





Defining and classifying migratory habitats as sources and sinks: the migratory pathway approach

Richard A. Erickson¹  | Jay E. Diffendorfer² | D. Ryan Norris³ | Joanna A. Bieri⁴ | Julia E. Earl⁵  | Paula Federico⁶ | John M. Fryxell³  | Kevin R. Long⁷ | Brady J. Mattsson⁸ | Christine Sample⁹  | Ruscena Wiederholt¹⁰ | Wayne E. Thogmartin¹

¹Upper Midwest Environmental Sciences Center, U.S. Geological Survey, La Crosse, WI, USA

²Geosciences and Environmental Change Science Center, U.S. Geological Survey, Denver Federal Center, Denver, CO, USA

³Department of Integrative Biology, University of Guelph, Guelph, ON, Canada

⁴Department of Mathematics and Computer Science, University of Redlands, Redlands, CA, USA

⁵Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK, USA

⁶Department of Mathematics, Computer Science and Physics, Capital University, Columbus, OH, USA

⁷Department of Mathematics and Statistics, Texas Tech University, Lubbock, TX, USA

⁸Institute of Silviculture, University of Natural Resources and Life Sciences, Vienna, Austria

⁹Department of Mathematics, Emmanuel College, Boston, MA, USA

¹⁰School of Natural Resources & the Environment, The University of Arizona, Tucson, AZ, USA

Correspondence

Richard Erickson
Email: rerickson@usgs.gov

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Abstract

1. Understanding and conserving migratory species requires a method for characterizing the seasonal flow of animals among habitats. Source-sink theory describes the metapopulation dynamics of species by classifying habitats as population sources (i.e. net contributors) or sinks (i.e. net subtractors). Migratory species may have non-breeding habitats important to the species (e.g. overwintering or stopover habitats) that traditional source-sink theory would classify as sinks because these habitats produce no individuals. Conversely, existing migratory network models can evaluate the relative contribution of non-breeding nodes, but these models make an equilibrium assumption that is difficult to meet when examining real migratory populations.
2. We extend a pathway-based metric allowing breeding habitats, non-breeding habitats and migratory pathways connecting these habitats to be classified as sources or sinks. Rather than being based on whether place- or season-specific births exceed deaths, our approach quantifies the total demographic contribution from a node or migratory pathway over a flexibly defined yet limited time period across an organism's life cycle. As such, it provides a snapshot of a migratory system and therefore does not require assumptions associated with equilibrium dynamics.
3. We first develop a generalizable mathematical notation and then demonstrate how the metric may be used with two case studies: the common loon (*Gavia immer*) and Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*). These examples highlight how stressors can impact stopover and wintering habitats (loons) and habitat management targeting migratory pathways can improve population status (trout).
4. *Synthesis and applications.* Each of the two case studies presented describes how effects at one location are felt by populations in another through the seasonal flow of individuals. The contribution metric we present should be helpful in allocating regulatory and management attention to times and locations most critical to migratory species persistence.

KEYWORDS

common loon, conservation, invasive species, metapopulations, network model, waterfowl, Yellowstone cutthroat trout

1 | INTRODUCTION

Understanding the contribution of seasonally occupied habitats to the population dynamics of migratory species is crucial for developing ecological theory and conservation strategies (Doak, 1995; Donovan, Thompson, Faaborg, & Probst, 1995; Pulliam, 1988). This knowledge of key habitat for a migratory population can aid in designing reserves, optimizing conservation funding and maintaining population viability (Battin, 2004; Martin et al., 2007; Naranjo & Bodmer, 2007). A population's proportional dependence on a location can be defined as the degree to which that location contributes to the entire population's maintenance (i.e. births and deaths; Semmens, Diffendorfer, López-Hoffman, & Shapiro, 2011). However, despite our ability to conceptualize the idea of population dependencies, precisely defining and estimating this value poses challenges when depicting migratory species population dynamics and corresponding needs for conservation and management.

Within metapopulation theory, several approaches have been put forth to identify the relative contribution of sources and sinks (Caswell & Shyu, 2012; Krkošek & Lewis, 2010; Ovaskainen & Hanski, 2003; Strasser, Neubert, Caswell, & Hunter, 2012). Runge, Runge, and Nichols (2006) developed a contribution metric. This metric is defined as the per capita contribution, C , to the next generation of a member of the focal subpopulation, r (Runge et al., 2006, p. 928). This C can be used to classify subpopulations within a metapopulation as sources ($C > 1$) or sinks ($C < 1$). An advantage of this metric is that it can be used to assess the relative contribution of individual habitats using "snapshots" of data, such as those collected during annual monitoring, sampled across an otherwise spatiotemporally variable network. This differs from assessments of habitat contributions in traditional network models (e.g. Taylor & Norris, 2010) which assume a dynamical system at equilibrium.

Metrics such as C are useful for identifying sources and sinks but cannot be readily applied to migratory organisms. By definition, migratory organisms use more than one habitat over the course of a year, but most species only breed during specific time periods and in a subset of all habitats. Applying the traditional source-sink definitions to migratory organisms would, therefore, classify non-breeding habitats as sinks because these habitats do not produce offspring. However, these non-breeding habitats play an important, often essential, role in migratory species dynamics (Martin et al., 2007; Norris, Marra, Kyser, Sherry, & Ratcliffe, 2004) and should not automatically be classified as deleterious (Taylor & Hall, 2012). Wiederholt et al. (2017) demonstrated how the C metric could be adapted to a migratory network with two stationary seasons; their approach, however, does not include a method for generalizing the metric to more complex networks (e.g. shorter periods of habitat residency represented by migratory stopovers).

