

A guide to calculating habitat-quality metrics to inform conservation of highly mobile species

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Abstract

Many metrics exist for quantifying the relative value of habitats and pathways used by highly mobile species. Properly selecting and applying such metrics requires substantial background in mathematics and understanding the relevant management arena. To address this multidimensional challenge, we demonstrate and compare three measurements of habitat quality: graph-, occupancy-, and demographic-based metrics. Each metric provides insights into system dynamics, at the expense of increasing amounts and complexity of data and models. Our descriptions and comparisons of diverse habitat-quality metrics provide means for practitioners to overcome the modeling



challenges associated with management or conservation of such highly mobile species. Whereas previous guidance for applying habitat-quality metrics has been scattered in diversified tracks of literature, we have brought this information together into an approachable format including accessible descriptions and a modeling case study for a typical example that conservation professionals can adapt for their own decision contexts and focal populations.

Considerations for Resource Managers

- Management objectives, proposed actions, data availability and quality, and model assumptions are all relevant considerations when applying and interpreting habitat-quality metrics.
- Graph-based metrics answer questions related to habitat centrality and connectivity, are suitable for populations with any movement pattern, quantify basic spatial and temporal patterns of occupancy and movement, and require the least data.
- Occupancy-based metrics answer questions about likelihood of persistence or colonization, are suitable for populations that undergo localized extinctions, quantify spatial and temporal patterns of occupancy and movement, and require a moderate amount of data.
- Demographic-based metrics answer questions about relative or absolute population size, are suitable for populations with any movement pattern, quantify demographic processes and population dynamics, and require the most data.
- More real-world examples applying occupancy-based, agent-based, and continuous-based metrics to seasonally migratory species are needed to better understand challenges and opportunities for applying these metrics more broadly.

KEY WORDS

demographic model, graph, metapopulation, migration, network, occupancy



1 | INTRODUCTION

The population distribution of mobile species varies spatiotemporally, and movement strategies differ greatly both among and within migratory species. The spatial structure of highly mobile populations can be characterized in many ways, including classic metapopulations (Hanski, 1994), seasonal migratory systems (Mattsson et al., 2012; Nicol, Fuller, Iwamura, & Chades, 2015), nomadic systems (Dean, 2004), and even biophysical marine circulation systems (Cowen, Paris, & Srinivasan, 2006). The question of where and how to manage or conserve these species presents an enormous challenge that requires joint innovations in science and policy. For instance, many North American landbird species range across the western hemisphere, occupying habitat scattered across a number of tropical and subtropical nations in winter before migrating to temperate and boreal habitat in Canada and the United States (Fraser et al., 2012; La Sorte, Fink, Hochachka, & Kelling, 2016). Migratory insects, most notably the monarch butterfly (*Danaus plexippus*) and the common green darner (a dragonfly, *Anax junius*), move from breeding habitat as far north as southern Canada to wintering habitat in Mexico (Flockhart et al., 2017; May, 2013; Oberhauser et al., 2017). Managing such spatially structured but temporally dynamic populations is challenging for management agencies, because these species often cross political boundaries leading to social, economic, and political management challenges across multiple jurisdictions (Dallimer & Strange, 2015; Kirby et al., 2008; Lopez-Hoffman et al., 2017a; Robinson et al., 2009). As a result, many of the world's most spectacular migrations have either disappeared due to human activities or are in steep decline (Harris, Thirgood, Hopcraft, Cromsigt, & Berger, 2009; Wilcove & Wikelski, 2008).

Quantitative tools can help identify habitats and migratory pathways that are most important for maintaining this dynamic network of movements and, in turn, achieving particular management objectives (Erickson et al., 2017; Nicol et al., 2016; Wiederholt et al., 2017). This information is especially useful for informing the allocation of limited resources to manage or conserve highly mobile species (Martin et al., 2007; Runge, Martin, Possingham, Willis, & Fuller, 2014). Furthermore, this information can be used in listing species as threatened or endangered under the US Endangered Species Act (Earl et al., 2017). Quantitative information on the relative importance of habitats also provides a means of understanding where ecosystem services provided by migratory species originate, and whether imbalances exist between ecologically and economically important parts of the range (Lopez-Hoffman et al., 2017b; Semmens, Diffendorfer, Lopez-Hoffman, & Shapiro, 2011). All these applications highlight the importance of quantitative tools for informing the management and conservation of migratory and other highly mobile species, but raise questions about which tools are appropriate in particular contexts.

Nicol et al. (2016) developed a framework for choosing among available habitat-quality metrics to quantify the quality of habitats used by spatially structured populations within a management context. The framework provides guidance for selecting metrics based on the management objectives, management actions, and available data for a population-specific context. In their paper, they identified eight candidate management objectives and four types of management actions for conserving migratory populations. For each objective-action combination, they presented appropriate habitat-quality metrics arising from three broad classes: graph-based metrics, occupancy-based metrics, and demographic-based metrics. Here, we define habitat quality as the relative or absolute contribution of a discrete habitat or pathway to the population dynamics of a spatially structured population; a metric would then comprise some proxy or direct quantitative measure of this habitat quality. Although guidance for selecting the appropriate metric in a given decision context is crucial, still missing is a concise guide for calculating the appropriate habitat-quality metric and understanding the underlying metric assumptions.



The goal of this paper is to build the mathematical background needed to employ the metrics suggested by Nicol et al. (2016). This work aims to give a concise description of the mathematics behind the habitat-quality metrics and to develop a case study to help managers understand the benefits and drawbacks for using a particular method. We work to greatly expand the mathematical descriptions offered in Nicol et al. (2016), however, this work is not intended to present an exhaustive formulation of mathematical approaches for each metric, but rather seeks to establish a foundation from which resource managers can build mathematical models to support specific objective/action pairs. We also focus a majority of our attention on metrics that can be applied to seasonally migratory populations. We use a simple case study as an example tutorial to illustrate how habitat-quality metrics are calculated in a practical application to inform management of a migratory population. We then summarize the advantages and disadvantages of available habitat-quality metrics for particular contexts and suggest avenues for future data and modeling needs. A list of mathematical symbols used can be found in Table A1.

2 | HABITAT-QUALITY METRICS

For each of the metric categories defined in Nicol et al. (2016), we will discuss the general framework for calculating the primary metrics within the context of four management actions: add/remove a habitat, enhance/degrade a habitat, add/remove a pathway, and enhance/degrade a pathway. Each of these four management actions seeks to improve the habitat for a mobile species by either increasing the quantity or quality of occupied habitat or increasing connectivity among habitats; such actions will for most species increase population size, reduce instability in population dynamics, and lower risk of extirpation.

To calculate any of the habitat-quality metrics, a set of *habitats* (also called nodes or vertices) must be identified. These habitats are connected by *pathways* (also called edges). Pathways represent routes along which migration or dispersal occurs. Together, the habitats and pathways form a *network* (also called a graph) that represents a species and its movements. Any of the available habitat-quality metrics can be built from such a network structure by layering additional information about the use or demographics within habitats and along pathways. In the mathematical formulation, we have worked to use notation as close as possible to the main source reference. However in some cases, notation had to be altered to keep consistent notation here. A table of mathematical variables can be found in Appendix A.1. The mathematical level is intended to be approachable for a broad range of resource managers, so the habitat-quality metrics described here form the foundation of much broader calculations. In all cases, references for more in-depth study are provided.

To illustrate a practical application of the habitat metrics, we model a population of elk (*Cervus canadensis*) for which there are sufficient data to calculate a diverse suite of metrics. The focal population occurs near Cody, Wyoming and consists of two groups. One group is nonmigratory, while the other migrates seasonally from shared overwintering grounds near Cody to breeding grounds in Yellowstone National Park (Middleton et al., 2013). The system is therefore useful for demonstration because of the mixed migratory strategies, which is commonly found in nature (Chapman, Brünmark, Nilsson, & Hansson, 2011). The network structure, model parameters, and density-dependent assumptions are based on three studies of this population: Singer, Harting, Symonds, and Coughenour (1997), Taper and Gogan (2002), and Middleton et al. (2013).

We model the elk population using three habitats overlaying the geographical breeding and overwintering areas (Fig. 1). Habitat 1 represents the high elevation summer breeding range inside Yellowstone National Park, henceforth breeding-only habitat. Habitat 2 is the region where a portion of the

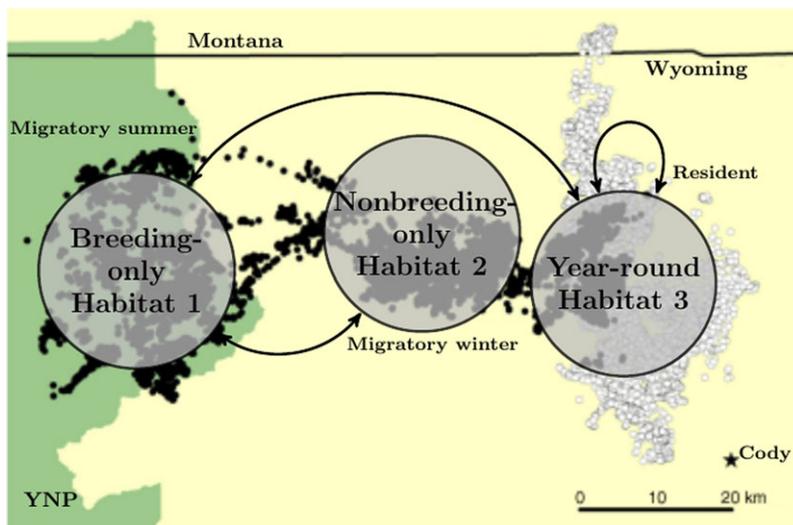


FIGURE 1 Geographical network structure for migratory elk population in Wyoming. Habitats (also called nodes or vertices) are the circles that are connected by pathways (also called edges) represented with arrows. The habitats and pathways form a network (also called a graph) that represents the annual cycle of the elk population. Map from Middleton et al. (2013)

migratory population overwinters just east of Yellowstone National Park, henceforth nonbreeding-only habitat. Habitat 3 is located near Cody and contains both a resident population (that breeds and overwinters at that location) and a portion of the migrating population that winters in the area, henceforth year-round habitat.

The annual migratory cycle is divided into two 6-month time intervals: summer/fall, which includes breeding and fall migration; and winter/spring, which includes overwintering and spring migration. The breeding-only habitat is occupied during summer/fall, the nonbreeding-only habitat is occupied during winter/spring, and the year-round habitat is occupied during both seasons. Detailed descriptions of model formulation and parameterization are provided in Appendix A.2.

