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Research

Estimating the per-capita contribution of habitats and pathways in a migratory network: a modelling approach

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Every year, migratory species undertake seasonal movements along different pathways between discrete regions and habitats. The ability to assess the relative demographic contributions of these different habitats and pathways to the species' overall population dynamics is critical for understanding the ecology of migratory species, and also has practical applications for management and conservation. Metrics for assessing habitat contributions have been well-developed for metapopulations, but an equivalent metric is not currently available for migratory populations. Here, we develop a framework for estimating the demographic contributions of the discrete habitats and pathways used by migratory species throughout the annual cycle by estimating the per capita contribution of cohorts using these locations. Our framework accounts for seasonal movements between multiple breeding and non-breeding habitats and for both resident and migratory cohorts. We illustrate our framework using a hypothetical migratory network of four habitats, which allows us to better understand how variations in habitat quality affect per capita contributions. Results indicate that per capita contributions for any habitat or pathway are dependent on habitat-specific survival probabilities in all other areas used as part of the migratory circuit, and that contribution metrics are spatially linked (e.g. reduced survival in one habitat also decreases the contribution metric for other habitats). Our framework expands existing theory on the dynamics of spatiotemporally structured populations by developing a generalized approach to estimate the habitat- and pathway-specific contributions of species migrating between multiple breeding and multiple non-breeding habitats for a range of life histories or migratory strategies. Most importantly, it provides a means of prioritizing conservation efforts towards those migratory pathways and habitats that are most critical for the population viability of migratory species.



Introduction

Understanding the relative contribution of discrete habitats to the dynamics of spatially structured populations, such as populations of migratory species, is important both for the advancement of ecological theory (Keeling et al. 2000, Kneitel and Miller 2003, Kerr et al. 2006) and for the proper allocation of conservation effort (Thogmartin 2010, Sheehy et al. 2011). Many migratory animals have shown severe declines over the last century (Wilcove and Wikelski 2008), yet effectively managing and conserving migratory animals presents great challenges because it involves not only understanding how individuals use habitats and pathways throughout the annual cycle but the relative importance of these areas within the larger network (Taylor and Norris 2010, Thogmartin 2010, Mattsson et al. 2012, Bauer and Klaassen 2013, Iwamura et al. 2013, Wiederholt et al. 2013). Here, we present a generalized approach to estimate the habitat- and pathway-specific contributions of species migrating between multiple breeding and multiple non-breeding habitats (i.e. a migratory network; Taylor and Norris 2010).

The purpose of this approach is to predict demographic contributions of discrete habitats and pathways to population dynamics. Habitats can be defined as areas containing the essential resources a species needs to survive and complete its life cycle in terms of both consumed resources (e.g. food) and physical sites (e.g. nesting sites; Dennis et al. 2003, Vanreusel et al. 2007). Because migratory species spend portions of the annual cycle in multiple habitats (e.g. breeding, non-breeding, or stopover sites), the contribution of any one habitat to population dynamics is not a product of that habitat alone. Rather, a habitat's contribution may be affected by habitat dynamics in the migratory network to which individuals migrate over the annual cycle. Our contribution approach takes this phenomenon into account. The framework also accounts for annual probabilities of survival, reproduction, and migration between habitats and tracks migratory cohorts or groups of individuals adopting a particular migratory or non-migratory transition between seasons.

Our framework builds upon past studies that have developed habitat contribution metrics in other types of spatially structured populations (Hanski and Hanski 1999, Ovaskainen and Hanski 2003, Runge et al. 2006, Krkosek and Lewis 2010, Caswell and Shyu 2012, Strasser et al. 2012, Vanbergen et al. 2013). However, the application of these metrics to migratory networks is problematic because migration is a fundamentally unique spatial process (Marra et al. 2006) differing from the existing source-sink and metapopulation conceptualizations. At least four key attributes of migratory species are not captured by traditional metapopulation models (Taylor and Hall 2012). First, migrating species exhibit cyclical, directed movements from one location to another. Seasonal migration is not the same as dispersal among local habitats (Hill et al. 1996, Semlitsch 2008). Although migration and dispersal may maximize fitness by enhancing survival and reproduction, they may be

performed at different spatial scales and are either repeated events (migration) or one-time events (dispersal) (Winkler 2005). Second, the life stages of migratory species are separated across space and time with reproduction occurring only during part of the year and in particular areas (Newton 2010). This is not compatible with a key tenet of source-sink theory that sources are habitats where birth rates exceed death rates and where emigration exceeds immigration (Pulliam 1988). According to source-sink theory, non-breeding habitats occupied by migratory species would be classified as a sink (Pulliam 1988), but for migratory species this is problematic as non-breeding habitats are often critical to population maintenance. Third, in migratory populations, regular alterations in habitats and biotic interactions occur, usually with the change of seasons, resulting in predictable annual movements of migratory individuals between habitats (Newton 2010). These predictable seasonal movements distinguish a migratory population from the traditional metapopulation, where any habitat may be inhabited at any point in the annual cycle. Fourth, seasonality means that migratory systems are subject to carry-over effects (i.e. cross-seasonal effects) where the population dynamics in one season may depend on processes or event in the previous season (Ratikainen et al. 2008). A typical example of a carry-over effect is when quality of the non-breeding habitat influences an individual's body condition and timing of spring migration, which in turn has consequences for its reproductive success on the breeding grounds (Norris 2005).