Our goal was to develop an approach for assessing the relative contribution of all types of habitats throughout the annual cycle of migratory species. We do so by developing contribution metrics (for both habitats and pathways) accounting for any number of time periods and types of habitats or "nodes" (e.g. breeding habitat, stationary non-breeding habitat and migratory stopovers). To correctly value non-breeding habitats, we use a pathway concept from network models (Taylor & Norris, 2010) for following groups of individuals using the same migratory pathway. We outline this approach and then apply it to two example migratory species: the common loon (*Gavia immer*) and Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*).

1.1 | The network approach

One approach for describing the spatial and temporal dynamics of migratory populations is to use network theory (Taylor & Hall, 2012; Taylor & Norris, 2010). Habitats within a spatially structured population can be defined as "nodes" connected by "edges" (Taylor & Norris, 2010). For seasonally breeding migratory animals, a network contains two general node "sets": breeding and non-breeding nodes (Taylor & Norris, 2010). Edges allow for dispersal between nodes (i.e. migration). We develop a metric for migratory networks that addresses the following issues: (1) some nodes may be unoccupied in a given period and (2) non-breeding nodes (e.g. stationary overwintering habitat, stopover habitats) should not necessarily be classified as sinks even though they do not produce offspring.

2 | MATERIALS AND METHODS

2.1 | Metrics

2.1.1 | Metric formulation

Our formulation must account for both spatial and temporal variables while, ideally, being compact, clear and generalizable. We begin by considering a landscape comprised of N nodes (Taylor & Norris, 2010) or "habitat patches" (Runge et al., 2006), denoted using subscripts (e.g. parameter x for node 1: x_1). Nodes are connected by edges, denoted using a subscript that includes the starting and ending nodes (e.g. parameter x for the edge between nodes 1 and 2: $x_{1,2}$). A simple network might include three nodes and two time periods: node 1 occupied only during summer as a breeding node, node 2 occupied year-round and node 3 only occupied during winter (Figure 1).

A pathway is a route a group of individuals takes over the course of a set time period (typically a year). For example, a group of individuals spending the summer at node 1, the winter at node 2, and then returning to node 1 use pathway $1 \rightarrow 2 \rightarrow 1$ and parameter x for the pathway

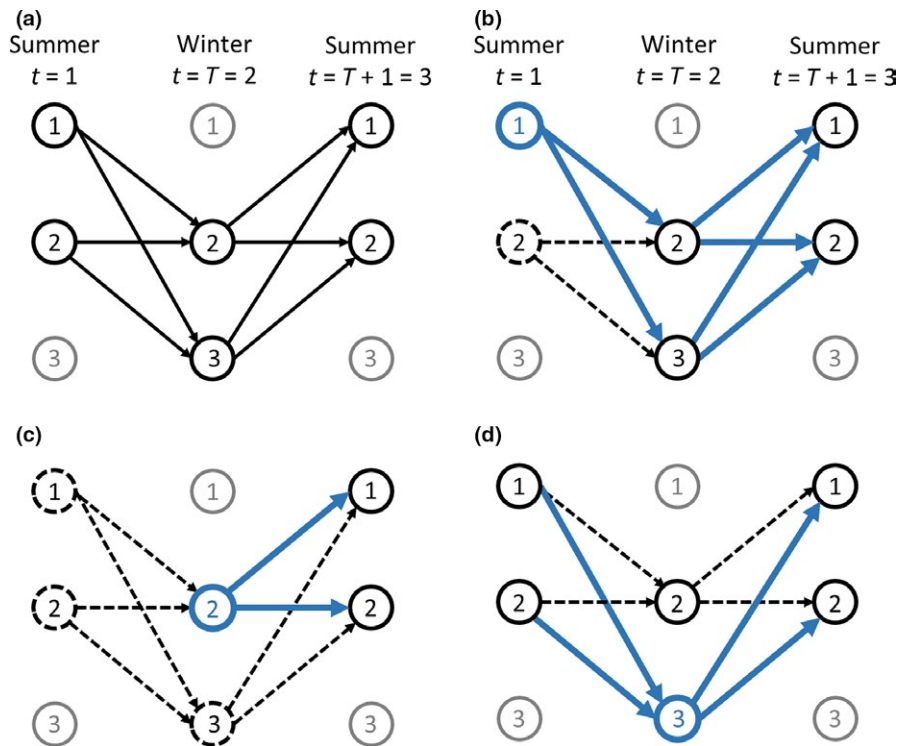


FIGURE 1 Examples of three different approaches for calculating node contributions in a complete-migratory network with three nodes and two time periods ($T = 2$). Circles are nodes, and arrows are edges depicting migratory transitions between successive time periods. (a) It illustrates the complete network and all pathway transitions starting at origin nodes (left-hand column) and ending at destination nodes (right-hand column). Node 1 is occupied only during summer, node 2 is occupied all year and node 3 is occupied only during winter. (b–d) Solid arrows indicate migratory movements considered when calculating contribution of the focal node, whereas the dashed arrows indicate migratory movements existing in the network but not part of the focal node contribution calculation. (b) It illustrates calculation of C_1 , the per capita contribution of origin node 1. (c) It illustrates calculation of ${}_3F_3$, the flow-through contribution from node 3. (d) It illustrates calculation of ${}_2E_2$, the fixed-end contribution from node 2 starting at beginning of winter and ending at end of spring migration

would be $x_{1,2,1}$. The group of individuals using a pathway is considered to be a **subpopulation**, and all of the subpopulations (i.e. all individuals) comprise the global population. The start and end time of the pathway depends on the life history, monitoring and management of the species.

