible to predict changes in population size of migratory animals without information on how populations are connected between seasons and the dynamics of each site within a migratory network. Our model provides predictions that can be tested in real-world migratory networks and suggest that one of the keys will be to accurately estimate patterns of connectivity between sites throughout the annual cycle. Such information will also be critical for developing sound conservation plans (Martin et al. 2007), some of which will have to span international borders.

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