While several of the aforementioned attributes of migration can occur in metapopulations – such as ephemeral habitats driving metapopulation structure (Hernández Cienfuegos 2005) – metapopulation approaches do not consider the combination of all four attributes. The framework we present here fills this gap in theoretical approaches by incorporating the unique characteristics of migratory populations into focal-habitat and focal-pathway contribution metrics.

In this paper, we adapt the method for estimating patch-specific contributions in a source-sink system developed by Runge et al. (2006) to the case of migratory species. First, we briefly discuss current modeling approaches used for migratory species. Then we present an approach for modeling the per-capita contributions for habitats, seasonal transitions between habitats (either migratory or non-migratory), and pathways (a series of transitions through the annual cycle), by tracking movements of individuals. To illustrate this approach, we model a hypothetical species migrating among habitats in a four-habitat system, which allowed an investigation of how contrasting habitat quality between multiple breeding habitats and between multiple non-breeding habitats affects per capita contributions. Because methods to estimate the contributions of a migratory species' various habitats to its population viability is a critical need for management (McGowan and Ryan 2009, Iwamura et al. 2013), we conclude by discussing applications of our contribution metric to migratory species conservation and management.

Habitat-specific contributions in spatially-structured populations

There are a number of approaches to modeling the population-level responses of migratory species to alterations of habitat or to environmental change (Norris 2005, Taylor and Norris 2010, Bunnefeld et al. 2011, Sheehy et al. 2011, Mattsson et al. 2012, Taylor and Hall 2012, Bauer and Klaassen 2013, Wiederholt et al. 2013). Most of these studies involve measuring population responses to perturbations, such as altering habitat attributes or removing habitats (Ovaskainen and Hanski 2003).

An alternative to perturbations is to directly estimate the demographic contribution of a habitat in a migratory network using one of at least two metrics: 1) lifetime reproductive success (Krkosek and Lewis 2010); or 2) a per capita contribution that accounts for reproduction, survival, and dispersal (Runge et al. 2006). While both metrics build upon source-sink theory (Pulliam 1988, Diffendorfer 1998), the per capita contributions can be adapted to annual time steps, which may be feasible to estimate for many species. Although methods already exist for estimating per capita contributions, they were developed for metapopulations, where habitat patches are connected through one-way dispersal events. As such, they are unable to account for either seasonality or differences in habitat types (i.e. breeding vs non-breeding seasons and habitats), or migration (i.e. regular movements between habitats) between these habitats. Our model, described below, considers both breeding and non-breeding habitats and regular movements between habitats to develop a per-capita contribution metric that can be used for migratory animals.

The contribution of discrete habitats to migratory networks

Here, we extend the method of estimating per capita contributions of discrete habitats to migratory species. Our model is flexible in that it can account for residency (i.e. a segment of migratory population that is non-migratory) and can be applied to many types of spatially-structured populations that can be represented as a migratory network. The metric estimates the per capita contribution of individuals using discrete habitats, pathways, and transitions to the entire population in the next year. The metric is based on migratory individuals accounting for survival, reproduction, and movement during transitions between seasons (either a migratory transition between two habitats or a transition within a habitat that represents residency), and particular pathways between habitats (which follow a series of transitions through the annual cycle).

Runge et al. (2006) defined the metric C as the annual per-capita contribution of local population r to the entire metapopulation. If $C > 1$ then the local population contributes more individuals to the population than it loses through mortality, and is defined as a source. If $C < 1$ then the local

population loses more individuals through mortality than it contributes to the population through reproduction, and is defined as a sink (Runge et al. 2006). In this approach, breeding takes place in all habitats and this metric considers dispersal events (irregular one-way movements, not seasonal migrations). In contrast, migratory networks are somewhat unique because non-breeding habitats, by definition, do not produce individuals, which means their contributions using the original C metric would be < 1 . However, non-breeding habitats are critical for the persistence of migratory species. Thus, to account for their contribution, we account for their role in allowing individuals to survive the non-breeding season and return to reproduce on breeding grounds. For example, summer reproduction in the breeding grounds should count toward the annual per capita contribution for any given non-breeding location that provides habitat for migratory individuals between breeding seasons. The rationale behind this construct is to allow for carry-over effects and the fact that non-breeding grounds are necessary for supporting the energetic requirements for migration and breeding (Ratikainen et al. 2008).

Extending the contribution metric C to the case of migratory species leads us to replace the term 'local population' used in Runge et al. (2006) with 'habitat' (meaning a node within a migratory network) to highlight that our approach is scale independent and can accommodate habitats ranging from small patches up to large regions. For example, our approach accommodates species that undergo altitudinal migrations between habitats distributed across a mountainous landscape (e.g. American dippers *Cinclus mexicanus*; Loucks et al. 2003, Gillis et al. 2008) or species migrating across entire continents but occupying discrete breeding and non-breeding regions (e.g. Mexican free-tailed bats *Tadarida brasiliensis mexicana* or northern pintail ducks *Anas acuta*; Mattsson et al. 2012, Wiederholt et al. 2013).