To generalize our metric, we specify T time periods (indexed by t) within the annual cycle (e.g. four time periods might be summer; fall; spring; and winter, or two time periods might be summer/fall and winter/spring). Each time period includes growth and survival at the node and a subsequent transition. For example, a species migrating between temperate North America and Central America could have two 6-month time periods in the annual cycle: (1) summer through fall migration and (2) winter through spring migration (Figure 1). A slightly more complex migration might have three unequal time periods: (1) summer through arrival at a fall stopover node, (2) fall through arrival at a winter node and (3) winter and the spring transition back to breeding nodes. All nodes in the migratory network, including seasonally unoccupied nodes, are present in the system for each time period. This arrangement allows for simpler notation and for partial migration (i.e. a portion of the individuals using a given node migrate while others remain in that node year-round). Potentially occupied nodes during time step t are denoted as $i_t \in \{1, \dots, N\}$, where i indexes N nodes in the network. The pathway used by any given subpopulation throughout the time period $t = 1$ to T

is denoted by the sequence of nodes occupied: i_1, i_2, \dots, i_{T+1} . The final node in the sequence represents the destination node, which is necessary to specify in order to properly account for the final transition in the sequence of occupied nodes in the pathway from i_T to i_{T+1} .

2.1.2 | Pathway contributions

The pathway is the basic building block for calculating demographic contributions within a migratory network (Figure 1). Each pathway has two types of growth parameters. First, node growth parameter ${}_iS_i$ quantifies survival and births within node i for a specific time period t (e.g. ${}_3S_1$ is growth for node 1 during time period 3). The time period is indexed within a subscript before the variable name, whereas the node is indexed within a subscript after the variable name. Second, edge growth parameter ${}_{t,t+1}S_{ij}$ quantifies survival and births between time periods t and $t + 1$ when transitioning from node i to node j , where i indexes any of N nodes potentially occupied during time period t and j indexes any of N nodes potentially occupied during time period $t + 1$ (e.g. ${}_{5,6}S_{1,2}$ is growth for the migration between nodes 1 and 2 between time periods 5 and 6). If no births occur at a node or an edge, the growth parameter is survival. A pathway's growth parameter is the product of all the growth parameters for that pathway:

$$S_{i_1, i_2, \dots, i_T} = \prod_{t=1}^T S_{i_t, i_{t+1}}$$

where we use a more complex notation to represent the sequences of transitions between successive time periods ($t = 1, 2, \dots, T$) and correspondingly between nodes ($i = 1, 2, \dots, N$) comprising each pathway in the network. Left of the equal sign, subscript i_1, i_2, \dots, i_T shows the sequence of T nodes (indexed by i) comprising a focal pathway. To the right of the equal sign, S_i is node growth and is defined above. The right-most term $S_{i_t, i_{t+1}}$ is pathway growth, whose subscript indicates the transition between two nodes within the sequence of nodes (i.e. i_1, i_2, \dots, i_T) comprising a particular pathway. When focusing on a single transition, pathway growth can be written as it was originally, $_{t,t+1}S_{ij}$. Pathway growth is equal to the annual per capita contribution for the pathway and ranges from 0 to the theoretical maximum increase in individuals between $t = 1$ and T .

We define transition probability $_{t,t+1}p_{ij}$ as the probability a subpopulation at node i will transition to node j between time periods t and $t + 1$ (e.g. probability of going from node 1 to node 2 between time periods 3 and 4 is $_{3,4}p_{1,2}$), which uses notation analogous to that of the edge growth parameter $_{t,t+1}S_{ij}$. All transition probabilities leaving a given node for a given time period must sum to 1, accounting for all transitions from a node, including remaining at a node. The probability an individual uses pathway i is the product of all transition probabilities between the sequence of nodes occupied within that pathway:

$$P_i = P_{i_1, i_2, \dots, i_T} = \prod_{t=1}^{T-1} p_{i_t, i_{t+1}}$$

where we use the more complex subscripting that is also used for pathway growth.

A pathway's contribution metric is

$$C_i = C_{i_1, i_2, \dots, i_T} = P_{i_1, i_2, \dots, i_T} \times S_{i_1, i_2, \dots, i_T}$$

representing the probability pathway i is used multiplied by survival and births of individuals using it. A pathway's contribution metric provides a relative indicator of the pathway's importance (i.e. a larger contribution metric indicates a pathway contributes more than one with a smaller metric), but it is not a per capita metric and should not be used for assessing source-sink status of a pathway.

2.1.3 | Node contributions

Pathways are used to calculate the contribution of any focal node to population-level change from $t = 1$ to T (Figure 1). The approach for calculating node contribution depends on whether that node is occupied at $t = 1$ (henceforth, origin node). The per capita contribution of an origin habitat node r is the sum of all contributions from pathways originating from that node (Figure 1b):

$$C_r = \sum_{i \in {}_1Y_r} C_i \quad (1)$$

where ${}_1Y_r$ is the set of all pathways with an origin node r , ${}_1Y_r = \{i_1, i_2, \dots, i_T \mid i_1 = r\}$, and C_i is the contribution of each pathway (indexed by i) including origin node r .

2.1.4 | Contributions of unoccupied nodes at $t = 1$

To this point, we described how to calculate the demographic contribution of a given origin node to the entire population. For a node that is unoccupied at $t = 1$ (i.e. non-origin node), there are at least two ways to calculate its contribution (Data S1). A flow-through metric (${}_tF_r$; Figure 1c) sums the contributions from all pathways "flowing" through a non-origin node, which accounts for demographic contributions from individuals using the focal non-origin node during a specified time period. Alternatively, the fixed-end (destination) contribution metric (${}_tE_r$; Figure 1d) quantifies the per capita contribution of a non-origin node to the entire population starting during a time period when the focal node is occupied and ending at a fixed time that is consistent for all nodes. When calculated for an origin node, the flow-through metric is equivalent to C_r (Equation 1).

