Habitat Distribution Affects Connectivity and Population Size in Migratory Networks

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Habitat distribution affects connectivity and population size in migratory networks

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Abstract Population dynamics of migratory species can be modeled using spatial bipartite networks in which breeding and winter regions, or nodes, are distributed longitudinally and connected by links representing migratory movements. Understanding the factors that influence the connectivity and population size of such networks is important for effective conservation. In migration ecology terminology, *strong* migratory connectivity is a network with low node degree and *weak* or *diffuse* connectivity is a network with high node degree. We present a model of migration networks using a Lotka-Volterra system of differential equations in which each winter-breeding link is represented as a subpopulation which competes with other subpopulations that share breeding or winter regions. We use persistence theory to determine which links coexist with one another under different parameter regimes in a 2×2 network where only three patterns of connectivity (weak, moderate, and strong) are possible. We find that, in the absence of dispersal among subpopulations, strong connectivity occurs when winter habitat has the same longitudinal distribution as breeding habitat, and/or costs of cross-longitudinal migration are high. Moderate connectivity arises otherwise. Total population size is maximized when each longitudinal region has the same amount of breeding habitat as winter habitat and decreases with the costs of migration. Including any degree of dispersal leads to weak connectivity and also reduces population size. Our results suggest that actions that conserve habitat so as to preserve

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matching habitat distributions and minimize costs of migration would be most effective.

Keywords Migration networks · connectivity patterns · coexistence · Lotka-Volterra

1 Introduction

Animal migration, in which individuals move back-and-forth between winter and breeding grounds over the course of an annual cycle, has fascinated scientists since ancient times and migratory species are important components of biodiversity in many ecosystems [Dingle, 2014]. Migration can be found in many taxa, including insects, bats, and ungulates but probably the best studied is birds and at least 19% of extant bird species are migratory [Kirby et al., 2008]. Recent studies have drawn attention to severe declines in migratory avifauna in North America [Rosenberg et al., 2019] and Europe [Inger et al., 2014]. These population trends have been detected primarily by analysis of repeated, widespread, annual counts in just one season (often the breeding season) which are available through large-scale, citizen science monitoring programs such as the North American Breeding Bird Survey (BBS; [Sauer et al., 2017]). Analysis of BBS or other large datasets often reveals considerable spatial variation in trends across a species’ monitored range. Since declines can be caused by events in seasons in which the species is not monitored, understanding the causes of trends in migratory birds requires knowledge of migratory connectivity, i.e., how breeding regions are linked spatially to regions used during the non-breeding seasons [Webster et al., 2002].

The need to understand population trends has caused an explosion of studies to measure migratory connectivity for avian and other migratory species using various technologies to track individuals across seasons within an annual cycle [Bridge et al., 2011]. These technologies, which continue to be developed rapidly, can be either intrinsic or extrinsic markers. Intrinsic markers include genetic assignments of individuals sampled in the winter season to genetic groups within a genoscape [Ruegg et al., 2014] and stable isotope signatures of tissues grown (e.g., feathers molted) in a different part of the annual cycle [Hobson, 2005]. Extrinsic markers include satellite and GPS tags and light-level geolocators [Lisovski et al., 2020]. These tracking studies, however do not address the more fundamental problem in migration ecology that we start to address here, namely to understand what factors lead to different migratory connectivity patterns.