2.1 | Graph-based metrics

Graph-based metrics are developed from the mathematics of graph theory. When the management objective is concerned primarily with the connectivity or structure of a network, then graph-based approaches are appropriate. Graph-based metrics require the least amount of data of the three metric categories; many can be parameterized using only map or geographic information system data describing the location and connectivity of populations. Low data requirements make graph-based metrics particularly efficient for spatially expansive regions with many habitats. For a minimal graph-theoretic model, only information about the locations and areas of the habitats along with connectivity between areas is required. However, more information can be overlaid if the data are available. Graph-theoretic models can perform well in identifying the most important habitats compared to spatially explicit population models (Minor & Urban, 2007), but models including some measure of habitat quality tend to outperform simpler metrics (Visconti & Elkin, 2009; Wiens, 1989). For each management action, we discuss the type of graph that is required and which metric could be calculated to aid in conserving a migratory population. The use of graph-based metrics are applicable to both large and small networks. They assume that the structure of the network is most important to addressing the management objective.



A graph is *directed* if its pathways have a direction associated with them, *undirected* otherwise. A pathway connecting a habitat to itself is called a *loop*, which represents individuals of a habitat remaining resident through one or more time steps when modeling a spatially structured population. A graph is *weighted* if its habitats or pathways have been assigned weights, or numerical values, that quantify attributes; for example, a pathway could have a migration distance associated with it. An important idea in network analysis is the idea of a *path* through a network, defined as a sequence of distinct connected habitats and pathways through the graph, we will refer to this as a *migratory path*. A graph is *connected* when there is a migratory path between every pair of habitats. In general graphs are static, not dependent on time, however dynamic properties can be incorporated with a *temporal network*, in which the weights and directions of pathways and habitats could be seasonally dependent and represented by a time series of static graphs. Figure A2 depicts four examples of graphs with these properties.

A population of highly mobile individuals can be represented as a spatially structured population moving among a set of habitats. The same population can be modeled with a variety of graphs of differing complexity (Dale & Fortin, 2010; Urban, Minor, Treml, & Schick, 2009), see Appendix A.3 for examples of graph types. Choosing the appropriate model will depend on the specific decision context and available management actions. The simplest graph is an undirected and unweighted graph, with pathways connecting any two habitats (e.g., breeding and wintering areas used by a migratory bird) between which there is movement. A directed graph represents the direction of movement along each pathway, and this is useful, for example, when deciding how to conserve postspawning downstream or prespawning upstream migrations of salmonids (Fullerton et al., 2011; Schick & Lindley, 2007). A weighted graph is used to incorporate habitat-specific information, such as habitat size or habitat characteristics (e.g., percent natural cover) (Minor & Urban, 2007). Habitat weights may be calculated based on the size of the habitat or some measure of habitat quality. Pathways may also have weights such as distance and likelihood of movement (Saura & Pascual-Hortal, 2007). A time dimension may also be incorporated with a temporal network, in which the existence of each pathway is time-dependent.

Unlike other spatially structured populations, migratory populations are characterized by seasonal movement (Erickson et al., 2017; Wiederholt et al., 2017). In some cases, such as where practitioners are interested in annual predictions of population size for a single habitat, it is sufficient to build annual models incorporating all seasonal movement data into a single model time step (Iwamura et al., 2013; Nicol et al., 2015); however, for many other applications, capturing seasonal dynamics is critical. This time criticality suggests that a temporal network approach is appropriate for capturing migration dynamics (Blonder, Wey, Dornhaus, James, & Sih, 2012; Holme & Saramaki, 2012). These seasonally dependent graphs will have the same set of habitats, but with different pathways (directed or undirected) and possibly different habitat and pathway weights. The identity and weight of pathways may change in response to the removal or addition of habitats and pathways, thus changing the structure of a network (Blonder et al., 2012; Dhanjal-Adams et al., 2017). If a habitat used by a migratory population is eliminated, individuals may migrate to another habitat under relevant timescales. Modelers can turn to methodological approaches that are only recently being applied to study dynamics of ecological networks (Blonder et al., 2012; Dhanjal-Adams et al., 2017; Holme & Saramaki, 2012; Nicosia et al., 2013). Alternatively, one may represent the time-varying network with a multilayer network, in which each season is represented by a layer and the same habitat may have a different set of connected pathways in each layer (Boccaletti et al., 2014). Time-dependent pathway characteristics may be defined using information from Autonomous Fixed Arrays (AFA). For example, AFA can specify the time that an individual (or group of organisms) leaves one habitat or the length of time spent along a pathway until it arrives at another habitat. These models give the frequency with

which the directed movement occurred (Jacoby & Freeman, 2016). Similarly, Martensen, Saura, and Fortin (2017) developed spatiotemporal depictions of network connectivity which explicitly consider the amount of habitat reachable by dispersing organisms, habitat which may be available or unavailable over the course of time; they demonstrated that most spatiotemporal connectivity occurred through habitats lost or gained between time steps, habitats which served to facilitate movement to more durable habitat.

Many graph-based metrics exist, and selecting the appropriate metric poses a challenge. Rayfield, Fortin, and Fall (2011) provided a framework for classifying over 60 graph measures so that decision makers can select and apply appropriate measures. Metrics to quantify habitat connectivity were divided into two classes: topological indices (considers only the presence or absence of a pathway between habitats) and weighted indices (considers the weights of habitats and pathways). They also classified measures into the structural level in which they can be applied—namely, element (habitats and pathways), first-order neighbor (spatially adjacent habitats), component (group of interconnected habitats), and network. The selected metrics should correspond with the management objectives and actions at hand (Nicol et al., 2016). Here, we illustrate some of the common graph-based metrics corresponding with decreasing levels of resolution of focus, which we classify as element-, component-, and network-level metrics.

2.1.1 | Element-level metrics

Centrality indices are used to identify the most important habitats within a network. We focus on two of several centralities (degree and betweenness) to illustrate that the most informative measure will depend on the management context. The *degree* of a habitat is the number of pathways incident to the habitat, with loops counted twice. For directed graphs, typically two separate measures are given: *indegree* (number, or sum of weights, of incoming pathways) and *outdegree* (number, or sum of weights, of outgoing pathways). Indegree and outdegree may aid in distinguishing sources (i.e., habitats that are high quality and supporting the population as a whole) and sinks (i.e., habitats that are low quality and supporting population decline). Degree is the simplest measure and useful for identifying habitats that have the most direct connections to other habitats. The *betweenness* (also called the betweenness centrality) of a given habitat is the number of shortest migratory paths passing through the habitat. Given a connected graph, there exists at least one shortest migratory path between any two habitats such that the number of pathways that the migratory path traverses (for unweighted graphs) is minimized. Betweenness is useful for identifying stopover habitats, which will typically have higher betweenness than breeding and nonbreeding sites, demonstrating their importance to connectivity and movement across the landscape.

Metrics of pathway quality require that the graph is weighted, and the choice of weighting method is informed by the management context. If the objective is to minimize increases in mortality during migratory periods as a function of management actions, then pathway length (i.e., geographic distance between two habitats occupied in two successive time periods) is an appropriate weight. Dijkstra's algorithm identifies the shortest migratory path in weighted networks when weights represent the cost of transition (Dijkstra, 1959) and has been used to prioritize conservation sites in a migratory network (Martin et al., 2007). Most graphs define pathway weights based on connection strength (e.g., movement probability) rather than on survival or indicators of survival along them (e.g., distance between habitats), so in this case pathway weights need to be reversed before directly applying Dijkstra's algorithm. One may also extend the algorithm to incorporate the number of intermediate habitats a migratory path passes through (Brandes, 2001; Newman, 2001; Opsahl, Agneessens, & Skvoretz, 2010).

Applying these ideas to the elk population, we find that the year-round habitat has the highest degree (Fig. 2), which in the absence of additional information (such as habitat abundance) would indicate that

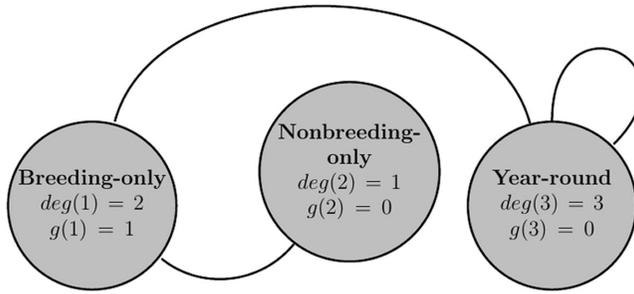


FIGURE 2 The degree, $deg(i)$, and betweenness, $g(i)$, for each habitat $i = 1, 2, 3$ in the undirected and unweighted graph

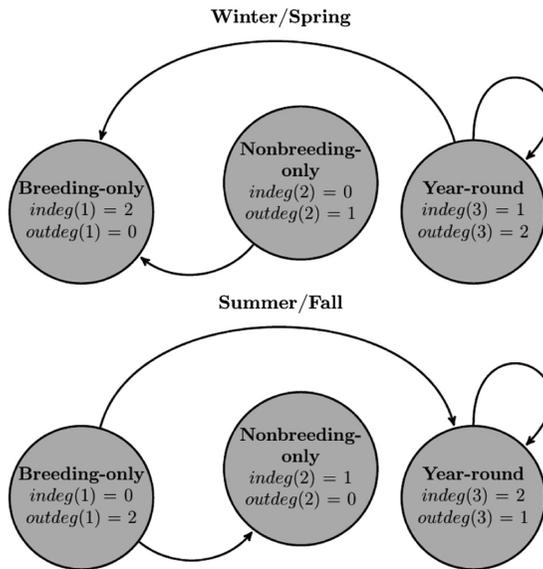


FIGURE 3 Indegree, $indeg(i)$, and outdegree, $outdeg(i)$, for each habitat $i = 1, 2, 3$ in a directed unweighted temporal graph

perturbing the year-round habitat may have a large effect on the overall population. The breeding-only habitat has the highest betweenness, here we observe that shortest way to traverse the network from the year-round habitat to the nonbreeding-only habitat is by passing through the breeding-only habitat, no other habitat in this network has a “flow-through” position along a migratory path. This suggests that perturbing the breeding-only habitat may have a large effect on the population, as individuals would no longer be able to travel between the remaining two habitats.