2.2 | Case studies

We chose two case studies based on conservation concerns and species life histories that make other source-sink criteria inappropriate. Our case studies simplify the life histories of the species but demonstrate how different spatially explicit subpopulations contribute to system dynamics. The first example is the common loon, a species of least concern but with a rate of population change decreasing in recent decades (Gear et al., 2009). The second example is the Yellowstone cutthroat trout, a distinct subspecies living in Yellowstone Lake, Wyoming, and surrounding tributaries (Gresswell, Liss, & Larson, 1994).

For each case study, we developed a migratory network model (Figures 2 and 3) parameterized primarily based on available literature for each species. When no parameter values could be found in the literature, we used our own knowledge and logic to specify them for the models. We then examined potential impacts of spatially explicit threats on growth and contribution of each pathway along with contribution of each node. When calculating node contributions, we compared values from the flow-through and fixed-end metrics. We

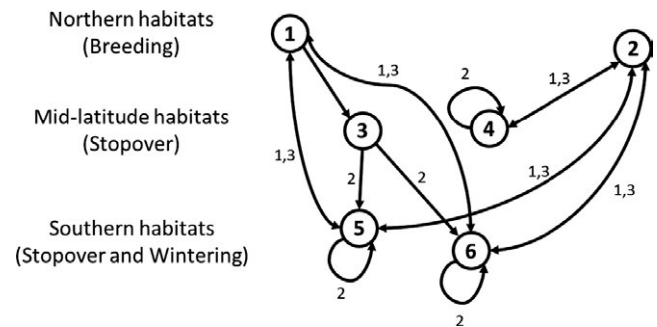


FIGURE 2 Habitat nodes and edges used by common loons in the eastern US. Circles are nodes, and the arrows depict edges used for migration. Node 1 is the Upper Midwest, 2 is New England, 3 is Lake Michigan, 4 is the Mid-Atlantic Coast, 5 is the Gulf Coast of Florida and 6 is the Atlantic Coast of Florida. Numbers next to edges are time periods in which an edge is used

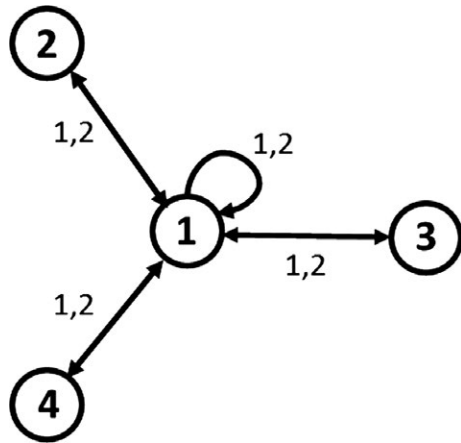


FIGURE 3 Habitat nodes and edges used by Yellowstone cutthroat trout in Wyoming, US. The circles are nodes and the arrow depicts edges used for migration. Node 1 is Yellowstone Lake, and nodes 2 through 4 are tributaries. Numbers next to edges are time periods in which an edge is used

calculated each node contribution metric using multiple start dates if the focal habitat was occupied during multiple seasons, with start dates corresponding to these occupied seasons. We, therefore, computed one node contribution value for every node and occupied-season combination. Pathways with a growth parameter >1 and nodes with a contribution metric >1 were considered sources, whereas the remainder were considered sinks. We also conducted a sensitivity analysis for the common loon case study (Supporting Information).

2.2.1 | Common loons of the eastern United States

Common loons are migratory waterbirds breeding in northern latitudes and overwintering in southern latitudes in the Nearctic (Gear et al., 2009). Within the Eastern United States, two breeding habitats exist: the Upper Midwest (primarily Wisconsin and Minnesota) and New England (primarily New York, New Hampshire, and Maine; Figure 2; Gear et al., 2009; Kenow, Meyer, Evers, Douglas, & Hines, 2002). All birds breeding in the Upper Midwest and some breeding in New England overwinter in the Gulf or Atlantic Coasts of Florida. Remaining New England birds overwinter off the mid-Atlantic coast near Rhode Island, Massachusetts and New Jersey (Gear et al., 2009; Kenow et al., 2002). Nearly all subpopulations are seasonally sympatric (i.e. their pathways intersect at nodes) except for the subpopulation in the Upper Midwest, which is allopatric from the one wintering along the mid-Atlantic coast. All subpopulations exhibit complete migration.

In developing the migratory network structure for loons, we simplified the spatial structure while retaining salient features of interest: eastern and western breeding nodes (nodes 1 and 2); a fall stopover node on Lake Michigan (Node 3); and overwintering nodes on the mid-Atlantic (node 4), Gulf (node 5) and Atlantic Coasts (node 6; Figure 2). Three time periods were chosen for loons: (1) breeding period (roughly late-spring and summer); (2) fall stopover period; and (3) overwintering period (roughly winter and early-spring). Each of these periods

corresponds with the start of a stationary time period (e.g. breeding) when loons are not migrating and reside in one of the habitats in the network for 3–4 months.

For model parameterization, we first developed a reference scenario representing current understanding of loon demographics in this system (Data S2). As is often the case, demographic estimates do not exist for all habitats and migratory routes (Hostetler, Sillett, & Marra, 2015). Gear et al. (2009) used survival estimates published in the peer-reviewed literature and long-term monitoring data of loon productivity and abundance to parameterize deterministic matrix models for Upper Midwest and New England loon populations. The Upper Midwest breeding population exhibited lower fecundity but higher probability of a juvenile growing into the adult class. With this information and their reported population rate of change, we tuned our model to reflect parameters reported in Gear et al. (2009). There are no published estimates of loon survival during migration, so we assumed longer migratory routes incurred greater mortality (e.g. $S_{1,3} = 0.98$ vs. $S_{1,5} = 0.96$) and that mortality was equal to or greater during migration compared to non-breeding stationary periods (e.g. $S_5 = 0.98$; Taylor & Norris, 2010). Based on work by Gear et al. (2009), we assumed 60% of the population occurred in the Midwest and 40% in the Northeast. We chose migratory transitions reflecting observations of loons tracked with satellite transmitters throughout their range (Kenow et al., 2002, 2009), where the majority of loons (e.g. $P \geq 0.9$) frequented stopover locations and the majority of those who continued onward stayed within their flyway (e.g. Upper Midwest birds overwintering in the Gulf of Mexico).