The strength of migratory connectivity can be described as a continuum from weak (diffuse) to strong. Under weak connectivity, individuals from multiple regions in one season are well-mixed in another season whereas under strong connectivity, a population from one region in the breeding season will migrate to population-specific non-breeding areas ([Webster et al., 2002, Finch et al., 2017]). Findings from studies of avian species show that connectivity patterns are often longitudinal, birds from eastern breeding regions travel to

eastern winter regions and migratory connectivity appears to be strong when measured at a large (continental) scales, but weak when measured at smaller spatial scales. For example, barn swallows *Hirundo rustica* tracked from 3 locations less than 100 km apart all travelled to the same, widely-spaced, winter regions [Liechti et al., 2015]. In contrast, Hahn et al. [2013] tracked common nightingales *Luscinia megarhynchos* from 3 widely separated breeding locations and found that they wintered in breeding population-specific clusters from west to central Africa, a strong connectivity pattern. Other species tracked at large scales that show strong or moderate connectivity include Wood thrush *Hylocichla mustelina* [Stanley et al., 2015], Pied Flycatcher *Ficedula hypoleuca* [Ouwehand et al., 2015], European Bee Eater *Merops apiaster* [Hahn et al., 2019], Great Reed warbler *Acrocephalus arundinaceus* [Koleček et al., 2016], and Herring Gulls *Larus argentatus* [Anderson et al., 2019]. This general pattern of large-scale strong or moderate connectivity and small-scale weaker connectivity can also be found within a species. For example, [Hallworth et al., 2015] found complete separation of eastern and western populations of ovenbirds, *Seiurus aurocapilla*, and at a smaller scale, [Hallworth and Marra, 2015] found that the non-breeding population boundaries of two breeding populations within the eastern (Maryland and New Hampshire) were closer, although still non-overlapping. A large scale study that analyzed tracks of 133 Tree Swallows *Tachycineta bicolor* from across their North American breeding range identified three distinct clusters of (breeding and non-breeding) locations that corresponded to western, central, and eastern North American flyways. Within each of these clusters, connectivity was considerably weaker than across the entire breeding range [Knight et al., 2018]. However, this pattern is certainly not universally true, several species show weak connectivity at large scales, for example Blue winged warblers (*Vermivora cyanoptera* [Kramer et al., 2018], Prothonotary warblers *Protonotaria citrea* [Tonra et al., 2019], Common Tern *Sterna hirundo* [Bracey et al., 2018] Finch et al, [Finch et al., 2017] reviewed multiple studies where birds had been tracked using geolocators and concluded that connectivity was weak in most species but also found that the strength of connectivity tended to increase with mean distance between breeding sites.

Spatial networks or graphs are a convenient way to represent populations and connectivity of migratory animals and provide a framework for many kinds of dynamical population models and analyses. In this work, we study connectivity patterns through rigorous mathematical analyses of a population dynamics model that represents the network of migrating populations (termed a migratory network [Taylor and Norris, 2010]). The most straightforward type of migratory network is bipartite with nodes of two types representing breeding (breeding nodes) and over-winter regions (winter nodes) and edges representing migratory movements between nodes of different types. Previous work with bipartite networks has represented each edge as a different subpopulation, and modeled three processes: survival during migration (along edges) which declines with increasing distance, density-dependent survival during winter (at winter nodes), and density-dependent reproductive success (at breeding nodes). This work has relied on simulations and numerical solutions of differ-

ence or differential equations to estimate how perturbations to networks affect connectivity patterns and hence, did not allow for rigorous precise statements about connectivity patterns [Taylor and Norris, 2010].

One factor likely to affect connectivity is dispersal among nodes. Previous models typically assume that individuals will remain faithful to their migration “strategy” (choice of winter and breeding node) throughout their life and that their offspring will inherit the same strategy as their parents. This may not be a terrible assumption when nodes represent very large regions but at smaller scales, we expect birds to disperse among breeding and winter regions. We particularly expect first year birds to disperse away from their natal regions [Cresswell, 2014]. Taylor [2019] incorporated natal dispersal into a tripartite network model and found that the resulting pattern of connectivity depended on the relative strength of density-dependence in each season and the degree and constraints of dispersal. Again, these findings were determined by numerically solving difference equations rather than analytically.