Because the elk population has seasonally dependent migration, we consider temporal networks to expand our discussion. Figure 3 shows the elk network for the temporal-directed-unweighted graph with measures of indegree and outdegree. In this case, the nonbreeding-only habitat in both seasons does not rank highest in measures of indegree or outdegree. Illustrating that the habitat is relatively more disconnected and perhaps less important to the network. This is consistent with the results from the undirected graph, however we gain information from the directed graph about the seasonal flow of migrants into or out of the habitats. In a temporal network, we recognize that migration is represented by a time-ordered sequence of pathways. For example, if one season is ignored then all habitats would

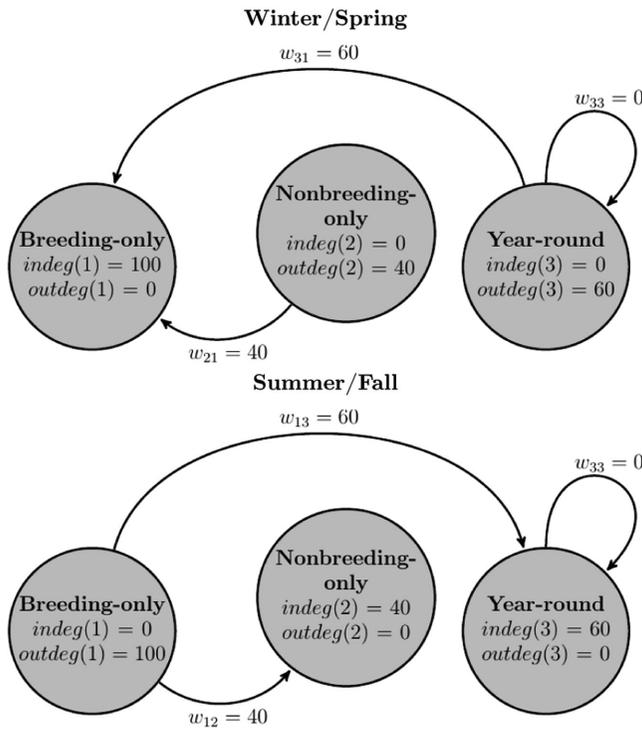


FIGURE 4 Indegree, $indeg(i)$, and outdegree, $outdeg(i)$, for each habitat $i = 1, 2, 3$ in a weighted directed temporal graph. Here, pathway weights, w_{ij} , represent distance (in km) for migration between centroids of habitat i and j . Note that the pathways change direction from one season to the next, but the weights remain the same

have a betweenness of 0. The pathway from the year-round habitat to the nonbreeding-only habitat via the breeding-only habitat is absent unless both seasons are considered.

Figure 4 shows the temporal-directed-weighted graph for the elk network, where pathway weights represent distances between habitats. Indegree represents a measure of distance traveled by immigrants and outdegree represents distance traveled by emigrants. Here, the year-round habitat has the lowest average indegree across seasons. If traveling long distances is expected to weaken the population, then this measure would indicate that the population at the year-round habitat is most robust. We also see that the breeding-only habitat has the highest average indegree, implying that this local population has endured a longer migration. This example highlights the fact that measures of indegree and outdegree are highly dependent on assumptions about pathway weights.

2.1.2 | Component-level metrics

Large networks may have multiple, smaller, possibly disconnected, subnetworks, called components or groupings. Component-level metrics are concerned with groupings of habitats that are interconnected both directly and indirectly. For small networks, containing only one component, component-level metrics will describe the full network. The *diameter* of a grouping of habitats is the greatest distance between any two habitats at the component level. This is determined by finding the shortest migratory path D_{ij} between each pair of habitats i and j (i.e., geodesic path) in the grouping and selecting the greatest of any of these. We can also define the *average path length*, which averages the shortest migratory paths over all pairs of connected habitats. Average path length is typically calculated by excluding self-loops, however, paths that have the same origin and destination node are important



TABLE 1 Shortest migratory path between habitats in the temporal weighted directed graph starting in either season

	Breeding-Only	Nonbreeding-Only	Year-Round
Breeding-only	$D_{11} = 80$	$D_{12} = 40$	$D_{13} = 60$
Nonbreeding-only	$D_{21} = 40$	$D_{22} = 80$	$D_{23} = 100$
Year-round	$D_{31} = 60$	$D_{32} = 100$	$D_{33} = 0$

TABLE 2 Shortest temporal path between habitats in the temporal weighted directed graph, starting in either season

	Breeding-Only	Nonbreeding-Only	Year-Round
Breeding-only	1 year	6 months	6 months
Nonbreeding-only	6 months	1 year	1 year
Year-round	6 months	1 year	6 months

Notes: One time step is 6 months and two time steps is 1 year.

in our application—they represent either resident populations or migratory populations that return to the same habitat after 1 year. For this reason, the arithmetic mean will be used to find the average path length for seasonally migratory species. In the case of a temporal graph, we define *temporal path length* as the time it takes to traverse a migratory path and *average temporal path length* and *temporal diameter* as the analog to static metrics discussed above (Nicosia et al., 2013).

Metrics of pathway quality require that the graph is weighted, and the choice of weighting method is informed by the management context. If the objective is to minimize increases in mortality during migratory periods as a function of management actions, then pathway length (i.e., geographic distance between two habitat occupied in two successive time periods) is an appropriate weight (Brandes, 2001, Newman, 2001; Opsahl et al., 2010).

Turning to the case study, we consider the directed weighted graph of Figure 4 and sum pathway weights to find the topological distance. For example, the distance of the migratory path from the year-round habitat to the nonbreeding-only habitat is $60 + 40 = 100$. Table 1 contains the shortest distance between each possible origin and destination habitats. The average path length (mean distance) is 62 and diameter (largest distance) is 100. To find the shortest temporal distance, we note that each time step is 6 months long and then count how many time steps it takes to traverse the shortest migratory path (Table 2). In this case, the average temporal path length is 8.7 months and the temporal diameter is 1 year, meaning it takes on average 8.7 months to get from any one node to any other node, and the longest duration of such a path is 1 year.

Changes to these graph metrics as habitats or pathways are removed can be important in quantifying habitat or pathway importance. The average path length and diameter (topological and temporal) for habitat removal and pathway removal are shown in Tables 3 and 4. By removing the breeding-only habitat, pathway 1-2 or pathway 1-3, the average path length and diameter are infinite, implying that the population can no longer move from one habitat to any other habitat (habitats are disconnected). This indicates the importance of the breeding-only habitat to the flow of migration. It is also interesting to note that the removal of pathway 3-3 forces all members of the population to become migratory and thus, increases average (topological and temporal) migratory path length and diameter.

2.1.3 | Network-level metrics

There exist many network measures to help quantify network-wide properties. *Node (edge) connectivity* measures the minimum number of habitats (or pathways) needing to be removed to disconnect a graph. The greater the connectivity, the more robust the network is to habitat removal. A set of habitats critical



TABLE 3 Average migratory pathway length and diameter, and average temporal pathway length and temporal diameter, for habitat removal

	Full Network	Breeding-Only Removed	Nonbreeding-Only Removed	Year-Round Removed
Average length	62	∞	60	60
Diameter	100	∞	120	80
Average temporal length	8.7 months	∞	7.5 months	9 months
Temporal diameter	1 year	∞	1 year	1 year

Notes: In the cases where the average length and diameter are infinite, habitats have become completely disconnected from the network due to removal of another habitat.

TABLE 4 Average migratory pathway length and diameter, and average temporal pathway length and temporal diameter, for pathway removal

	Full Network	Pathway 1-2 Removed	Pathway 1-3 Removed	Pathway 3-3 Removed
Average length	62	∞	∞	76
Diameter	100	∞	∞	120
Average temporal length	8.7 months	∞	∞	9.3 months
Temporal diameter	1 year	∞	∞	1 year

Notes: In the cases where the average path length and diameter are infinite, a habitat has become completely disconnected from the network due to pathway removal.

to the population may be found by identifying the minimal cut, or number of habitats, that renders the graph disconnected with their removal.

Degree distribution is a useful metric when considering very large networks. It is defined as the probability distribution of degrees over a whole network. In other words, given a degree, it reports the proportion of habitats that share that degree. Degree distribution can give information about which degree measure is most or least often realized in a single network along with measures of whether there is a large or small range of degree measures in the network. Degree distribution provides information about the robustness of the network to habitat removal. For example, scale-free networks (degree distribution follows a power law) are robust to random removal of habitats but fragile to removal of habitats that are most connected (have a high degree) (Fortuna, Gómez-Rodríguez, & Bascompte, 2006). These highly connected habitats can be particularly important in migratory networks, where stopover “bottleneck” sites often support large proportions of the population (Iwamura et al., 2013; Myers, 1983).

If we consider any of the network (graph) structures in the elk model, we find that the node connectivity is 1, because removing any single habitat, in particular the breeding-only habitat (called a cut node), will disconnect the graph. The edge connectivity is also 1, because removing the pathway connecting the breeding-only and year-round habitats or the pathway connecting the breeding-only and year-round habitats will disconnect the graph. Thus, the network structure is fragile to the removal of the breeding-only habitat or any pathway connected to it.

2.2 | Occupancy-based metrics

Occupancy-based metrics are built using the metapopulation framework, where metapopulations are defined as assemblages of spatially delineated local populations, coupled by some degree of movement among populations (Hanski & Gaggiotti, 2004). Metapopulation theory is well studied both theoretically and empirically and has been used in a wide range of conservation applications (Han-



ski, 1999). Management objectives focused on increasing persistence, maximizing time to extinction, increasing colonization rates, or maximizing the number of occupied habitats are readily addressed, when faced with low data availability, using occupancy-based metrics.

Data requirements are larger for occupancy-based metrics than for basic graph-based metrics. Similar to graph-based metrics, occupancy models use a network structure of habitats and pathways. However, the metrics require information on the presence or absence of a species in each habitat. The general approach requires information about the area of each habitat, the distance along the pathways between habitats, and some estimate of intrinsic colonization and extinction rates for each habitat, which can be estimated using observations about patch occupancy, with parameter estimates improving as the number of observations increases. These models can be formulated using either deterministic or stochastic (Markov process) approaches. Occupancy-based approaches assume that local populations, within the habitats, have a substantial risk of extinction, that patches are not so isolated that it would prevent recolonization, and that the dynamics among the local populations are not completely synchronous. These approaches are also most suitable for populations with a large number of habitats and pathways.