For comparison with the reference scenario, we examined three hypothetical stressor scenarios (Data S2). The species faces a wide range of threats, including disturbance from summer tourism, land-use change, acid deposition and mercury toxicity (Gear et al., 2009). We chose to model the effects of black flies on the breeding grounds (Weinandt, Meyer, Strand, & Lindsay, 2012), botulism mortality on Lake Michigan (Chipault, White, Blehert, Jennings, & Strom, 2015) and landscape-scale industrial accidents on the Gulf Coast (Paruk et al., 2014). These effects are geographically specific and important ongoing conservation concerns for loons.

2.2.2 | Cutthroat trout of Yellowstone Lake

The Yellowstone cutthroat trout, a distinct subspecies of cutthroat trout, lives in Yellowstone Lake but spawns in its tributaries (Gresswell et al., 1994). The species faces population declines, and metapopulation dynamics are known to be important for conservation (Gresswell et al., 1994). It faces several spatially explicit threats including fishing (Gresswell & Varley, 1988), predation from white pelicans (*Pelecanus erythrorhynchos*; Gresswell et al., 1994), and competition from invasive brook trout (*Salvelinus fontinalis*) in the tributaries (Dunham, Adams, Schroeter, & Novinger, 2002) and lake trout (*Salvelinus namaycush*) in Yellowstone Lake (Ruzycski, Beauchamp, & Yule, 2003). The Yellowstone cutthroat trout migrates upstream to spawn during summer, but not all migrants spawn, not all spawners die and some individuals spawn multiple times (Gresswell et al., 1994; Varley &

Gresswell, 1988). Survival for different tributaries ranges from 23% to 48% (Varley & Gresswell, 1988).

We created a simplified, tributary-lake system to demonstrate how a migratory source-sink metric may be used to guide conservation efforts (Figure 3; see Data S2 for parameter values). Cutthroat trout winter in Yellowstone Lake (node 1) and some migrate up tributaries to spawn in summer (nodes 2, 3 and 4). We therefore assumed two time periods: (1) summer and (2) winter. The model specified that, in summer, some proportion of fish spawn in one of the tributaries, whereas the remainder remain in the lake and do not breed. All fish spawning in tributaries return to the lake in winter, such that all fish are in the lake during winter.

We developed a reference scenario based on reported temporal variation among an array of vital rates (e.g. fecundity and mortality) and population parameters (i.e. annual rate of change) measured from cutthroat trout sampled in Yellowstone Lake between 1995 and 2009 (Gresswell et al., 1994). Growth parameter values varied among the three modelled tributaries to reflect observed heterogeneity in vital rates. Population growth rate for Yellowstone Lake was set to 0.90, whereas for the three tributaries, it was set to 1.30, 1.25 and 1.20, coherent with reproduction occurring only in the tributaries. Transition probabilities were set such that 40% of fish remained in the lake, with the remainder distributed among tributaries in a fashion matching the tributary population growth rates (i.e. 0.25, 0.20 and 0.15 respectively). Transition survival parameters were equal except for the resident Yellowstone Lake population, which had higher survival to reflect a benefit of avoiding migration. We compared the reference (i.e. no management) scenario to three scenarios for managing mortality

risk in tributaries, Lake Yellowstone, and in both locations combined (Data S2).

3 | RESULTS

3.1 | Common loon

Under the reference scenario, all pathways and breeding habitats were sources, whereas the fall stopover and winter habitats were sinks (Figures 4 and 5). Each of the three stressors (i.e. black flies, botulism poisoning and industrial accident) converted pathways containing the perturbed habitat from sources to sinks (Figure 4). Black flies on the breeding grounds had the largest impact and turned eight pathways (all originating from the perturbed Upper Midwest node) into sinks, demonstrating how a stressor at a breeding node can percolate throughout a network. Conversely, the industrial accident caused two pathways to become sinks: subpopulations originating from the perturbed node spending both fall and winter on the Florida Gulf Coast. Increased levels of botulism in Lake Michigan (node 3) caused all four subpopulations migrating through this perturbed node to become sinks.

The two node contribution metrics were similar when comparing effects of the three stressors relative to the reference scenario (Figure 5). The magnitudes were the same for the two breeding habitats (nodes 1 and 2) but differed for the wintering and fall stopover habitats. The differences were greatest for the two wintering habitats (nodes 5 and 6). The flow-through metric indicated these nodes contained a small portion of the population, whereas the destination