Here, we construct a Lotka-Volterra system of differential equations to represent population dynamics on the four edges of a bipartite, 2×2 (2 breeding by 2 winter nodes) network assuming density-dependence in both seasons and distance-dependent migration costs. We incorporate dispersal of varying levels (including none) and analyze the system to determine how different connectivity patterns arise. We specifically address how dispersal, habitat structure, and differential costs of migration affect connectivity and total population size and determine, analytically, the conditions for persistence of different connectivity patterns.

2 Model and Methods

To understand bird migration networks, we treat each edge of the network, or pathway, as a distinct population and use differential equations to model its dynamics. Specifically, we study a scenario with two winter sites and two breeding sites, indexed as 1 and 2, arranged longitudinally, with breeding and winter habitats 1 in the western range and breeding and winter habitats 2 in the eastern range. This gives a total of four possible migratory pathways. This simple scenario enables us to derive analytical results that provide interesting insight into the factors that influence connectivity patterns.

We let x_{ij} be the population density of the birds that breed in site i and winter in site j , i.e. that migrate over the path from i to j . Each site has a different habitat quality, which we represent through its carrying capacity, labeled K_{bi} and K_{wj} , for breeding site i and winter site j , respectively. The carrying capacity of each winter and breeding site results in competition amongst migrating populations. Each population competes with all other migrating populations with which it shares winter or breeding sites. Additionally, we assume that the path between breeding site i and winter site j is associated with a cost of migration that causes pathwise mortality at a rate m_{ij} . We study two different sets of equations: (1) no dispersal, i.e., offspring fol-

low the same migratory path as their parents and never switch paths and (2) with dispersal, i.e., offspring may choose a different migratory path than their parents or switch at some point in their lifetime.

2.1 No Dispersal

Building from the above assumptions, we model the migrating populations with the following differential equations

$$\frac{dx_{ij}}{dt} = r_{ij}x_{ij}\left(1 - \frac{\sum_k x_{ik}}{K_{bi}} - \frac{\sum_k x_{kj}}{K_{wj}}\right) - m_{ij}x_{ij} \quad (1)$$

where r_{ij} is the intrinsic growth rate of the population from breeding site i to winter site j . For all i and j , we assume that $m_{ij} < r_{ij}$, since otherwise the population would always have negative growth and hence not exist. Defining $c_{ij} = \frac{1}{1-m_{ij}/r_{ij}}$ and $\tilde{r}_{ij} = r_{ij}c_{ij}$, rearranging leads to

$$\frac{dx_{ij}}{dt} = \tilde{r}_{ij}x_{ij}\left(1 - \frac{c_{ij}\sum_k x_{ik}}{K_{bi}} - \frac{c_{ij}\sum_k x_{kj}}{K_{wj}}\right) \quad (2)$$

Since we study a system with two breeding and two winter sites, this yields a four-dimensional Lotka-Volterra differential equation model, one for each edge (Figure 1A). In this Lotka-Volterra model, we refer to the part in the parantheses as the per-capita growth rate of path ij . Furthermore, c_{ij} can be interpreted as the cost associated with the path between breeding site i and winter site j . When there is no pathwise mortality, then $c_{ij} = 1$. On the other hand, as the rate of pathwise mortality approaches the intrinsic growth rate, c_{ij} approaches infinity.

2.2 With Dispersal

As many migratory species may follow different paths than their parents or switch paths during their lifetime, we build from the previous model to add dispersal. We assume that some birds from pathway ij will switch to using the the pathway kl and let d_{ijkl} denote this dispersal rate. Including this dispersal, we have the following set of differential equations

$$\frac{dx_{ij}}{dt} = \tilde{r}_{ij}x_{ij}\left(1 - \frac{c_{ij}\sum_k x_{ik}}{K_{bi}} - \frac{c_{ij}\sum_k x_{kj}}{K_{wj}}\right) - \sum_{k,l} d_{ijkl}x_{ij} + \sum_{k,l} d_{kl ij}x_{kl} \quad (3)$$

Here the last sum represents the birds dispersing into path ij from all other paths and the second to last sum represents the birds dispersing out of path ij to other paths.