Occupancy-based metrics have their mathematical foundations in the well-known Levins Model (Levins, 1970), which tracks the proportion of habitats occupied in a metapopulation connected by dispersal. Extending this theory to a “spatially realistic metapopulation theory,” Ovaskainen and Hanski (2001, 2003) developed a model and a series of metrics for a finite set of habitats with dissimilar attributes (e.g., habitat size) and distance-dependent migration. Ovaskainen and Hanski modeled rate of change of the probability of habitat i being occupied, p_i , using an ordinary differential equation

$$\frac{dp_i}{dt} = C_i(\mathbf{p}(t))(1 - p_i) - E_i p_i, \quad (1)$$

where $C_i(\mathbf{p})$ is colonization rate, E_i is extinction rate, and \mathbf{p} represents the vector containing all occupancy probabilities, p_i . Equation (1) could be written in discrete form by replacing the derivative with a difference $\frac{dp_i}{dt} = p_i(t+1) - p_i(t)$; in the discrete case, the modelers are assuming that very little, or no, change happens to the occupancy probability within one time step. If we are considering the discrete case, then the habitat occupancy is only measured at discrete time intervals and we can define the incidence of occupancy Hanski (1994), or stationary probability that habitat i is occupied, as

$$J_i = \frac{C_i}{C_i + E_i}.$$

An important assumption being made here is that the colonization rate and extinction rate are constant from one step to the next, or at least changes are so small that they can be ignored. The functional dependence of $C_i(\mathbf{p})$ and E_i are highly dependent on ecological assumptions; we will outline a few approaches below.

Two examples of the functional dependence and assumptions for the colonization rate include the Spatially Realistic Levins Model and the Incidence Function Model (Ovaskainen & Hanski, 2001). The Spatially Realistic Levins Model assumes that colonization is a constant multiple of the connectivity of the patch, with connectivity defined as

$$H_i(\mathbf{p}(t)) = \sum_{j \neq i} A_j^{\zeta_{em}} p_j(t) e^{-\alpha d_{ij}}, \quad (2)$$

where A_j is the area of the origin habitat, ζ_{em} the scaling of emigration by habitat area, d_{ij} is the distance between habitats, and α is a scaling parameter for distance such that $\frac{1}{\alpha}$ represents the average



pathway distance. Biologically this implies that the colonization rate is higher in a habitat that is closely connected to large habitats with a high probability of occupancy.

Given these assumptions, the colonization rate becomes

$$C_i(\mathbf{p}(t)) = cH_i(\mathbf{p}(t)),$$

where c is the species-specific colonization parameter. Alternatively, the Incidence Function Model, formulated by Hanski (1994), assumes that the colonization rate is related in a nonlinear way to the flow of immigrants from other patches and that the flow of immigrants is proportional to the connectivity, as defined in equation (2).

$$C_i(\mathbf{p}(t)) = \frac{H_i(t)^2}{H_i(t)^2 + 1/c}.$$

The habitat extinction rate E_i is often assumed to be inversely proportional to the habitat size, $E_i = \frac{e}{A_i^{\zeta_{ex}}}$, which assumes that the larger area habitats have larger populations and therefore a smaller risk of extinction (Hanski & Ovaskainen, 2000). Here, ζ_{ex} is the extinction by habitat area scaling factor and e is the species-specific extinction parameter. This model is based on the assumption that occupancy probabilities in the discrete habitats are uncorrelated, at least temporarily. This approach also assumes that there are no external sources of migrants, that there are no completely isolated habitats, and that occupied habitats make a positive or zero contribution to the colonization of empty habitats.

Taylor and Hall (2012) extended this model to seasonally migratory species by considering a discrete-time version of this model and distinguishing between breeding and nonbreeding habitats. The definitions of occupancy, colonization, and extinction also need to be extended in the seasonally migratory case. Occupancy implies that a habitat is used during its relevant season so one does not count a breeding habitat as “unoccupied” if it is empty during the nonbreeding season but occupied during the breeding season. Colonization means that the habitat is unoccupied in a previous year and becomes occupied by individuals arriving from habitats of the opposite type (e.g., breeding versus nonbreeding habitat). Extinction implies that a habitat that was occupied in a previous year fails to be occupied in a subsequent year by individuals arriving from habitats of the opposite type (Taylor & Hall, 2012). This means that each of these measures is taken once per annual cycle and that they do not change within a season.

Habitats in a seasonally migratory metapopulation system must be separated into types. In the simplest case, this separation would be breeding habitats p_i and nonbreeding habitats q_i , but one could imagine assigning more habitat types for stopovers, swarming areas, or other migration events. Following the work of Taylor and Hall (2012), habitats are ordered sequentially with breeding habitats $i = 1, 2, \dots, n_B$ and nonbreeding habitats $i = n_B + 1, \dots, n_B + n_w$. This model requires that individuals exhibit full migration, or that colonization is strictly sequential, however it is reasonable that habitats that allow for a resident population could be assigned to both categories with linked attributes and a migration distance of zero. We note that occupancy-based metrics are appropriate for larger networks with habitats that are occupied in some years and unoccupied in other years, that is when probabilities of interannual extinction and colonization are greater than 0 and less than 1.

The elk in our case study reliably use all three habitats every year and therefore occupancy-based metrics (which depend on interannual variation in occupancy) for quantifying the quality of habitats and pathways are not clearly applicable. We therefore use theoretical parameter values to demonstrate occupancy-based metrics and note that conclusions will be limited in this instance. We modify the directed graph by, adding appropriate habitat and pathway weights (see Fig. 5). We note that the

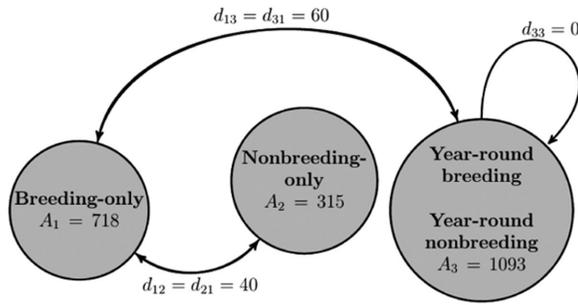


FIGURE 5 Network structure for migratory elk occupancy model with parameters A_i , area of habitat i , and d_{ij} , distance between habitats i and j . Distances and areas are approximated using map locations from Middleton et al. (2013) with distances measured to the approximate center of the habitat

year-round habitat supports a nonmigratory population that both breeds and winters there, thus we allow for breeding and nonbreeding seasons in a single habitat by defining the year-round habitat as both a breeding and nonbreeding habitat, with the resident population traveling a distance of zero during the migration period. To correspond with the notation in equations (3) and (4), we define season-specific persistence probability for each habitat as follows:

$$p_1 = \text{breeding-only}$$

$$p_2 = \text{year-round breeding}$$

$$q_1 = \text{nonbreeding-only}$$

$$q_2 = \text{year-round nonbreeding}$$

where p_i represents the i th habitat during the breeding (summer/fall) season and q_i represents the i th habitat in the nonbreeding (winter/spring) season. While we go ahead with calculations for illustrative purposes, many of the metapopulation assumptions are weak for our focal population and thus any conclusions drawn should be taken as theoretical.

2.2.1 | Equilibrium persistence probability approaches

The probability of population persistence within a habitat can be estimated based on the equilibrium occupancy of that habitat. Time series of presence/absence data are required for estimating persistence probability. The definition in equation (1) is extended to allow for dynamic migration, discrete time steps, and two distinct habitat types (i.e., breeding and wintering; Taylor & Hall, 2012).

$$p_i(t+1) - p_i(t) = c_B \sum_{j=n_B+1}^{n_B+n_W} q_j(t) A_j^{\zeta_{em}} e^{-\alpha d_{ij}} (1 - p_i(t)) - \frac{e_B}{A_i^{\zeta_{ex}}} p_i(t), \quad (3)$$

$$q_i(t+1) - q_i(t) = c_W \sum_{j=1}^{n_B} p_j(t) A_j^{\zeta_{em}} e^{-\alpha d_{ij}} (1 - q_i(t)) - \frac{e_W}{A_i^{\zeta_{ex}}} q_i(t). \quad (4)$$

These equations differ from Taylor and Hall (2012) only by adding the area-scaling factor for the extinction ζ_{ex} and emigration ζ_{em} . Area-scaling factors are particularly important when modeling large habitat areas, so the computations remain stable and results realistic.



This model can be numerically simulated to estimate persistence probability (i.e., equilibrium occupancy probability) of each breeding and nonbreeding habitat. Persistence probabilities can be estimated under alternative scenarios by removing or altering attributes of individual habitats or pathways from the network. If the management action includes enhancing or degrading pathways, for example, then modelers could change distance measures d_{ij} , where this can represent not just the Euclidean distance between habitats but also some measure of migration difficulty. Habitat areas could be reduced to test habitat importance. Similarly colonization and extinction rates could be altered to test the relative importance of these processes.

The *metapopulation size* is the weighted sum of the equilibrium persistence probabilities, as calculated numerically from equations (3) and (4) above. A direct extension of this to migrating populations requires that equilibrium occupancy probability vectors are denoted as p^* and q^* for the breeding and nonbreeding habitats, respectively, then similar to Ovaskainen and Hanski (2003), the metapopulation size, defined as an appropriate average of the habitat occupancy probabilities in each season, can be calculated as

$$S_B = \sum_{i=1}^{n_B} ws_i p_i^*, \quad S_W = \sum_{i=n_B+1}^{n_W} ws_i q_i^*,$$

where ws_i is a weight that is consistent with the biological context. For example, if $ws_i = 1$ for each habitat i , then S_B and S_W would measure the number of occupied habitats in the breeding or nonbreeding seasons, respectively. Alternately, if $ws_i = A_i$ then S_B and S_W would measure the proportion of area occupied in the breeding or nonbreeding seasons. If assuming that population density is proportional to area, and is consistent across habitats, this measure would be an index of abundance. From this measure of metapopulation size, one can define the *contribution of habitat o to the overall metapopulation size* in the breeding and nonbreeding seasons as

$$U_{B,o}^L = S_B - S_B^o, \quad U_{W,o}^L = S_W - S_W^o,$$

where S_B^o and S_W^o represent the size of the metapopulation in the network with habitat o removed during the breeding and nonbreeding seasons respectively. This idea of comparing metapopulation size after perturbations can easily be extended to removal or addition of a pathway, or to enhancement/degradation actions by changing distance or area parameters.

Additional metapopulation metrics exist; for example, long-term contribution to colonization, time to extinction, or contributions to persistence. However, these measures have not been formulated for seasonally migratory metapopulations. Valuable future work in this area of research would include a thorough mathematical generalization of the work of Ovaskainen and Hanski (2001, 2003) to seasonally migratory metapopulations, including generalizations allowing for more than the two, breeding and nonbreeding, habitat types described in this review.