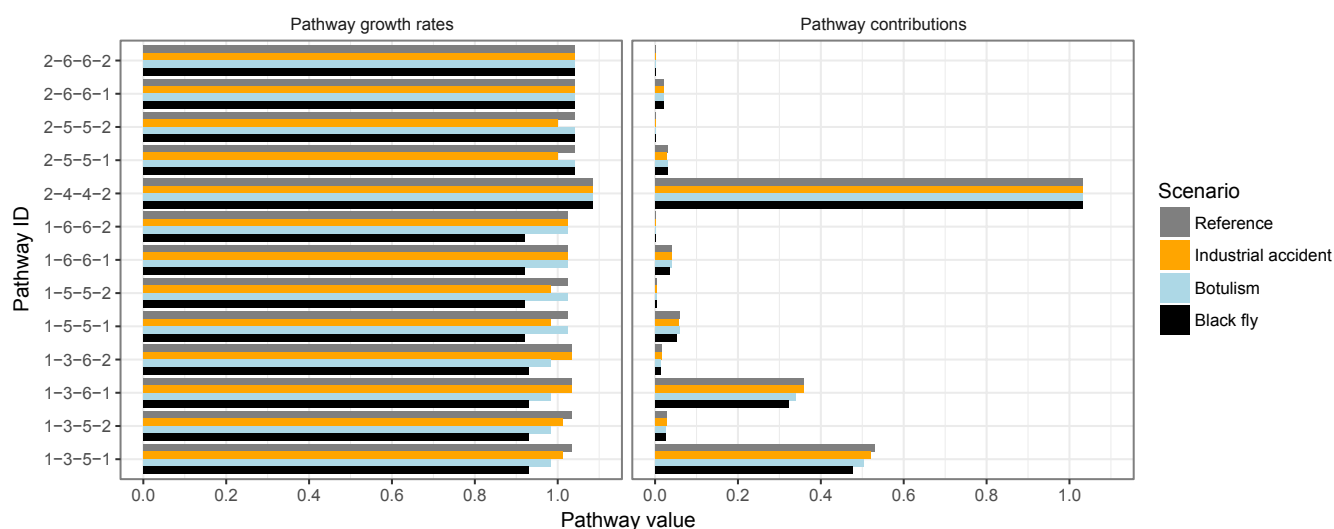


FIGURE 4 Pathway growth rates (S) and pathway contributions (C) for the common loon in the eastern US. Pathway growth rate is the net demographic contribution of individuals using a pathway including survival and recruitment. Pathway contribution is the product of a pathway's growth rate and use probability and is the contribution of a pathway to the population. The pathway ID is comprised of the sequence of nodes used by a focal subpopulation. The "reference" scenario provided a baseline demography unaffected by the tested stressors, the "black fly" scenario reduced reproduction in node 1, the "botulism" scenario decreased survival in node 3, and the "industrial accident" scenario decreased survival in node 5. For a given scenario, pathways with growth rates >1 are considered sources and those with growth rates <1 are considered sinks. Nodes are defined as habitats connected by migration in Figure 2

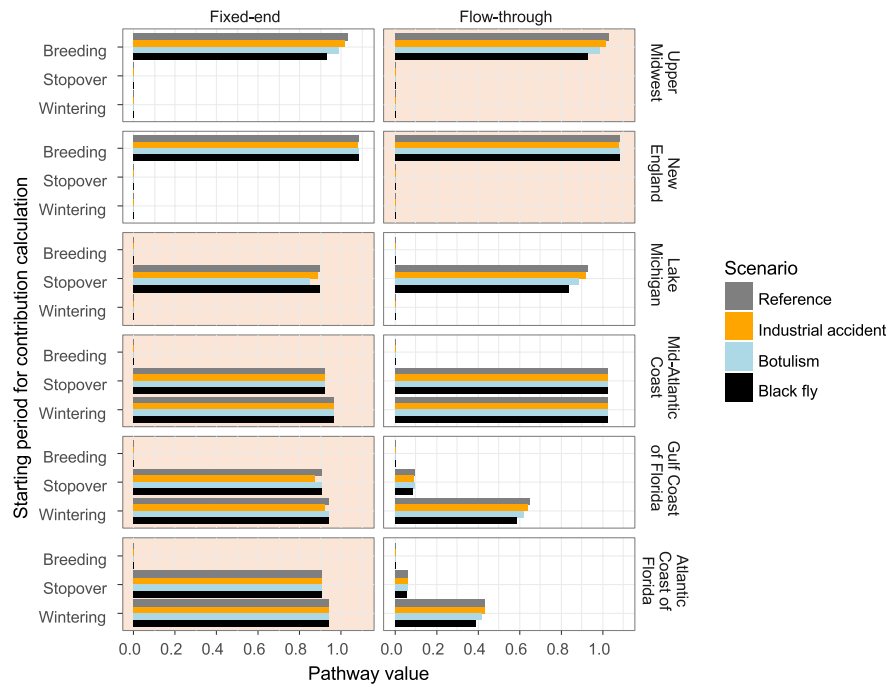


FIGURE 5 Demographic contributions of each habitat node using the flow-through metric (F_i) and the fixed-end contribution metric (E_i) for the common loon in the eastern US. The flow-through metric sums all of the pathway contributions intersecting a node during one complete annual cycle. The fixed-end contribution metric quantifies per capita contribution for a focal node during a portion of one annual cycle by summing contributions of all pathways intersecting that node, but only including a time window beginning when that node is first occupied and ending at a fixed-end date (here, the end of wintering) regardless of whether the annual cycle has been completed. Salmon-coloured facets indicate per capita contributions suited for determining source-sink status for each node. For a given scenario, nodes with contributions >1 are considered sources and those with contributions <1 are considered sinks. Scenarios are as in Figure 4 and nodes are defined as habitats connected by migration in Figure 2

metric showed that per capita contribution of individuals using these nodes was comparable to that of other nodes.

3.2 | Cutthroat trout

Under the reference scenario, all pathways and habitats were sinks (Figures 6 and 7). Tributary management converted six of nine pathways with complete migration (i.e. tributary–lake–tributary) into sources, which were pathways originating in tributaries with higher reference growth rates (node 2 or 3). Conversely, lake management alone allowed only one pathway (2–1–1) to become a source, which was the pathway with the highest growth rate under the reference scenario. By contrast, the 12 pathways with ≥ 0.7 growth rate under the reference scenario became sources when both lake and tributary management were applied. These were also the pathways originating in tributaries instead of in the lake; all tributaries had higher reference growth rates compared to the lake.