We refer to the paths between corresponding sites as “direct” paths and paths between one site in the western range and the other in the eastern as

“cross” paths. We assume that the costs of the cross paths are greater than the costs of the direct paths, i.e., $c_{ij} \geq c_{ii}$ and $c_{ij} \geq c_{jj}$ for $i = 1, 2$ and $j \neq i$.

By treating each migratory pathway as a distinct population that interacts only with other populations at shared sites and writing down a Lotka-Volterra model, we make use of the well-developed theory of Lotka-Volterra equations and persistence theory (see Methods below) to analyze connectivity patterns. We analyze how the relative size of the breeding and winter sites, the costs associated with traveling between the sites, and the dispersal affect the connectivity.

2.3 Analysis

To analyze how habitat distribution affects connectivity, we determine the conditions on our model parameters that lead to each type of connectivity pattern (weak, moderate, or strong; Figure 1A ; See Supplementary Information Figure 1 for all possible connectivity patterns). First, we non-dimensionalize the habitat structure parameters by scaling out the total habitat as follows. We let K be the total combined carrying capacity of all four habitats and let s be the fraction of this total found in the western range (so $(1-s)$ is the fraction in the eastern range). Additionally, we let γ_1 and γ_2 be the fraction of breeding habitat (versus winter habitat) in the western and eastern range, respectively. We choose this non-dimensionalization, as opposed to other possibilities, because it facilitates the analysis. Collectively, we call these parameters the habitat distribution ratios (see Figure 1B) and we show how they influence the connectivity pattern and population size.

For models without dispersal, we use a community assembly and persistence theory approach to find the conditions needed to achieve each type of connectivity pattern. Specifically, we start with a single migrating population, determine its equilibrium, and then test which, if any, of the excluded migrating populations can invade, i.e., have positive per-capita growth rates, at this equilibrium. For each of these populations, we determine the new equilibrium that results from this invasion. There are two possibilities: either both the original and the invading population coexist or the invading population excludes the original. According to the classical Lotka-Volterra theory, if the two populations coexist, then there is a unique equilibrium in which both populations have positive density. We continue by testing if any remaining excluded populations can invade the new equilibrium until we reach communities in which no excluded populations can invade, which we call an end state (see Supplementary Information). Generally, such an approach may lead to never ending cycles. However, under the assumptions of our model, this does not happen.

After identifying the end states, we determine if the migrating populations in that end state coexist, using the mathematical theory of persistence ([Hofbauer and Sigmund, 1998], [Schreiber, 2006]). Heuristically, persistence ensures that the density of each population in that end state stays above some

lower bound for all of time, as long as it was initially present. In other words, each population between two habitats in that end state will continue to exist, as long as it initially existed. Altogether, this provides a set of conditions on the parameters that ensures that a certain connectivity pattern persists over time. In the following section, we give the main results and leave the details of the analysis to the Supplementary Information.

3 Results

3.1 Connectivity with no dispersal.

Using a community assembly approach and persistence theory, we find that the final possible end states that occur are either (i) both direct paths (strong connectivity) or (ii) both direct paths along with one cross path (moderate connectivity). Hence, with no dispersion, the connectivity pattern is either strong or moderate; weak connectivity is not possible.