Applying this formulation to the elk, we assume the intrinsic colonization and extinction rates are equivalent among habitats, $c_b = c_w = 0.75$ and $e_B = e_w = 0.25$. These values match the default parameter values from Taylor and Hall (2012). We then assume the extinction and emigration rates by habitat area as $\zeta_{ex} = 0.10$ and $\zeta_{em} = 0.10$, respectively, which we deemed reasonable given the large habitat size. We estimated habitat persistence probabilities p_i and q_i for breeding and wintering habitats, respectively, based on the discrete iterative equations (3) and (4). We ran numerical calculations to equilibrium, 200 steps. Persistence probabilities for the habitats under the baseline scenario, rounded to the nearest tenth, are as follows: $p_1 = 0.80$, $p_2 = 0.92$, $q_1 = 0.71$, and $q_2 = 0.93$. Here, all habitats have relatively high occupancy probabilities, with the year-round habitat being highest in both seasons.



TABLE 5 Metapopulation size, S_B^o and S_W^o , and contribution to metapopulation size, $U_{B,o}^L$ and $U_{W,o}^L$, for elk occupancy case study with complete habitat removal perturbations, with subscripts B and W denoting breeding and non-breeding seasons, respectively

	Breeding-Only Removed	Year-Round Breeding Removed	Nonbreeding-Only Removed	Year-Round Nonbreeding Removed
S_B^o	3009	1861	4288.27	1585
S_W^o	3009	3222	3029	695
$U_{B,o}^L$	1725	2874	446	3149
$U_{W,o}^L$	704	492	685	3018

TABLE 6 Persistence probabilities for the elk habitats and cohorts with pathway degradation perturbations

	Breeding-Only (p_1)	Year-Round Breeding (p_2)	Nonbreeding-Only (q_1)	Year-Round Nonbreeding (q_2)
Baseline	0.80	0.92	0.71	0.93
Pathway 1-2 degraded	0.80	0.92	0.60	0.93
Pathway 1-3 degraded	0.83	0.92	0.80	0.92

Notes: In each case, the pathway distance was doubled to model an increase in migration difficulty.

We also estimate the equilibrium metapopulation size during each of the seasons. Here, $ws_i = 3A_i$, ecologically this implies that overall expected population density would be 3 elk per square mile, consistent across all habitats. Thus assuming occupancy probability is related to percent area use, the metapopulation size, S , measures the expected number of individuals at each of the habitats. We find that $S_B = 4735$ and $S_W = 3713$ during the breeding and nonbreeding seasons, respectively.

To assess the relative importance of habitats for persistence of the metapopulation as a whole, we removed individual habitats and recalculated metapopulation persistence. From this, we calculate both the metapopulation size (assuming $ws_i = 3A_i$), and the contribution to metapopulation size (Table 5). Because metapopulation size is weighted by habitat area, removal of a large habitat is expected to have a larger impact on the population. Interestingly, the removal of the year-round non-breeding habitat has a slightly larger impact on the metapopulation size compared to removal of the year-round breeding habitat, likely because both the migratory and resident populations use that non-breeding habitat.

To focus on pathway importance, we perturb pathway lengths. In Table 6, we change the pathway distances independently, modeling an increase in migration difficulty, and compare population persistence probabilities. When migration distance is doubled along the pathway from the breeding-only to the nonbreeding-only persistence at the nonbreeding-only habitat is reduced. When migration distance is doubled along the pathway connecting the year-round and breeding-only habitats, persistences remain high with increases to persistence in the breeding-only and nonbreeding-only habitats. We also note that this level of pathway perturbations has little effect on the year-round habitat. We could not equally perturb the nonmigratory pathway 3–3 because its length is zero.

2.2.2 | Landscape matrix approaches

The migratory metapopulation persistence capacity, λ_{MM} , is a measure that allows us to assess whether conditions are favorable for the population to reach the nonzero equilibrium state, enabling long-term persistence. λ_{MM} is defined as the dominant eigenvalue of the migratory metapopulation landscape (or dispersal) matrix, \mathbf{M} . Taylor and Hall (2012) showed that migratory metapopulations persist when metapopulation persistence capacity exceeds the persistence condition, i.e., $\lambda_{MM} > \sqrt{\frac{e_B e_W}{c_B c_W}}$, where c

and e still represent colonization and extinction rates and subscripts B and W represent breeding and nonbreeding habitat values, respectively. To formulate the landscape matrix in the seasonally migratory example, consider the block matrix

$$\mathbf{M} = \begin{pmatrix} \mathbf{0} & \mathbf{A} \\ \mathbf{A}^T & \mathbf{0} \end{pmatrix},$$

where the elements of the submatrix \mathbf{A} are $A_{ij} = A_i^{\zeta_{ex}} A_j^{\zeta_{em}} e^{-\alpha d_{ij}}$. A_{ij} gives the contribution that habitat j makes to the colonization of habitat i multiplied by the expected lifetime of patch i . Ovaskainen and Hanski (2003) argue that A_{ij} may be viewed as measuring the fraction of time that patch i would be occupied if habitat j was its only source of migrants. In this formulation, we have slightly generalized the work Taylor and Hall (2012) by adding the area-scaling factor for the extinction, ζ_{ex} , and emigration, ζ_{em} . Elements of \mathbf{A} are zero if both source and destinations habitats are of the same kind. For example, two breeding habitats are not directly connected as migrants must travel sequentially from to a nonbreeding habitat before moving to a new breeding habitat.

Ovaskainen and Hanski (2001) defined the *relative patch value for long-term persistence*, which measures the relative decrease or increase in metapopulation capacity due to the removal, V_o^- , or addition, V_o^+ , of habitat o . For a seasonally migrating network, the set of all habitats is defined as $\mathcal{Q} = \{p_1, \dots, p_{n_B}, q_1, \dots, q_{n_W}\}$. The value of a removed habitat can be expressed as

$$V_o^- = \frac{\lambda_{MM}(\mathcal{Q}) - \lambda_{MM}(\mathcal{Q} \setminus \{o\})}{\lambda_{MM}(\mathcal{Q})},$$

where $\lambda_{MM}(\mathcal{Q})$ is the persistence capacity for the full network and $\lambda_{MM}(\mathcal{Q} \setminus \{o\})$ is the persistence capacity for the network with habitat o removed. Similarly, one can define the value of an added habitat

$$V_o^+ = \frac{\lambda_{MM}(\mathcal{Q} \cup o) - \lambda_{MM}(\mathcal{Q})}{\lambda_{MM}(\mathcal{Q})},$$

where $\lambda_{MM}(\mathcal{Q} \cup o)$ represents the persistence capacity for the full network with the added habitat. This definition can be extended to represent the value of smaller perturbations, where instead the metapopulation capacities are compared for the case of habitat degradation or enhancement, or pathway contributions, where the metapopulation capacities are compared for pathway perturbations.

Applying this analysis to the elk population, we determine whether conditions are favorable for network-level persistence under the baseline situation where all habitats can receive and export individuals. The migratory metapopulation landscape under baseline conditions is created using the submatrix:

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & 1.03 & 0.64 \\ 0 & 0 & 0 & 4.05 \\ 1.03 & 0 & 0 & 0 \\ 0.64 & 4.05 & 0 & 0 \end{pmatrix},$$

where each element represents the fraction of time that habitat i would be inhabited if its only source of immigrants were habitat j . For example, comparing $A_{13} = 1.03$ and $A_{14} = 0.64$, would indicate that the pathway between the breeding-only and nonbreeding-only habitats is more important to the breeding-only habitat than the pathway coming from the year-round habitat. Based on this matrix, we find the metapopulation persistence capacity, $\lambda_{MM} = 4.11$ (i.e., dominant eigenvalue of \mathbf{M}). We then



TABLE 7 Metapopulation persistence capacity, λ_{MM} , and relative habitat value, V_o^- , for the elk occupancy case study with habitat-removal perturbations

	Breeding-Only Removed	Year-Round Breeding Removed	Nonbreeding-Only Removed	Year-Round Nonbreeding Removed
λ_{MM}	4.05	1.94	4.09	1.26
V_o^-	0.01	1.12	0.005	2.25

use the intrinsic extinction and colonization rates to compute the persistence condition:

$$\sqrt{\frac{e_b e_W}{c_m c_w}} = 0.33.$$

The persistence capacity exceeds the persistence condition so we would expect the population to persist.

It is useful at this point to calculate metapopulation persistence capacity for the case of habitat removal, allowing us to calculate the relative habitat value (Table 7). This analysis shows that in all cases λ_{MM} exceeds the condition for migratory metapopulation persistence so at the level of perturbation we examined we would not expect metapopulation extinction. However, removing the year-round nonbreeding habitat has the largest effect on persistence. This indicates that protecting the year-round nonbreeding population could have the greatest impact on the overall population. Also, removal of the nonbreeding-only habitat has the least effect on metapopulation persistence, which is expected as individuals can still winter at the year-round nonbreeding habitat. An important assumption is that the population “mixes” at the year-round nonbreeding habitat and that individuals could change migration strategies, which may not be realistic for our case study species. We also note that removal of the breeding-only habitat is theoretically troublesome, since this disconnects our network and makes metapopulation assumptions invalid.

2.3 | Demographic-based metrics

Of the three metrics presented in Nicol et al. (2016), demographic-based metrics require the most data, which are necessary for estimating survival, reproduction, and movement probabilities. These metrics are most useful for examining consequences of management actions for objectives such as population abundance, growth rate, resilience to climate change and other dynamic stressors, and maximizing ecosystem goods and services (Erickson, Thogmartin, Diffendorfer, Russell, & Szymanski, 2016; Wiederholt et al., 2013). Metrics accounting for these objectives can be derived using per capita approaches, elasticity and sensitivity analysis, and measures of abundance and growth rates. After describing the parameterization of demographic parameters in a graph, we distinguish two types of demographic-based metrics including instantaneous approaches and perturbation-analysis approaches. Demographic approaches are suitable for small or large networks, although for large networks identifying demographic parameters for each node and path requires extensive data. Parameter estimates for the elk case study and mathematical formulations are provided in Appendix A.2.

2.3.1 | Demographically weighted graph approaches

Habitat and pathway quality can be quantified by weighting a graph based on demographic information along the pathways and within the habitats. In particular, a node-weighted graph, or graph in which habitats are weighted proportional to the ecological context, is required to examine the demographic effects of adding or removing an entire habitat or pathway. For example, habitats may be characterized by their quality-weighted area, equal to habitat size multiplied by habitat quality, where habitat quality

is assumed to be related to reproductive potential in the habitat (Minor & Urban, 2007). Alternatively, habitats may be characterized by their per-capita fecundity and mortality rates.