Per capita contributions

For migratory species, the per capita contribution of a focal habitat, year-long pathway, or seasonal transition can be defined as the number of individuals in the entire population at year $T + 1$ that are generated from the average individual at year T that occupied the focal habitat, pathway, or transition at some point during the annual cycle (Fig. 1). The time interval over which the contribution is evaluated is one year for any given focal pathway, habitat, or transition. The annual time step T is broken into four seasons: breeding, breeding to non-breeding transition, non-breeding, and non-breeding to breeding transition. For example, for a long-distance temperate-tropical migrant, the per capita contribution of a focal pathway can be calculated from start of summer \rightarrow fall \rightarrow winter \rightarrow spring \rightarrow start of following summer. Correspondingly, habitat and transition-specific demographic parameters are classified into two stationary time periods or anniversary dates (i.e. when none of the individuals in the population are migrating) that depend on which habitat, breeding or non-breeding, is being considered. We refer to habitats as

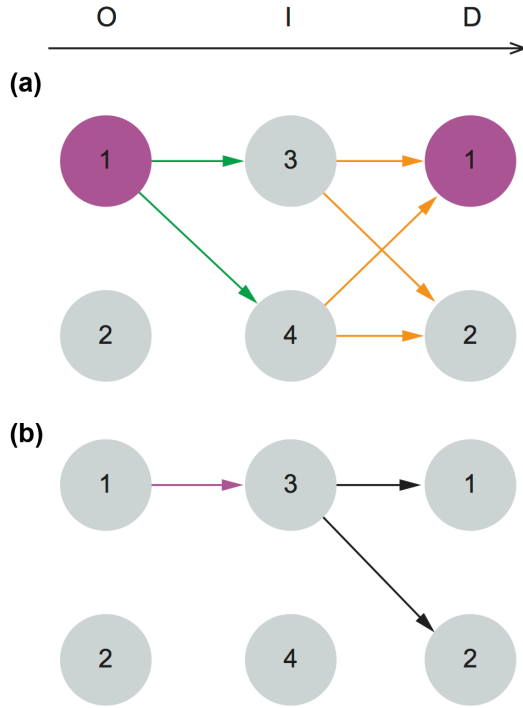


Figure 1. Depiction of per capita contributions for focal pathways, habitats, and transitions in a migratory network with 4 habitats, for a species with complete migration. When the annual cycle begins with the breeding habitat the order is: 1) origin (o) = breeding season through start of fall transition in year T ; 2) intermediate (i) = non-breeding season from end of fall transition through start of spring transition, and 3) final destination (d) = end of spring transition and start of breeding season in year $T + 1$. For non-breeding habitats the order is as follows: 1) origin (o) = non-breeding season through start of spring transition in year T ; 2) intermediate (i) = breeding season from end of spring transition through start of fall transition, and 3) final destination (d) = end of fall transition and start of non-breeding season in year $T + 1$. In (a) the focal breeding habitat 1 (dark-shaded circle) is occupied during the breeding season (origin time period, o) and is linked by migration to two habitats 3 and 4 that are occupied during the non-breeding season (intermediate time period, i). Then individuals migrate to either breeding habitat 1 or 2 for the final time period, d . In (b), focal transition 13 represents individuals moving from habitat 1 to 3 during migration, then, they migrate to either breeding habitat 1 or 2.

seasonally occupied during the origin o , intermediate i , or destination d time periods (Fig. 1).

We first calculate per capita contributions from migratory cohorts, or groups of individuals following a specific pathway. For instance, after the breeding season, individuals migrate from a breeding habitat o (origin) to a non-breeding habitat i (intermediate), and, after the non-breeding season, individuals migrate from a non-breeding habitat i to a breeding habitat d (destination). Per capita contributions can be calculated for any pathway from o to i to d (Eq. 1–4), for each discrete habitat in the network (Eq. 5) or for any seasonal transition (o to i , or i to d) within a pathway (Eq. 6). Resident cohorts

that remain in one habitat year-round can be accounted for by specifying $o = i = d$. A unique feature of our metric is that it can be used to estimate contributions of not only habitats, but also transitions and pathways within a migratory network. Supplementary material Appendix 1 compares our approach with the original Runge et al. (2006) formulation.

First, we define adult survival probability (A^{oid}) and per-capita juvenile recruitment (J^{oid}) for a focal pathway oid (migratory route) during their annual cycle. In the following equations, each vital rate can be specified separately for each migratory cohort oid , and the superscript a represents parameters for adults, while j represents parameters for juveniles. While most of the equations are the same regardless of anniversary date, the equations for juvenile recruitment (Eq. 2, 3) vary according to anniversary date. The probability of adult survival is the same regardless of the anniversary date (when in the annual life cycle we start). For the pathway oid is as follows:

$$A^{oid} = s_o^a \cdot s_{oi}^a \cdot s_i^a \cdot s_{id}^a \quad (1)$$

where s_o^a represents the adult survival probability for any individual using habitat o , s_{oi}^a represents the survival probability for adults transitioning between habitats o and i , s_i^a represents the adult survival probability for adults in habitat i , and s_{id}^a represents the survival probability during the transition from habitat i to habitat d (Fig. 2, Table 1). When $o = i$ and $i = d$, s_{oi}^a and s_{id}^a represent resident survival probabilities for non-migratory cohorts.