Furthermore, we find that the habitat distribution determines which of these connectivity patterns will eventually be reached. If we assume that there is no mortality along the direct paths, i.e., $c_{11} = c_{22} = 1$, then the population of the cross path between breeding site i and winter site j is able to coexist with the direct paths (i.e., moderate connectivity) if

$$1 - (\gamma_i - \gamma_j) < \frac{1}{c_{ij}} \quad (4)$$

A more general condition including cases when $c_{11} \neq c_{22} \neq 1$ is provided in the Supplementary Information. We observe from this condition that, if the costs of the direct paths are equal to 1, then, the proportion of habitat in west vs east, s , does not affect whether cross paths are occupied. Rather, this only depends on the cost of the cross path and the difference between the proportions of habitat in the breeding ranges (Figure 1B). If costs are fixed, the population between the eastern breeding site and western winter site exists if the γ_2 is high and γ_1 is low, i.e., most of the eastern range is breeding habitat and most of the western range is winter habitat. Intuitively, this is the case for two reasons. First, in the eastern range, the relatively small winter site limits how large the direct populations can become reducing the competition in the larger breeding site. Secondly, in the western range, the relatively small breeding site limits the competition from the western direct path.

Additionally, we observe that the condition for the two cross populations to exist are mutually exclusive. This means that if the cross population between breeding site i and winter site j exists then the other cross population cannot and vice versa (Figure 2). Finally, there is some range of parameters for costs and the difference between the breeding habitat in the eastern and western range for which neither cross path population coexists. In this case, the migration network will eventually reach a strong connectivity pattern.

3.2 Total Population Size with no dispersal

Next, we ask how is the total population size supported by the network affected by the distribution of the habitats. In particular, how does the habitat distribution affect the total population?

If we have strong connectivity (i.e., with only two direct populations), then the two populations do not directly interact and the community approaches an equilibrium given by

$$x_{11}^{str} = \gamma_1(1 - \gamma_1)sK, \quad x_{22}^{str} = \gamma_2(1 - \gamma_2)(1 - s)K \quad (5)$$

Hence, the total population size is

$$[\gamma_1(1 - \gamma_1)s + \gamma_2(1 - \gamma_2)(1 - s)]K \quad (6)$$

From this expression, we can see that how the habitat is distributed amongst the winter habitats and breeding habitats affects the total population size that is supported. If the total habitat available in the east or the west is fixed, then the total population size is maximized when the habitat is split evenly between the breeding and winter site (i.e., when $\gamma_1 = \gamma_2 = \frac{1}{2}$). In other words, the more uneven the breeding and winter distribution, the lower total population that is supported.

If we have moderate connectivity with the cross population between breeding site 1 and winter site 2, and assume $c_{11} = c_{22} = 1$, then the population size using each pathway goes to an equilibrium, given by

$$x_{11}^{mod} = \left[1 + \frac{1-s}{\gamma_1} \left(1 - (\gamma_1 - \gamma_2) - \frac{1}{c_{12}}\right)\right] \underbrace{\gamma_1(1 - \gamma_1)sK}_{x_{11}^{str}} \quad (7a)$$

$$x_{12}^{mod} = -\left(1 - (\gamma_1 - \gamma_2) - \frac{1}{c_{12}}\right)s(1 - s)K \quad (7b)$$

$$x_{22}^{mod} = \left[1 + \frac{s}{1 - \gamma_2} \left(1 - (\gamma_1 - \gamma_2) - \frac{1}{c_{12}}\right)\right] \underbrace{\gamma_2(1 - \gamma_2)(1 - s)K}_{x_{22}^{str}} \quad (7c)$$

The total population size with moderate connectivity including the path between breeding site 1 and winter site 2 is the sum of these three expressions. There are a few things to notice from these expressions. First, in the expression of x_{11}^{mod} and x_{22}^{mod} , the terms outside the square brackets in the curly underbrace are the equilibrium with strong connectivity. Secondly, the expression in the parantheses within the square brackets of x_{11}^{mod} , and x_{22}^{mod} is reminiscent of condition (4), which determines whether moderate connectivity is supported. If the condition is met, then this term is negative. Hence, this gives us that if we have moderate connectivity, then the population density using direct paths decreases, since the expression in the square brackets is less than one. Notably, the amount that the populations of x_{11} and x_{22} decrease is scaled by $1 - s$ and s , respectively, i.e., the proportion of habitat in the opposite range.