The two node contribution metrics were the same for nearly all habitats and seasons but they differed greatly for the lake during winter. In particular, the flow-through metric value was greater than the fixed-end metric for this node and season, reflecting all trout being in Yellowstone Lake in winter. The fixed-end metric for the lake yielded a per capita contribution for winter similar to that for summer.

4 | DISCUSSION

We extended a method for calculating demographic contributions of migratory habitats and pathways. This extension allows for any number of habitats and time steps of potential occupancy during the annual cycle, for source-sink classification, and for quantifying relative importance of migratory subpopulations and habitats for population growth. Our approach allows contributions of habitats and subpopulations to be compared across time periods and space even if some individuals migrate. It also allows for the contribution of particular habitats to be classified as sources or sinks even if no individuals produce offspring within the habitats, which was not possible with previous methods (e.g. Runge et al., 2006).

Comparing the contribution metrics with two case studies revealed important insights, particularly effects of localized management on the source-sink status of pathways and habitats in the networks. Adding a stressor within a particular focal loon habitat converted migratory pathways containing this habitat from sources into sinks. For example, an increase in black flies within Upper Midwest breeding habitat converted the habitat itself and migratory pathways emanating from it into sinks. Increasing levels of botulism in Lake Michigan also converted all pathways including this stopover habitat into sinks. An industrial accident along the Gulf Coast, however, converted only a subset of

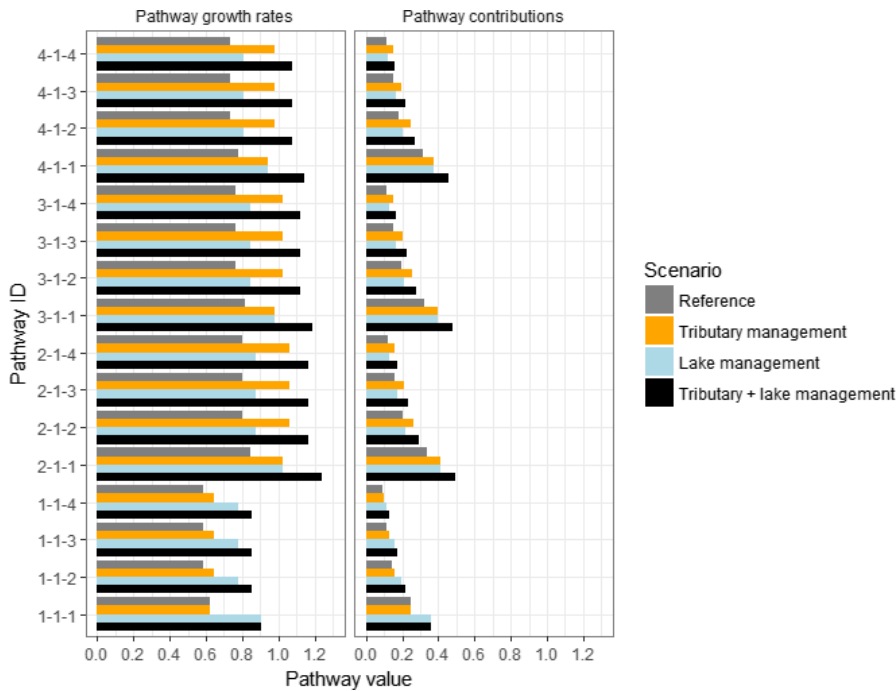


FIGURE 6 Pathway growth rates (S) and pathway contributions (C) for the Yellowstone cutthroat trout in Wyoming, USA. The “Reference” scenario imposed no management, the “Lake Management” scenario increased survival in Yellowstone Lake (node 1), the “Tributary Management” scenario increased tributary survival (nodes 2–4) and the “Tributary + Lake Management” scenario increased survival in both habitats. For a given scenario, pathways with growth rates >1 are considered sources and those with growth rates <1 are sinks. Nodes are defined as habitats connected by migration in Figure 3

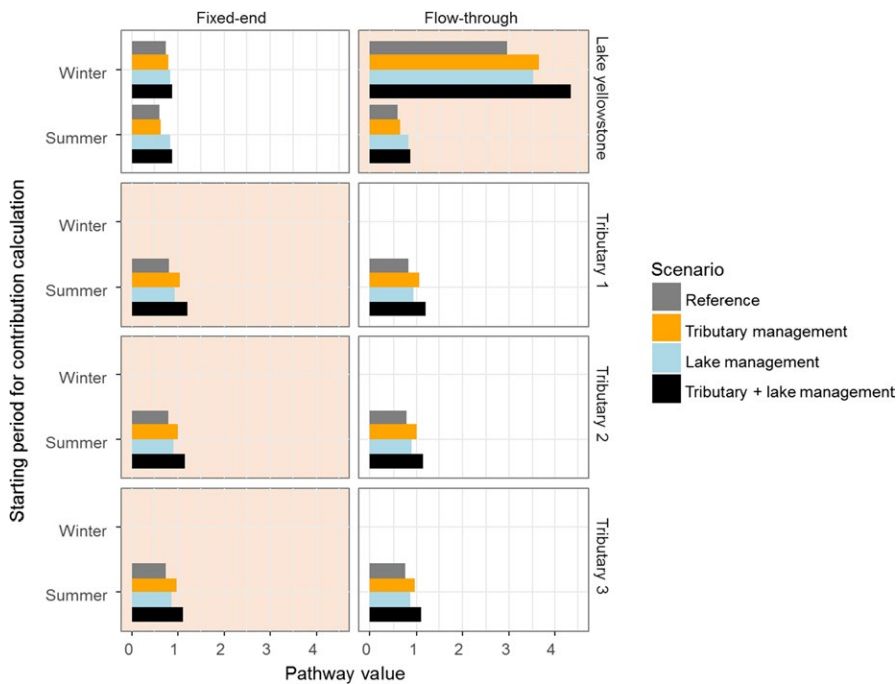


FIGURE 7 Demographic contributions of each habitat node using the flow-through metric (F_T) and the fixed-end contribution metric (E_T) for the Yellowstone cutthroat trout in Wyoming, USA. Brook trout are present in nodes 2–4 and lake trout are present in node 1, both of which compete with cutthroat trout. Salmon-coloured facets indicate per capita contributions suited for determining source-sink status for each node. Scenarios are as described in Figure 6, and nodes are defined as habitats connected by migration in Figure 3