If the proposed management action is to add or remove a habitat from the network, then the modeler may consider weighting the habitats by abundance that will allow for estimating how much the population size will change under alternative scenarios for wholesale habitat gains or losses. Abundance metrics are generally fairly simple and rely on identifying sites supporting a large proportion of the total population. For example, sites that support >1% of the total flyway population (Conklin, Verkuil, & Smith, 2014), or staging sites supporting >0.25% of the population (Bamford, Watkins, Bancroft, Tischler, & Wahl, 2008). If the proposed management action is to add or remove a pathway, one may consider measures of connectivity (i.e., how much will the population abundance change if pathways are removed). One may additionally compare the betweenness and other centralities of stopover sites in a demographically parameterized graph to determine which sites are most vital to the population. This concept has been developed into a bottleneck index for migratory species, which quantifies the importance of a migratory habitat using the proportional habitat change and the proportion of a population passing through a habitat during migration (Iwamura et al., 2013).

To effectively study demographic consequences of a management action that enhances or degrades a pathway, a node-weighted and edge-weighted directed graph becomes necessary. To parameterize such a graph, demographic information about pathways is needed. A common demographic metric describing movements of individuals along pathways is *flux*, which is calculated by assigning a quality-weighted characteristic to the starting habitat and then multiplying by the movement probability from the starting habitat to the destination habitat (Erickson et al., 2017; Minor & Urban, 2007). A quality-weighted characteristic could be size of the starting habitat multiplied by an index of survival and/or reproduction in that habitat, where the index is scaled from 0 to 1. The sums of flux for all incoming and outgoing pathways are called *influx* and *outflux*, respectively. A pathway with high flux indicates that a large number of individuals move between the two habitats and suggests a lower rate of habitat extinction (Minor & Urban, 2007).

In a network with seasonal migration, comparisons of habitat quality via weights based wholly or partly on reproduction can only be made between habitats of the same type. That is, such weights can be compared between breeding habitats or between nonbreeding habitats, but not across habitat types. Otherwise the comparisons are confounded by the lack of reproduction, by definition, in the nonbreeding habitats.

Turning to the case study, we calculate habitat weights, w_i , based on the estimated per capita growth rates (Fig. 6). We then calculate the weight of each possible pathway as a flux by multiplying the weight of habitat i by the probability of moving from habitat i to j . The flux estimates indicate that the year-round habitat in the summer has the largest effect on the population, as it has the largest overall immigration and emigration rates (in/outdegree). It makes sense that fluxes are larger during fall migration as it follows the summer breeding season, when the population size is at its highest level within the year, especially in a nonmigratory population incurring the lowest mortality rate. During spring migration, the greatest flux occurs in the migratory group moving from the nonbreeding-only to the breeding-only habitat. If the management objective is to conserve the largest migratory movements between two habitats, then strategies that conserve migration from breeding-only to nonbreeding-only habitats would be effective.

2.3.2 | Instantaneous approaches

Based on source-sink theory (Pulliam, 1988), metrics have been developed to quantify the per capita contribution of habitats or pathways to the entire network within a specified time window or at

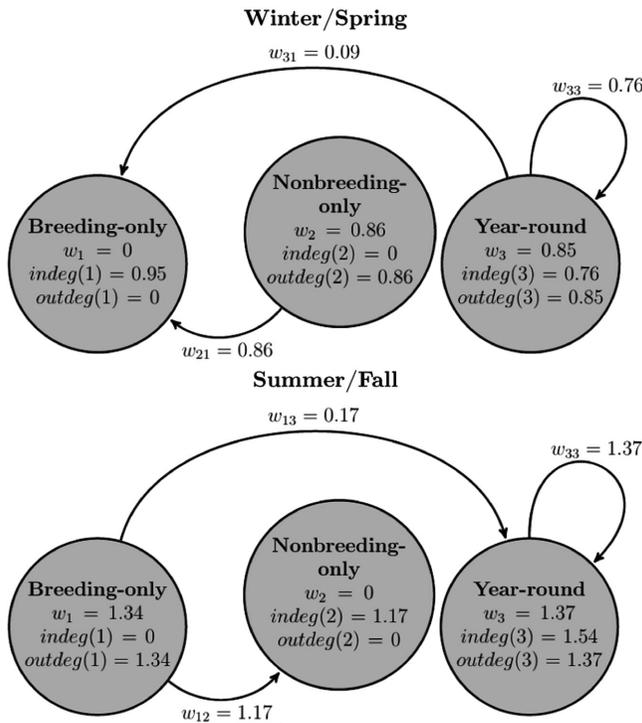


FIGURE 6 Weights for habitats, w_i , and pathways w_{ij} representing subannual dynamics (two 6-month seasons) in a demographically weighted graph. Pathway weights represent flux

equilibrium conditions (Erickson et al., 2017; Figueira & Crowder, 2006; Runge, Runge, & Nichols, 2006; Wiederholt et al., 2017). Because these metrics do not consider changes over time, we will refer to them as instantaneous approaches and opposed to dynamic, time-dependent, approaches. This class of metrics quantifies the number of individuals that an average individual contributes to the population at the network level during a snapshot in time. These metrics are very useful if the management objectives include understanding the relative value of a habitat or pathway for population dynamics at the network level (Nicol et al., 2016).

Recent approaches to estimating per capita contributions can incorporate emigration and immigration as well as survival and reproductive rates of residents and emigrants. For instance, one approach models the per-capita contributions for habitats, seasonal transitions between habitats (either migratory or nonmigratory), and pathways (a series of transitions through the annual cycle) by tracking movements of individuals (Wiederholt et al., 2017). This approach quantifies per capita contributions over the annual cycle, allowing for a comparison of the demographic importance of each habitat and pathway in the network within specified time windows. Another similar approach quantifies the total demographic contribution from a habitat or migratory pathway over a flexibly defined yet limited time period across an organisms life cycle. This approach focuses on pathway survival and reproduction and flows of individuals (Erickson et al., 2017).

To extend basic source sink theory to seasonally migrating species, the migratory path over the annual cycle must be considered. The general idea is to consider a focal habitat and then quantify how much of an impact a single adult individual, in a focal habitat, has on the overall population (by estimating the per capita contribution an individual generates at the next time step). Using the metric as defined in Wiederholt et al. (2017), the *annual per capita contribution* of a habitat can be



defined as

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

where the focal habitat is labeled o (origin). This quantity represents the sum of contributions over all possible migratory paths, C^{oid} (origin, intermediate, destination), through the network, over one annual cycle. Here, we are assuming two seasons and counting only pathways originating at the focal habitat. The contributions are further weighted by the probability that a migrant traversed a specific pathway (p_{oi} multiplied by p_{id}). The full term, $C^{oid} p_{oi} p_{id}$, is called the *migratory path flux*. To calculate the migratory path contributions, both per-capita juvenile recruitment and per-capita adult survival probability must be considered, i.e., $C^{oid} = a^{oid} + j^{oid}$. We specify these age-cohort-specific migratory path contributions as follows:

$$a^{oid} = s_o^a s_{oi}^a s_i^a s_{id}^a,$$

$$j^{oid} = \begin{cases} s_o^a r_o s_{oi}^j s_i^j s_{id}^j & \text{breeding occurs at the origin habitat,} \\ s_o^a s_{oi}^a s_i^a r_i s_{id}^j & \text{breeding occurs at the intermediate habitat,} \end{cases}$$

where s represents survival rate, subscripts indicate habitat or pathway, and superscripts indicate juvenile or adult. Here, r_o is the number of juveniles produced per adult in habitat o . The per capita contributions of subannual pathways can also be calculated. For instance, the contribution for the pathway during the transition from habitat o to i , is given by

$$C^{oi} = \sum_{d=1}^n C^{oid} p_{id}.$$

Note that habitats o and i may be at the same location but occupied during subsequent seasons, representing the transition of a nonmigratory cohort, for example from summer to fall.

In addition, the *population growth rate* at the network level is defined as

$$\lambda = \sum_{o=1}^n w_o C^o, \quad (5)$$

where w_o is the proportion of the total population in habitat o , calculated as the population size in habitat o divided by the total population size summed across all habitats in that season.

The benefit of contribution metrics is that they, along with population growth rates, can be calculated without the need for specifying initial population size. These methods do, however, require intrinsic survival rate for each habitat and each pathway, transition probability for each pathway, reproductive rate for each habitat, and the proportion of the population found in each habitat. These metrics cannot be used when examining multigenerational time windows during which the equilibrium assumption is often not met; for example, due to density-dependent effects. It is important to note that for populations with seasonal transitions, the per capita contribution metrics depend on the anniversary date. For example, the contribution of habitat o may have a different value if the anniversary date is the breeding season than if it is calculated starting in the nonbreeding season.

To estimate per capita contributions for the elk, we consider the population of females only across a single year. This approach assumes that reproduction is not limited by the number of males. The



TABLE 8 Per capita contributions, C^o , for each habitat as the origin considering each season as the anniversary date

Habitat	Anniversary Date	
	Summer/Fall	Winter/Spring
Breeding-only C^1	1.07	0
Nonbreeding-only C^2	0	1.14
Year-round C^3	1.14	1.22

Notes: A result of zero implies that the focal habitat is unoccupied during the anniversary date season.

TABLE 9 Per capita pathway contributions, C^{oi} , for each habitat as the origin considering each season as the anniversary date

Pathway	Anniversary Date	
	Summer/Fall	Winter/Spring
C^{12}	1.07	0
C^{21}	0	1.14
C^{13}	1.07	0
C^{31}	0	1.14
C^{33}	1.14	1.23

Notes: A result of zero implies that the focal pathway does not exist during the anniversary date season.

TABLE 10 Per capita migratory pathway contributions, C^{oid} , for each pathway as the origin considering each season as the anniversary date

Migratory Path	Anniversary Date	
	Summer/Fall	Winter/Spring
C^{121}	1.07	0
C^{131}	1.07	0
C^{133}	1.07	0
C^{331}	1.14	0
C^{333}	1.14	1.23
C^{313}	0	1.14
C^{312}	0	1.14
C^{212}	0	1.14
C^{213}	0	1.14

Notes: A result of zero implies that the focal pathway does not exist at the origin habitat during the anniversary date season.

network structure for the instantaneous approach can be found in Figure A1 in Appendix A.2.1. We find that the year-round habitat has the highest per capita contribution regardless of anniversary date (Table 8), suggesting that management actions in the year-round habitat would have the largest impact on the population at the network level. The greatest pathway contribution is for the nonmigratory population remaining in the year-round habitat (C_{33}) regardless of anniversary date (Table 9). Given the small differences among pathway contributions, management strategies that allocate equal effort among pathways are expected to have the largest effect on the population as a whole. Migratory path contributions differ by <10% (Table 10). When comparing annual migratory path contributions the nonmigrants in the year-round habitat, C_{333} contribute the most on a per capita basis to the overall population, whereas migrants spending the breeding season in the breeding-only habitat have the



lowest contribution. This is likely due to the lower reproductive rate in the breeding-only habitat (0.68) compared to the breeding habitat (0.86).