Given a fixed total habitat carrying capacity, we show how the total population size depends on the habitat distribution, in Figure 3. The values given are the total population supported relative to the total habitat carrying capacity. The dark curves delimit three regions of which migration network is supported by that habitat configuration: (a) direct paths with one cross path between winter site 1 and breeding site 2, (b) only direct paths and (c) direct paths with one cross path between winter site 2 and breeding site 1. These regions depend on condition (4) and in particular, the costs of the cross paths. For more costly cross paths, strong connectivity is expected over a wider range of the difference between γ_1 and γ_2 .

The total population is maximized when $\gamma_1 = \gamma_2 = \frac{1}{2}$ and only populations between direct paths exist. In this case, the distribution in the eastern range versus the western range does not impact the total population. The total population size decreases when γ_1 or γ_2 deviates from the optimal of $\frac{1}{2}$. For example, when the habitat is proportionally greater in the breeding habitat in both the eastern and western range (γ_1 and γ_2 are large), then only a small total population is supported (see (ii) in Figure 3). This reduction is alleviated if the relative ratio of breeding to winter habitat in the eastern range is opposite to that of the western range (e.g. γ_1 small and γ_2 large) because this allows for the population in the cross path to exist (see (i) and (iv) in Figure 3). Additionally, if the habitat is skewed to the west, then the relative ratio of breeding to winter habitat in the east, γ_2 , has a less pronounced impact on the total population than does the that in the west, γ_1 (Figure 3B).

3.3 Connectivity and total population size with dispersal

With path switching dispersal, there is always weak connectivity, since some of the population using any one path switches to every other path (provided all $d_{kl ij} > 0$). Hence, this path switching is one possible explanation for the weak connectivity patterns that are observed in real systems at small scales. As in the analysis with no dispersal, the relative population using each path is impacted by the habitat distribution amongst the four habitats as well as the costs, even though networks are always weak connectivity networks. When dispersal rates are low, the relative populations sizes at equilibrium are similar to those given by the equilibrium in the no dispersal case (Figure 4). When dispersal rates are high, the population is split roughly evenly into all possible paths, even if cross paths are very costly.

Dispersal from direct paths to cross paths causes a decrease in the total population compared with the case of no dispersal (Figure 4). This is because such dispersal leads to individuals switching paths to more costly paths. Together, the costs of the cross paths and dispersal have compounding effects on the total population. More costly cross paths have a more pronounced negative effect on the total population when dispersal is higher and vice versa (Figure 4).

4 Discussion

Our analysis of a migratory network model shows that connectivity patterns and population size are driven by the distribution of habitat amongst breeding and winter sites, the cost associated with migrating via a certain pathway, and the level of dispersal among paths. We found that, without dispersal, strong connectivity results when the longitudinal distribution of breeding habitat matches the longitudinal distribution of winter habitat or when costs of traversing cross pathways are high, whereas moderate connectivity results when breeding habitat has a different longitudinal distribution than winter habitat and costs of cross pathways are low. Additionally, total population size is highest when there are equal amounts of breeding and winter habitat in both eastern and western ranges and declines as this discrepancy increases. The addition of dispersal always results in weak connectivity and reduces population size at equilibrium, especially when cross-path migration costs are high because it leads to individuals using costly paths.

Networks have become a popular way to visualize and model connectivity, movement, and population dynamics in migratory species. Variants of the network model described here with the key assumptions of density-dependence in both seasons and route- or distance- dependent migration survival have been used for theoretical explorations and applied to understand the dynamics of real species. [Taylor and Norris, 2010] explored, theoretically, the effects of habitat loss on connectivity and population size. [Taylor, 2019] expanded the model to a tripartite network with natal dispersal and explored how habitat loss in differently- regulated networks with and without natal dispersal affected connectivity and population size. [James and Abbott, 2014] used a network with nodes arranged latitudinally rather than longitudinally to explore how migration distance and length of breeding season interact to affect population size. Variants of the model were used to estimate the unmeasured migratory connectivity in Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) [Wiederholt et al., 2013] and to discover reasons for population decline in a migratory songbird, Wood thrush [Taylor and Stutchbury, 2016].