Unlike adult survival, the calculation of juvenile survival depends on which season is considered for the anniversary date in the annual cycle. For a breeding season anniversary date, the per-capita recruitment of juveniles along pathway oid is:

$$J^{oid} = s_o^a \cdot r_o \cdot s_{oi}^j \cdot s_i^j \cdot s_{id}^j \quad (2)$$

where s_o^a is adult survival in the breeding season, r_o represents the number of juveniles produced per adult that survive in habitat o , s_{oi}^j represents the juvenile survival probability during the transition from habitat o to habitat i , s_i^j represents the non-breeding season juvenile survival probability in habitat i , s_{id}^j represents the juvenile survival probability during the transition from habitat i to habitat d (Fig. 2).

For a non-breeding season anniversary date, the per-capita recruitment of juveniles along pathway oid is:

$$J^{oid} = s_o^a \cdot s_{oi}^a \cdot s_i^a \cdot r_i \cdot s_{id}^j \quad (3)$$

where s_o^a is adult survival in the non-breeding season, where s_i^a is adult survival in the breeding season, and r_i represents the number of juveniles produced per adult that survive in habitat i , and s_{oi}^a and s_{id}^j are defined as above.

The per capita contribution of a pathway, C^{oid} , can be calculated by summing the adult survival and juvenile recruitment moving along the oid pathway:

$$C^{oid} = A^{oid} + J^{oid} \quad (4)$$

Second, we demonstrate how the per capita contribution of a particular focal habitat during their annual cycle can

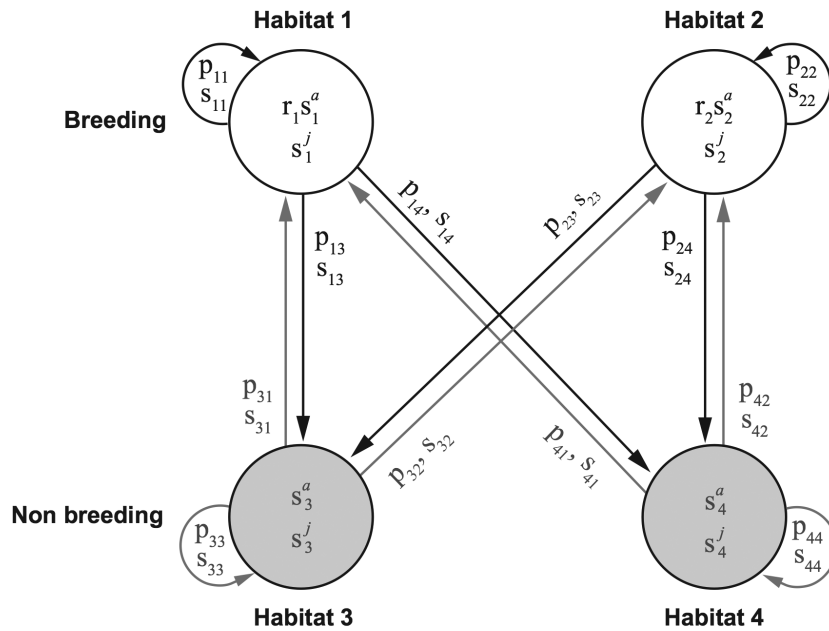


Figure 2. Vital rate parameters used for calculating per capita contributions within a hypothetical migratory network with four habitats, including two breeding (unfilled) and two non-breeding habitats (gray fill) that are connected by migratory pathways. Individuals choose among three migratory strategies according to a set of transition probabilities (p). They may either stay within their current habitat (non-migratory strategy) or migrate to one of two possible habitats. Reproduction (r) only occurs on the breeding habitats during the breeding season, and survival (s) can be specified for each habitat, age class (e.g. a = adults; j = juveniles), and season (not shown here for simplicity).

be derived from the pathway-specific contributions. A focal habitat's per capita contribution can be defined as follows:

$$C^o = \sum_{i=1}^n \sum_{d=1}^n (C^{oid} \cdot p_{oi} \cdot p_{id}) \quad (5)$$

where C^{oid} is defined in Eq. 3, p_{oi} represents the probability of individuals transitioning from habitat o to one of n

intermediate destinations indexed by i (including any habitat in the network), and p_{id} represents the probability of individuals transitioning from habitat i to one of n final destinations indexed by d (including any habitat in the network). When $o = i$ and $i = d$, p_{oi} and p_{id} are probabilities of not migrating from habitats o to i , or i to d , respectively, which represents non-migratory cohorts of the population.

Table 1. Baseline parameters for estimating per capita contributions to a hypothetical migratory population.