all pathways including this winter habitat from sources to sinks. Both Lake Michigan and the Gulf Coast habitats were sinks under the reference scenario, but the Gulf Coast had a much lower fixed-end per capita contribution compared to Lake Michigan. This difference reflects the proportionately lower usage of the Gulf Coast by loons and could explain why an industrial accident in this winter habitat would less consistently convert associated source pathways into sinks.

The trout example demonstrated that management actions for converting pathways from sinks to sources should be tailored to the movement strategy along target pathways. Managing tributaries, for

instance, would be more effective than lake management for creating source tributaries and pathways with complete migration from the Yellowstone Lake to one of its three tributaries. In contrast, lake management would be more effective than managing tributaries for creating source pathways for subpopulations that are partially migratory or non-migratory. Lake management, however, was not sufficient to convert Yellowstone Lake into a source.

In both case studies, effects of management on demographic contributions of some habitats differed depending on which node contribution metric was used. Although effects on source-sink status

were rather consistent, effects on the demographic contributions themselves differed substantially for winter habitats (i.e. intermediate nodes) in both case studies. The fixed-end and flow-through metrics are more suitable for origin and intermediate nodes respectively. Furthermore, the fixed-end metric may be more useful for quantifying contributions of habitats hosting at least some non-migratory individuals. For example, fisheries managers are interested in the per capita contribution of particular locations to inform decisions about stocking waters with non-migratory fish (Cowx, 1994). Nonetheless, having two metrics to quantify contributions for two respective node types undermines our ability to compare the importance among all habitats used by a migratory species. A single metric that is demonstrably suitable for both types of nodes would greatly advance our ability to understand the role of individual habitats in migratory networks (Wiederholt et al., 2017), while providing potentially useful guidance for achieving habitat-level goals for migratory species.

Analysing effects of particular stressors on demographic contributions can help managers identify spatially explicit conservation strategies for migratory species. Because consequences of management percolate through the migratory network, mitigation in one location can lead to positive population responses elsewhere in the network. Managers could explore different scenarios to evaluate the magnitude of these non-focal node consequences. Such a scenario analysis would allow examination into whether candidate management actions would change pathways and habitats from sinks into sources, helping to inform allocation of management efforts among habitats in the network.

Not only is the approach useful for informing management decisions but also estimating contributions of habitats and pathways in migratory networks provides insight into metapopulation ecology. Metapopulation theory allows connectivity of spatially structured populations to be considered across discrete and fragmented landscapes (Hanski, 1998). Expanding this theory to migratory populations allows stopover nodes to be considered within metapopulation theory as more than sink populations.

There are multiple avenues of additional research needed for examining migratory habitat and pathway contributions. First, long-term dynamics are not captured with our annual metric. Some contexts may require consideration of low-level stressors accumulating over long periods (Peterson et al., 2003; Wiens, 2014); methods developed by Taylor and Norris (2010) may be better for examining these stressors. On the other hand, calculating these contribution metrics within an annual cycle is consistent with sampling timeframes for monitoring of migratory populations. This timeframe creates opportunities for identifying short-term effects of mitigation strategies on source-sink status of pathways and habitats within a migratory network. Second, our approach requires a spatiotemporally discrete specification of a migratory network comprised of habitats and migratory routes; some populations, however, migrate continuously (e.g. wildebeests, *Connochaetes* spp.). Partial differential equations (Gockenbach, 2002) or individual-based models (DeAngelis & Mooij, 2005) may better represent these species, but would require development of corresponding metrics.

The third and perhaps most notable requirement of these methods is the need for demographic data across the annual life cycle

of migratory species. Without these data, uses of our metric will be limited to theoretical investigations or to a small number of species for which suitable datasets already exist. As noted by Hostetler et al. (2015), full-annual-cycle models require parameter estimates that may be expensive, difficult or impossible to collect. This limitation constrains all quantitative approaches and is not unique to our metric.

In conclusion, we provide a generalizable metric for population ecologists and conservation managers to properly account for the contribution of individual habitats and pathways used by a species over the course of its annual life cycle. For seasonally migrating species, this metric describes the demographic contribution of a location over flexibly defined time steps and habitats. The approach can be applied to examine diverse types of migratory networks defined by species life history and research or management questions at hand. Metrics available through this approach provide a method for classifying habitats and pathways as sources or sinks, improving understanding of the demographic consequences of environmental perturbations and providing guidance for conservation and natural resource management of migratory species.

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AUTHORS' CONTRIBUTION

This article originated as part of a NIMBioS Working group. R.A.E., J.E.D., D.R.N. and W.E.T. drafted an initial manuscript. All co-authors reviewed/contributed to the manuscript. R.A.E., J.A.B., J.M.F., P.F., K.R.L. and C.S. developed the mathematical notation; R.A.E. coded and J.A.B., P.F., W.E.T. and C.S. reviewed code.

DATA ACCESSIBILITY

Code used for this project is available at the USGS BitBucket Page <https://doi.org/10.5066/f7416v7z> (Erickson et al., 2017). The code is also available in Supporting Information, Data S3.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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