Previous modeling work on migratory network population dynamics has relied on numerical approaches with multiple breeding and winter sites to understand connectivity [Taylor and Norris, 2010]. Here, we use a simple 2×2 network to give precise analytical results about how the distribution of habitat impacts connectivity and population size. Specifically, our four differential equations are rearranged to be 4D Lotka-Volterra competitive equations, which have nice structure to them and facilitate analysis. In fact, the 2D and 3D competitive Lotka Volterra systems have been thoroughly analyzed and the possible qualitative dynamics completely classified [Zeeman, 1995]. A complete analysis of a general 4D competitive Lotka Volterra system has not been published, though it seems possible yet tedious. Here, we thoroughly analyze a 4D Lotka Volterra system with additional structure that a single population competes with at most two other populations and populations using direct paths have a competitive advantage over those using the cross paths. We find

that without dispersal, one cross population always goes extinct and hence, reduces to a 3D system.

While our results provide insights into migration network connectivity, there are many avenues to extend this work that may offer further insights. Migration is a complex behavior and events or effects of habitat quality in one season may “carry over” to affect vital rates such as reproductive success or survival in another season [Harrison et al., 2010] and these carry-over and seasonal interaction effects could be incorporated into network models [Norris and Taylor, 2006]. True migratory networks usually involve more than two types of habitat patches [Newton, 2010]. For example, most long distance migrants will use “stopover” or staging sites during migration to rest and refuel. To represent the habitat used during migration season, a multipartite network might be more appropriate [Taylor, 2019] or network models that use different approaches, e.g., [Iwamura et al., 2013]. While analytical analysis of an extended model with more than two winter and breeding habitats may be difficult, numerical solutions may help understand connectivity patterns. Migrating species are components of larger ecosystems and often experience interspecific interactions such as competition and predation [Bauer and Hoyer, 2014] that may also influence their persistence and hence, network connectivity.

4.1 Conservation Implications

Much of conservation planning for migratory birds makes use of the concept of flyways, defined as the geographical area covered by a migratory species (or group of species) over the course of its annual cycle, encompassing breeding and non-breeding grounds and the connecting migration route [Kirby et al., 2008, Boere and Stroud, 2006]. Effective conservation of a migratory species requires coordinated action along the entire length of its flyway. Since flyways often traverse political boundaries, the flyway concept has proved valuable for coordination of international conservation action. Flyways are often, although not always, oriented longitudinally (i.e. from south to north, and from north to south) [Newton, 2010]. The US FWS used four longitudinally oriented flyways (Atlantic, Mississippi, Central, and Pacific) for management of migratory waterfowl in North America [Fish and Wildlife Services] and migratory shorebird conservation initiatives have also been organized around flyways [Atlantic Flyway Shorebird Initiative, Pacific Flyway Shorebird Initiative].

In some cases, a single species is found in multiple flyways and will be categorized into flyway subpopulations. Underlying the use of the flyway concept within a species is the assumption of strong to moderate connectivity at large scales but weak connectivity at smaller scales. These assumptions have been borne out by tracking studies for many species that show strong connectivity at large scales and weak connectivity at smaller scales (e.g., [Kramer et al., 2018, Knight et al., 2018, Kolecek et al., 2016, Hallworth et al., 2015, Finch et al., 2017, Hallworth and Marra, 2015]). Our analysis demonstrates that a

species is expected to assemble into flyway subpopulations when habitat is matched longitudinally (i.e., a given flyway contains a similar proportion of total winter habitat as of total breeding habitat) and inter-flyway migration costs are high compared to intra-flyway costs. If there is mismatch in flyway distribution of winter versus breeding habitat combined with manageable costs of inter-flyway migration, then significant inter-flyway movements are expected and conservation for the species is better addressed either using a large flyway that encompasses its entire range or using a network concept. Our analysis shows changes to habitat that cause longitudinal mismatch of breeding and winter habitat may weaken connectivity, causing individuals to use more costly migration paths and reduce population size overall. Conservation actions that maintain similar longitudinal distributions of breeding and winter habitat across flyways will maximize global population size.