Parameters by season and habitat*†	Baseline parameter values‡
Breeding in habitat o or i	
$s_{o,a}^a$ Adult survival probability	0.96 [1 = 2]
$r_{o,a}$ Number of juveniles produced per adult that survive the breeding season	0.7 [1], 0.55 [2]
Transition from habitat o to i , or i to d [13 = 14 = 23 = 24]	
s_{oi}^a Adult survival probability	0.85
s_{oi}^j Juvenile survival probability	0.80
p_{oi} Migration probability	0.50
Non-breeding in habitat i or o	
$s_{i,o}^a = s_{j,o}^j$ Adult = juvenile survival probability	0.98 [3], 0.86 [4]
Transition from habitat i to d , or o to i [31 = 32 = 41 = 43]	
$s_{id,oi}^a$ Adult survival probability	0.85
$s_{id,oi}^j$ Juvenile survival probability	0.85
$p_{id,oi}$ Migration probability from habitat	0.50
Other parameters	
w_o Ratio of population size in habitat o to total population size in all habitats o	0.50 [1 = 2, 3 = 4]

Note: *habitat o represents the habitat of origin, habitat i represents an intermediate destination, and habitat d represents a final destination, †habitat and transition numbers are given in square brackets, some indicating when habitats or transitions had equivalent values.

In this case a habitat will have two contribution metrics, one starting at the beginning of the breeding season and one starting at the beginning of the non-breeding season.

We can also calculate per capita contributions of transitions. For instance, the contribution for the transition from habitat o to i , C^{oi} , is determined:

$$C^{oi} = \sum_{d=1}^n C^{oid} \cdot p_{id} \quad (6)$$

where p_{id} is defined above. This is a weighted summation of the pathway contributions, where the transition probabilities are the weights. When $o = i$ or $i = d$, Eq. 6 can represent non-migratory cohorts of the population.

The contribution metric developed by Runge et al. (2006) had a valuable property – the contributions, weighted by the fraction of the population they represented, added up to the population growth rate. This same property holds for all of the metrics we have developed. For example, using habitat-specific contributions, we can calculate the growth rate, λ :

$$\sum_{o=1}^n w_o C^o = \lambda \quad (7)$$

where w_o is the population size in habitat o divided by the total population size summed across all habitats in that season, and C^o is determined from Eq. 5. The growth rate equations can either be interpreted instantaneously or asymptotically. Methods for calculating λ from C^{oid} , C^{oi} and C^o , along with an equation for w_o are provided in Supplementary material Appendix 2.

Applying the contribution metric to hypothetical migratory networks

We used a simple, four-habitat network with two breeding habitats (habitats 1 and 2; Fig. 1) and two non-breeding habitats (habitats 3 and 4; Fig. 1) to explore habitat, pathway, and transition contributions via perturbation analyses. This migratory network is considered bipartite (sensu Taylor and Norris 2010) meaning that there are two set of habitats (breeding and non-breeding) that must be used by individuals over the course of the annual cycle and that pathways only connect habitats between habitat sets. Our parameterization was loosely based on a northern hemisphere migratory species, with intermediate survival probabilities, similar migration survival probabilities for adults and juveniles, and fairly low levels of reproduction (Table 1) (Sæther and Bakke 2000).

We developed two baselines, one heterogeneous and one homogeneous baseline (which is discussed solely in Supplementary material Appendix 3). The homogeneous baseline was developed to simply illustrate the effect of perturbations on contributions; these perturbations included changes to the population distribution, migration strategy and probability, and survival probability. It assumed all vital rates and migration probabilities were equal among habitats, and the baseline was used to test 5 basic scenarios (see Supplementary material Appendix 3 for results and discussion of these

scenarios). We ran additional scenarios based on a heterogeneous baseline with two high quality habitats (1 and 3) and two low quality habitats (2 and 4) (scenario 1 in Fig. 3). Non-breeding habitat 3 had higher survival than non-breeding habitat 4, and breeding habitat 1 had higher reproduction than breeding habitat 2 (Table 1). While we explore a limited set of five scenarios, these were selected to illustrate how habitat and pathway quality, and migratory flows and strategy may affect the per capita contributions and population viability. First, using the heterogeneous baseline, we explored a Heterogeneous baseline scenario (scenario 1 in Fig. 3), and a Rescue effect scenario (scenario 2 in Fig. 3), where we increased migration between high and low quality habitats (migration probabilities between habitats 1 and 4, and between 2 and 3 were increased by 50% to 0.75). Such a migratory pattern could occur if the routes connecting habitat 1 to 4, and 2 to 3 were less costly (e.g. a shorter distance) than the routes from habitat 1 to 2, and 2 to 4. In scenarios 3 (Low quality pathway) and 4 (Low quality pathway and partial migration), we lowered the quality of the pathway between habitats 1 and 3 by lowering spring and fall migration survival probabilities by 6%. This scenario could occur due to loss or degradation of stopover sites along the migratory route. In scenarios 4 (Low quality pathway and partial migration) and 5 (Low quality habitat and partial migration), we also added a partially migratory population where 25% of individuals stayed in breeding habitat 1 yr round and avoided using the low-quality pathway between habitats 1 and 3. For example, due to global change, some migratory species can now remain on their overwintering grounds year round, and a portion of the population may become non-migratory (Newton 2010). For these scenarios, habitat 1, transition 11, and pathway 111 have two contributions: one starting at the beginning of the breeding season, and the other starting at the beginning of the non-breeding season (because a non-migratory population occupies the habitat year-round). For scenario 4, winter survival in breeding habitat 1 was reduced to 85% of the survival probability for habitat 3 and 4, and survival during migration period increased by 5 to 89% for adults and 84% for juveniles. Finally, we tried a low-quality habitat and partial migration scenario where we lowered winter survival in habitat 3 by 12% to the level of habitat 4 (from 0.98 to 0.86; scenario 5 in Fig. 3). This scenario could occur due to habitat loss or degradation on the breeding grounds. The partially migratory population had the same characteristics as scenario 4 except that winter survival was lowered to only 89% of the survival probability for both habitat 3 and 4.