2.3.3 | Dynamic perturbation approaches

If practitioners wish to account for density-dependent effects (e.g., reproductive or harvest rates are dependent on the number of animals) or time-dependent effects (e.g., selection of migration path based on past migratory information), then dynamical perturbation metrics become useful. These metrics quantify the impacts of small changes to vital rates to understand the influences of parameter change on population-level responses, including abundance and population growth rate. They are well developed (Caswell, 2001, 2011; Caswell & Shyu, 2012) with sensitivity and elasticity analyses used to estimate impacts of perturbations of vital rates on the population growth rate (Caswell, 2001; Caswell & Shyu, 2012; Greene & Beechie, 2004). Perturbation analyses can also be used to estimate the contribution of a particular habitat to other objectives such as population size, age structure, extinction risk, or sustainable harvest levels (Bauer & Klaassen, 2013; Caswell & Shyu, 2012; Flockhart, Pichancourt, Norris, & Martin, 2015; Mattsson et al., 2012; Strasser, Neubert, Caswell, & Hunter, 2012; Sutherland, 1996, 1998; Taylor & Norris, 2010; Thogmartin et al., 2013). These approaches have been applied to a number of mobile species, such as soft shelled clams (Strasser et al., 2012), salmon habitats (Greene & Beechie, 2004), and birds (Hunter & Caswell, 2005).

Dynamic perturbation approaches make use of a discrete time stepping formulation, where the population at each season or time step can be calculated by

$$\mathbf{N}(t + 1) = \mathbf{L}_\star \mathbf{N}(t), \quad (6)$$

where $\mathbf{N}(t)$ is a vector containing the population at each habitat for each demographic class at time t and \mathbf{L}_\star is a season-long population projection matrix that may include both demographic and dispersal processes during time step \star . An identical formulation can be written without use of matrix notation as

$$N_i^\bullet(t + 1) = \sum_{j=1}^n s_{ji}^\bullet(t) p_{ji}^\bullet(t) f_j^\bullet(t), \quad (7)$$

where N_i^\bullet represents the population of migrants in habitat i and the superscript \bullet is a placeholder for specific classes, for example, $\bullet = \{a, j\}$ to represent an age-class model with adults and juveniles. The functions on the right-hand side are defined based on the ecological system. The right-most term $f_j^\bullet(t)$ is the update function for habitat population, representing habitat survival rates, reproductive rates, and transitions between classes (e.g., juveniles becoming adults). The functions $s_{ji}^\bullet(t)$ and $p_{ji}^\bullet(t)$ represent the pathway survival and transition probabilities. Each of these three functions could include density-dependent effects or other forms of spatiotemporal variation in vital rates. An extensive description of this modeling approach can be found in Sample et al. (2017).

Sensitivity is defined as the change in an output variable (e.g., network-level growth rate) when one or more system parameters (e.g., habitat-specific survival rate) is changed. These metrics have been developed for seasonally migratory populations using periodic matrix population models and vector permutation models (Caswell, 2008; Caswell & Shyu, 2012). The former accounts for cyclic temporal (seasonal or annual) variation, and the latter accounts for stage structure in the system. These two modeling frameworks can be combined for modeling populations with annual cycle migrations and stage structure. In these systems, equation (6) is generalized and population dynamics across the full



annual cycle of τ seasons is represented by

$$\mathbf{N}(t + \tau) = \mathbf{L}_\tau \dots \mathbf{L}_2 \mathbf{L}_1 \mathbf{N}(t).$$

We can then define the annual growth rate at time t as

$$\lambda = \frac{(\mathbf{N}(t))^T}{N_{\text{tot}}(t)} \mathbf{L}^T \mathbf{1}, \quad (8)$$

where \mathbf{L} is the full annual population projection matrix, $\mathbf{L} = \mathbf{L}_\tau \dots \mathbf{L}_2 \mathbf{L}_1$, $N_{\text{tot}}(t)$ is the total network population size at time t , superscript T represents the matrix transpose, and $\mathbf{1}$ is a column vector containing ones.

When considering multiple classes in which habitat demography is applied before pathway dispersal, we order entries in the population matrix by habitats:

$$\mathbf{N}(t) = \begin{pmatrix} N_1^1(t) \\ N_1^2(t) \\ \vdots \\ N_1^k(t) \\ N_2^1(t) \\ N_2^2(t) \\ \vdots \\ N_n^k(t) \end{pmatrix},$$

where the subscript denotes the habitat, the superscript denotes the stage or class (for example, adults and juveniles), and k represents the total number of classes. In this case, care must be taken in defining the projection matrix for season \star as

$$\mathbf{L}_\star = \mathbf{P}^T \mathbb{M}_\star \mathbf{P} \mathbb{B}_\star,$$

where \mathbf{P} is a vec-permutation matrix, \mathbb{M}_\star is the block diagonal matrix describing dispersal, and \mathbb{B}_\star is the block diagonal matrix describing demography for season \star . See 4 for descriptions of \mathbf{P} , \mathbb{M} , and \mathbb{B} . Also Hunter and Caswell (2005) has definitions for other orderings and arrangements, such as applying dispersal first then demography. If ξ is defined as a vector of output variables (e.g., network-level population size at equilibrium) and θ as a vector of input parameters (e.g., habitat-specific survival rate), then sensitivities are given by the derivative

$$\frac{d\xi}{d\theta^T} = \frac{d\xi}{d\text{vec}^T \mathbf{L}} \frac{d\text{vec} \mathbf{L}}{d\theta^T}. \quad (9)$$

Elasticity is defined as a proportional sensitivity and is calculated in a similar way to sensitivity. A mathematical definition of elasticity can be found in Caswell (2008). Use of these methods requires a background in matrix calculus, and for a complete mathematical treatment of these approaches see Caswell (2007, 2008) and Magnus and Neudecker (1985). Caswell and Shyu (2012) presents these methods for nonlinear periodic models and models with delayed density dependence.

To illustrate this method in the elk case study, we create a matrix model that accounts for the demography and movement of both adults and juveniles in the two-season network. Model formulation can be found in Appendix A.2.2. We chose to analyze a linear model so that survival rates and transition

**TABLE 11** Sensitivity of growth rate λ to habitat- and class-specific survival probabilities

	Winter-Spring Season	Summer-Fall Season
Breeding-only Juveniles	n/a	$\frac{d\lambda}{ds_1^j} = 0.092$
Breeding-only Adults	n/a	$\frac{d\lambda}{ds_1^a} = 0.393$
Nonbreeding-only Juveniles	$\frac{d\lambda}{ds_2^j} = 0.069$	n/a
Nonbreeding-only Adults	$\frac{d\lambda}{ds_2^a} = 0.337$	n/a
Year-round Juveniles	$\frac{d\lambda}{ds_{3,w}^j} = 0.142$	$\frac{d\lambda}{ds_{3,s}^j} = 0.142$
Year-round Adults	$\frac{d\lambda}{ds_{3,w}^a} = 0.593$	$\frac{d\lambda}{ds_{3,s}^a} = 0.537$

probabilities are nondensity-dependent (parameters are shown in Fig. A1). We also chose to focus on the sensitivity of growth rate to changes in habitat- and season-specific survival rates, although other output variables, such as habitat population size, and other input parameters, such as migration survival rates, may be used. Changes in survival rates correspond to enhancing/degrading a habitat.

The growth rate of the population, defined in equation (8), is given by the dominant eigenvalue of the projection matrix \mathbf{L} . We found that the growth rate is slightly smaller than one ($\lambda = 0.989$) suggesting a declining population. Small changes in the parameter values may produce a growth rate larger than 1 and determining the sensitivity of λ to changes in demography may therefore provide insightful information. Equation (9) provides the sensitivities, where the only output variable is λ and parameter vector θ contains habitat- and season-specific survival rates:

$$\frac{d\lambda}{d\theta^T} = \frac{d\lambda}{d\text{vec}^T \mathbf{L}} \frac{d\text{vec} \mathbf{L}}{d\theta^T}.$$

Details on how the derivative is calculated is given in Appendix A.2.3. Sensitivity results are provided in Table 11. It is evident that an increase in any of the survival rates results in an increase in growth rate (the derivative is positive). We also find that the growth rate is most sensitive to changes in adult survival at the year-round habitat, and least sensitive to changes in juvenile survival at the nonbreeding-only habitat.

For more complicated systems, information about sensitivity and elasticity can be approximated using numerical techniques. Numerical techniques are advantageous when density-dependent relationships are very complicated (highly nonlinear or discontinuous) or when multiple habitats and/or pathways are perturbed simultaneously. In this case, the population size, $N_j^*(t)$, as defined in equation (7), is explicitly tracked from one time step to the next until it reaches equilibrium. Perturbations can be carried out to examine the population's sensitivity to each of the management actions. For example, survival rates at habitats or density-dependent survival effects can be perturbed, the simulation can again be run to equilibrium, and results compared to a baseline. A population's *resilience* to changes in parameters can also be measured using numerical techniques. For example, one could change system parameters, such a survival at habitats, for a specific number of steps and then measure the time it takes for the population to return to equilibrium values.