In the longer term, though, strong connectivity likely leads to genetic differentiation and the formation of distinct genetic groups [Ruegg et al., 2020] and eventually, perhaps, to the formation of separate subspecies that do not interbreed and may not interact competitively in the same way even when they share habitat for part of the year [Lagass et al., 2020]. In these cases, this single species network model may not accurately predict changes to connectivity or changes to population sizes following perturbations to the network. There is a need to develop network models for differentiated species or groups of subspecies and to manage migratory animals can be so as to conserve genetic diversity as well as population sizes [Ruegg et al., 2020].

5 Statements and Declarations

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5.2 Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

5.3 Ethics Approval

Not applicable

5.4 Consent to Participate

Not applicable

5.5 Consent for Publication

Not applicable

5.6 Availability of data and material

Not applicable

5.7 Code availability

Mathematica code used in the analysis of this work is available in the supplementary information. We also provide a pdf of the code if a reader does not have access to Mathematica.

5.8 Author Contributions

Both authors contributed to the development and analysis of this project as well as the writing of this manuscript.

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Fig. 1 Schematic of connectivity and habitat distribution parameters. There are three types of connectivity patterns possible in our model (A). Strong connectivity is when only populations occupying direct paths exist and there is a one-to-one relationship between breeding (northern) and winter (southern) sites. Moderate connectivity is when one population occupying a cross path exists along with the two direct populations. Weak connectivity is when populations occupying all possible paths between breeding and winter sites exist. In (B), the nondimensionalized habitat distribution parameters are depicted. Parameter s is the proportion of total habitat capacity found in the western range, while γ_1 and γ_2 are the proportion found in the breeding habitat in the west and east, respectively.

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Fig. 2 Plot showing how the connectivity pattern depends on the costs of the cross paths (y-axis) and the difference between the breeding habitat in the eastern and western range (x-axis). The left and right shaded regions both indicate moderate connectivity. The left shaded region is with the cross path between the eastern breeding site and western winter site, while the right shaded region is with the opposite cross path. The white region in between indicates strong connectivity. The regions are determined from condition (4) given in the main text.

Fig. 3 Habitat distribution effects on population sizes with no dispersal. The color gradient in panels (A) and (B) gives the total equilibrium population size relative to the total combined carrying capacity, from equations (5) and (7). The dark black lines delimit the region with strong connectivity. Parameters are $c_{12} = c_{21} = 1.5$, $s = 0.5$ and $s = 0.75$ for panel (A) and (B), respectively. Panel (C) depicts the networks corresponding to points in panels (A) and (B). The size of the nodes represent the carrying capacity of that habitat and the thickness of the edges between nodes corresponds to the population density using that pathway.

Fig. 4 Dispersal rate and costs of cross paths affects the total population size. The color gradient gives the total equilibrium population size relative to the total carrying capacity. Parameters are $s = 0.75$, $\gamma_1 = 0.5$, $\gamma_2 = 0.25$. Panel (B) depicts the networks corresponding to five points in panel (A), with difference costs and dispersal rate: (i) $d = 0.8$, $c_{12} = c_{21} = 1.5$, (ii) $d = 0.5$, $c_{12} = c_{21} = 1.5$, (iii) $d = 0.2$, $c_{12} = c_{21} = 1.5$, (iv) $d = 0.5$, $c_{12} = c_{21} = 1.2$ and (v) $d = 0.5$, $c_{12} = c_{21} = 1.8$

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