We used R to program our models (R Core Team). Our model file, script file, and an excel sheet to calculate contributions are included in Supplementary material Appendix 4. The code uses a matrix notation which was necessary to generalize to any number of habitats in the network, which is included in Supplementary material Appendix 5. We attach a complete list of results in Supplementary material Appendix 3, including a discussion of our scenario hypotheses and results.

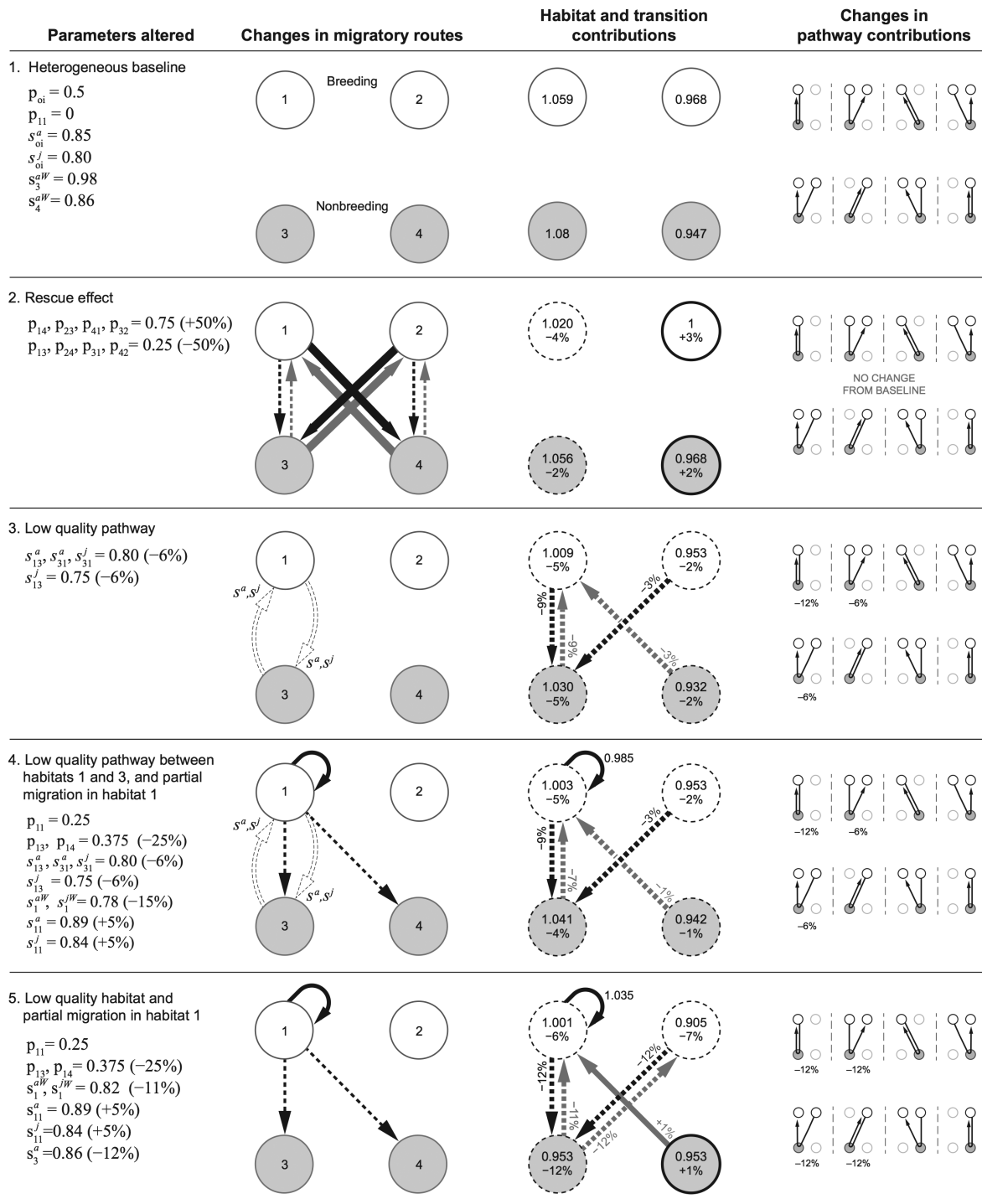


Figure 3. Per capita contributions from example migratory networks using the heterogeneous baseline. Parameters are altered (scenarios 2–5) are displayed, along with changes to the migratory network. Changes to transition and pathways contributions from the heterogeneous baseline for only the breeding season anniversary are displayed. Habitat contributions (and changes from the heterogeneous baseline) are displayed within the circles. The arrows that are shown represent changes from baseline. Dashed arrows or habitat outlines represent reduced migratory flow or contributions, while thick solid lines or habitat outlines represent increased migratory flow or contributions. The unfilled arrows in scenarios 3–4 display reduced adult and juvenile migratory survival. For a complete table of results see Supplementary material Appendix 3 Table A7–A10.

Results

As expected, with heterogeneous quality habitats (Heterogeneous baseline, scenario 1 in Fig. 3), habitats 1 and 3 had contributions above 1, while habitats 2 and 4 had contributions below 1. The population growth rate was slightly increasing ($\lambda = 1.01$). Pathways or transitions that originated or passed through the low quality habitats (2 and 4) had lower contributions than pathways that originated or passed through high quality habitats (Fig. 3, Supplementary material Appendix 3 Table A7–A11).

When migratory flow increased between high and low quality habitats (Rescue effect, scenario 2 in Fig. 3), the contributions of the high quality habitats (1 and 3) were lowered but the contributions of the low quality habitats (2 and 4) increased, and habitat 2's contribution increased above one. However, the population growth rate did not change from scenario 1 ($\lambda = 1.01$). Under the rescue effect, pathway and transition contributions were unaltered compared to scenario 1, as no parameters affecting per capita rates along the pathways were changed.

Lowering the quality of the pathway between habitats 1 and 3 in both directions (Low quality pathway, scenario 3, and Low quality pathway and partial migration, scenario 4 in Fig. 3) decreased the contributions of all habitats. The population growth rate was also decreasing for both scenarios ($\lambda = 0.98$ for both scenarios). Transitions or pathways that included the transition between habitats 1 to 3 also had lowered contributions (Fig. 3, Supplementary material Appendix 3 Table A7–A11).

Adding a resident population in habitat 1 (Low quality pathway and partial migration, scenario 4 in Fig. 3) caused the contribution of habitat 1 to decrease by different amounts depending on the anniversary date modeled. The contribution of habitat 1 from the start of the breeding season decreased slightly (compared to scenario 3), and its contribution from the start of the non-breeding season was reduced to below 1. Although fewer individuals used the low quality pathway between habitat 1 and 3, the lowered winter survival of the non-migratory population decreased habitat 1's breeding season contribution, and caused the non-breeding season contribution to be below one. The contribution for non-breeding habitats (3 and 4) and the spring transitions (31 and 41), although lowered compared to the baseline, increased slightly compared to scenario 3 because some migrants stayed in habitat 1 and had higher survival during the fall migration. The contributions for pathway 111 and transition 11 were below one (other partially migratory pathway results are discussed in Supplementary material Appendix 3).

Lowering the winter survival in habitat 3 with a partial migration population (Low quality habitat and partial migration scenario 5 in Fig. 3) caused the contributions of habitats 1, 2, and 3 to decline. The population growth rate also declined compared to the other scenarios ($\lambda = 0.95$). The contributions for habitat 4 and transition 41 increased slightly, because habitat 4 sent some migrants that remained

in habitat 1 that had a higher survival during fall migration compared to baseline where all individuals migrated. Habitat 1, however, still had a breeding season-anniversary date contribution above 1 because its partially migratory population buffered it from poor conditions in overwintering grounds. The non-breeding season-anniversary date contribution, on the other hand, for habitat 1 was below 1 because some juveniles moved along migratory pathways in fall (to habitats 3 or 4) that did not have the higher survival of non-migratory individuals. Contributions for pathways or transitions that used habitat 3 also declined compared to the baseline scenario 1 from the reduced winter survival (Fig. 3, Supplementary material Appendix 3 Table A7–A11). Pathway 111, and transition 11 had contributions above one despite low winter survival, because of the higher survival for non-migratory individuals in habitat 1 during the migratory seasons (other partially migratory pathway results are discussed in Supplementary material Appendix 3).

Discussion

We have developed a method for calculating the per capita contribution to the overall population of a migratory species of individuals using a particular habitat, pathway, or transition. Our contribution metric differs from those published earlier for other metapopulation structures in that it can be used not only to derive the demographic contributions of each habitat, but also to understand the importance of different migratory pathways and transitions. Our metric can be applied to any network (e.g. metapopulations, altitudinal migration, partial migration) and classifies migratory network elements as contributing (contribution > 1), maintaining (contribution $= 1$), or losing (contribution < 1) individuals to the overall population. Our method can be easily altered to accommodate smaller time steps to model stop-over sites used during migration, and can be adapted to any type of network (e.g. tripartite) and for other types of age or stage-structured populations (e.g. juveniles, immatures, and adults). Adults and juveniles can also be easily given different transition probabilities, as in some species the juveniles migrate separately from their parents. Our contribution metric expands upon previous approaches (Runge et al. 2006) by estimating demographic contributions for habitats and pathways through specification of migratory cohorts and illustrating the dependency of individual habitat contributions on vital rates in other habitats used during the annual cycle. Our approach is useful for addressing hypotheses about impacts from perturbations to migratory network and the adaptive advantages of particular life history strategies for spatially structured populations.

While our hypothetical 4-habitat network was relatively simple (2 breeding and 2 non-breeding habitats), our analysis illustrated four properties of migratory network dynamics. First, lowering the quality of a habitat lowers the contribution of that habitat (Heterogeneous baseline, scenario 1 in

Fig. 3). Second, the demographic contribution from one habitat is contingent on demographic processes in other habitats and pathways (Rescue effect, Low quality pathway, and Low quality habitat and partial migration, scenarios 2, 3, and 5 in Fig. 3; scenario B5 in Supplementary material Appendix 3). For example, increased migration from a high-quality habitat could raise the contribution of a low-quality patch to one, which demonstrates that migratory connectivity alone can have a ‘rescue effect’ on habitats in the network (Rescue effect, scenario 2 in Fig. 3). Our analysis also demonstrated that alterations during one season or one habitat may have reverberating effects throughout the migratory network. This has been reported in other models (Dolman and Sutherland 1995, Taylor and Norris 2010) and experiments (Betini et al. 2015) in migratory systems. For example, decreased survival in one habitat decreases the contribution of other habitats (Low quality habitat and partial migration, scenario 5 in Fig. 3, scenario B5 in Supplementary material Appendix 3). Similarly, other studies simulating habitat loss in more complex networks demonstrated ‘knock-on effects’, where a perturbation at a node can cause population increases or decreases at other nodes that are not directly connected (Taylor and Norris 2010, Betini et al. 2015). In addition, the position of the node within the network and its connectivity can either mediate or exacerbate the impacts of habitat loss (Taylor and Norris 2010). Such effects occur because of the dependence of migratory species on multiple habitats during the annual cycle, which indicates that management in one area can have consequences for population dynamics in all areas of occurrence (Taylor and Norris 2010).

Third, lowering the quality of a migratory route lowers the quality of not only habitats directly along this route but other habitats in the network are affected as well (Low quality pathway, and Low quality pathway and partial migration, scenarios 3 and 4 in Fig. 3). Lowered pathway quality had a large impact on contributions, showing the importance of focusing demographic studies of, and conservation efforts for, migratory species not only on habitat quality but also corridors, stopover sites, and migratory connectivity. This result is analogous with network modeling of migratory birds that showed that loss of flyway habitat caused a disproportionate decline of migratory flow (Iwamura et al. 2013). Fourth, a partially migratory population in a habitat with lowered winter survival can reduce the contribution of that habitat (scenario 4 in Fig. 3). However, if winter survival is also lowered in other habitats in the network, partial migration in a habitat with more moderate winter survival can maintain a contribution above one (scenario 5 in Fig. 3). This buffering effect may be a mechanism driving evolution of partial migration (Holt and Fryxell 2011). Although not directly tested in our analysis, partial migration could potentially help buffer against the complete loss of a habitat (if transition probabilities can change). By quantifying these coupled effects, our metric offers a tool for assessing consequences

of ongoing and future changes in climate and land use throughout a migratory network.

Our framework generates multiple areas for future research. A particularly important question is whether per capita contributions can serve as indicators for habitat that are crucial for maintaining population viability in the face of possible perturbations or disturbance. For instance, our modeling framework could be applied to real case study species to better understand which habitat areas are most important to maintain a stable or increasing population. Another area for future research could examine how network structures and migration strategies (e.g. metapopulations, partial or complete migration) affect contributions of network elements. Our framework can also be extended to accommodate density-dependence and carry-over effects by adding covariates for the demographic parameters (e.g. reproduction, r ; Betini et al. 2015), and contributions could be calculated for males and females separately.

One disadvantage of this approach is that contrasting time periods (offset by 6 months) for habitats occupied only during breeding versus those only occupied during non-breeding could be of concern if there is significant annual variation in demographic rates. In this case, the comparability of breeding and non-breeding-only habitat contributions could diverge with increasing temporal variation in quality of breeding and non-breeding habitats, and the quality and preference of transitions.

Conclusions

We have developed metrics for the per capita contribution of individuals using discrete habitats, pathways, and transitions to the population dynamics of spatially structured populations, including migratory populations. These metrics can be applied to species with varied life history traits, migratory strategies, and age structures, and can be extended to calculate contributions for density dependence and carry-over effects. These metrics are useful for studies of ecology and evolution, and most importantly provide a means of prioritizing conservation efforts towards those migratory pathways and habitats that are most critical for the population viability of migratory species.

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Supplementary material (Appendix ECOG-02718 at <www.ecography.org/appendix/ecog-02718>). Appendix 1–5.