For the elk case study, formulation of the pathway survival, transition probability, and habitat update functions can be found in Appendix A.2.4. After calculating baseline population size, perturbations to the baseline survival rates in each of the habitats simultaneously for both juveniles and adults were carried out. This would correspond to enhancing or degrading a habitat. Figure 7 shows the percent

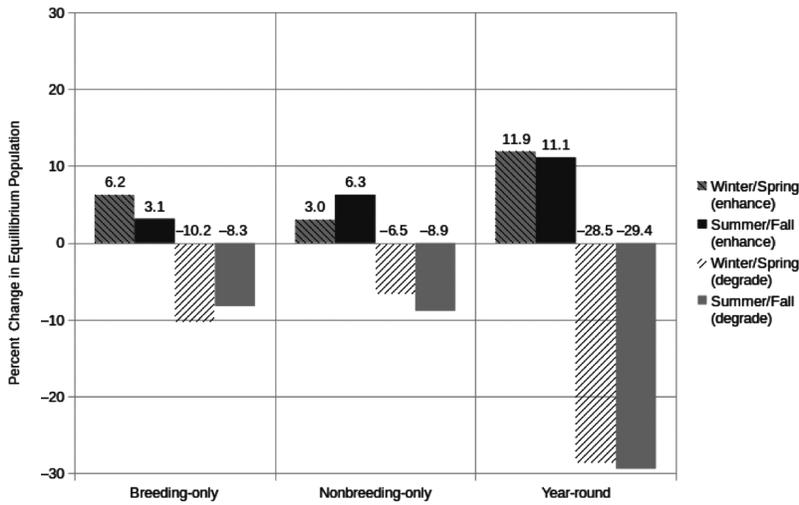


FIGURE 7 Percent change in total population size across perturbations to habitat- and season-specific survival rates based on the elk network population model. Here, baseline survival rates were changed by a factor of +0.2 to represent habitat enhancement or -0.2 to represent habitat degradation. In each case, the network simulation was run to equilibrium. When survival is density-dependent, the factor is applied after the density-dependent survival rate is calculated

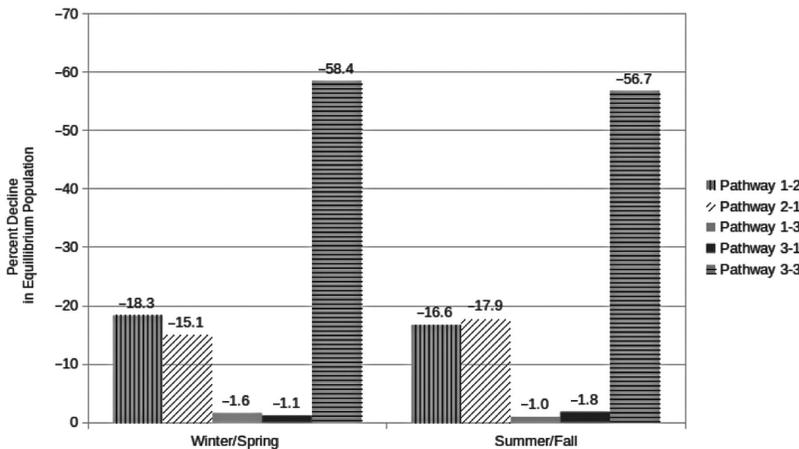


FIGURE 8 Percent decline in total population size across perturbations to pathway-specific survival rates based on the elk network population model. Here, baseline pathway survival rates were changed by a factor of -0.2 to represent pathway degradation. In each case, the network simulation was run to equilibrium

change in population size when survival rates are changed in the specified node by 20%. The greatest network-level impacts are observed after enhancing or degrading the year-round habitat, with habitat degradation causing the largest change in population. We also examined the consequences of degrading each of the subannual pathways by reducing survival from 100% to 80% along each pathway independently (Fig. 8). The results are consistent with the per capita contributions of subannual pathways C^{oi} results, with the nonmigratory pathway perturbation having the largest impact on the population. Reductions in survival along the pathway connecting the year-round habitat and the breeding-only habitat have the least effect on the overall population.

2.4 | Other approaches

Other modeling approaches that may be useful in assessing management actions include continuous network flow approaches and agent-based approaches. These models require the most data to fully parameterize but can often answer questions at finer spatial and temporal scales. At this point in time, however, fully described metrics for seasonally migratory populations have not been articulated to the extent necessary to make them practically available. These approaches are complex and demand considerable data or system knowledge. Agent-based models, for example, are computational simulations combining individual elements of decision-making, learning, adaptation, and evolution.

Agent-based models are sometimes called individual-based models because they model the decisions of individuals (agents), which accumulate to yield emergent properties relating to species status and trend at the population-level (Grimm, 1999; Grimm et al., 2005). These agents act independently, seeking to fulfill specific objectives, responding to and moving within their environment and, if appropriately programmed, learning and adapting their state and behavior in response to stimuli from other agents and the environment. Through simulation of differing configurations of the landscape, the consequences of enhancing, degrading, adding or removing habitat and pathways can be evaluated for any of the management objectives listed in Nicol et al. (2016, table 3). For instance, Lonsdorf et al. (2016) modeled the movement of mallard (*Anas platyrhynchos*)-like birds across North America as a function of caloric gains and losses, and then using marginal value analysis examined the consequences of changing caloric availability in a portion of the species migration via habitat management. They found that locations with decreased caloric availability reduced survival rates during migration. Beatty et al. (2017) took a similar approach to assess the influence of changing climate scenarios on spring dabbling duck migration using an agent-based model, finding that under all climate scenarios they evaluated, stopover duration and movement distances increased. Both approaches suggest migrational processes are pinched, narrowing the flow of individuals through an important subset of all possible locations; these pinchpoints are particularly important to address through management and adaptation to ensure species conservation. Linking these habitat-driven changes in agent movement and survival to consequences for network-level population dynamics would be an important next step.

Continuous modeling approaches play a large role in spatial ecology, addressing issues related to spatial population dynamics, animal movements, and community structure in heterogeneous environments (Cantrell, Cosner, & Ruan, 2010). The majority of this work focuses on both short-term animal movements and dispersal. Far fewer continuous approaches have been applied to seasonal migration or dispersal. A few examples of seasonal models incorporating continuous approaches include the modeling of “wave fronts” and the spread of species, including disease organisms (Mundt, Sackett, Wallace, Cowger, & Dudley, 2009), modeling of daily vertical migration of plankton (Han & Straskraba, 1998), using Brownian bridge movement to model migration pathways (Horne, Garton, Krone, & Lewis, 2007; Palm et al., 2015), and migratory flow network (MFN) models that assume a fluid dynamic flow of migrants along migratory paths (Taylor, Laughlin, & Hall, 2016). These continuous approaches could be useful in refining management actions, such as enhancing or degrading a habitat or pathway, by better specifying the mechanisms behind the cause of enhancement or degradation. For example, Taylor et al. (2016) relate the per capita rate of movement along a pathway as being proportional to the pressure toward and resistance to movement, where pressure and resistance can be related to seasonal changes, population density, or migration cost. They were also able to describe how the growth rate of a theoretical population of a migratory bird might be affected by climate-related phenology shifts and allow for various levels of ability to adapt migration strategies. Because metrics associated with continuous approaches to modeling migratory species to this point are difficult to generalize beyond a specific study or method, we do not consider them further.



3 | DISCUSSION AND SYNTHESIS

We demonstrated how diverse habitat-quality metrics are computed for highly mobile species in a generalized context and for a particular species based on empirical information. These demonstrations collectively provide an important resource for professionals managing or conserving migratory populations, bridging the gap between the metrics-selection framework provided by Nicol et al. (2016) and practical application of these metrics in real-world contexts. By demonstrating diverse habitat-quality metrics for a single migratory system, we confirmed that multiple metrics can be computed for a given migratory population and showed how these metrics can be applied according to several scenarios representing alternative decision contexts. An important insight is that not all classes of metrics will apply to every population structure. In the elk example, the population exhibits annual variation in habitat-specific population size but not in presence/absence (i.e., elk are present in each habitat every year), and therefore only the graph-based and demographic-based metrics were relevant. See Appendices 4 and 4 for tables summarizing comparisons of elk habitat and pathway quality metrics. The simulated elk population persisted in all habitats throughout all of the single-habitat and single-pathway degradation scenarios, indicating that the objective of maximizing population persistence (and therefore the class of occupancy-based metrics) is irrelevant in this case.

Our comparisons of habitat- and pathway-quality metrics applied to the elk example revealed key differences and congruences regarding rankings of importance that depended on the management context. Examining graph- and demographic-based metrics led to general agreement that the habitat occupied during only the nonbreeding season (Habitat 2) was generally of least importance to system dynamics. Using the graph-based approach, the most connected habitat is expected to have the greatest influence on system dynamics. In the elk example, we found that indeed the habitat with the highest degree (i.e., number of incoming and outgoing pathways) across seasons was the most important for population dynamics. The breeding-only habitat has the greatest betweenness as it is the only habitat in the network having two pathways linked to other habitats in the network, but perturbing survival in this habitat had little effect on the population at the network level. Choosing the appropriate graph-based metric in the absence of sufficient demographic information can be crucial for achieving objectives related to network-level population dynamics. Unlike the more data-intensive metrics, the graph-based metrics were unable to make a clear distinction between the relative value of the breeding-only and year-round habitats. Demographic-based metrics allowed for an additional insight that the relatively high importance of the year-round habitat is attributed to the comparatively high levels of reproduction by nonmigrants. A 27% advantage in reproduction for migrants compared to nonmigrants translated to a 7% greater per capita contribution of this year-round habitat compared to the other habitats.

Although much progress has been made in identifying and demonstrating the applicability of habitat-quality metrics for managing highly mobile species, there are several areas for future research on this topic. When management decisions are time-dependent or depend upon the density of individuals within habitats and pathways, generally only demographic-based metrics are sufficient for providing the insight needed. If, however, timing of the management action or the number of individuals that may be affected is less important, occupancy-based metrics are often suitable. When decisions are constrained by limited data or need to be rapidly concluded, the low data requirements of graph-based metrics are appealing. These graph-based metrics are more readily scalable, as well, allowing inclusion of tens if not hundreds of discrete habitats and the connections among them. This level of complexity, especially when accounting for spatial heterogeneity in demographics, often precludes the more data-intensive metrics. Thus, one area needing to be addressed is the scaling up of the more data-intensive



methods, allowing for more habitats and pathways, should data-gathering from remote sensing, for instance, or other means allow parameterization of specific habitats. This increased spatial complexity in how populations are depicted would provide increased granularity to the decisions a manager may make.

For the vast majority of systems, the information needed to parameterize these more data-hungry approaches simply will not be available in the interval of time a decision needs to be made. In these situations, graph-based approaches relying strictly on the spatial arrangements of populations may be sufficient for informing certain management decisions. However, as noted by Earl et al. (2017), for highly mobile species, occupancy is necessarily dynamic, demographically independent subpopulations may not exist, and therefore understanding population risk requires more sophisticated data and models. A more proactive approach to monitoring highly mobile species would ensure that these data are available when needed; it could also pay dividends in terms of our ability to anticipate and avoid problems before they become critical and require unpopular conservation measures. Furthermore, extending monitoring efforts to include the socioeconomic benefits of highly mobile species could elucidate cross-jurisdictional benefit flows and suggest alternative means of obtaining conservation funding (Semmens et al., 2018).

Generalizable approaches for computing habitat-quality metrics using agent-based and continuous models would provide important additions to the current selection of metrics, which would be especially useful for high-stakes decisions with large volumes of spatially explicit data on population dynamics. Another promising avenue is developing methods for incorporating habitat-quality metrics within decision-support systems that allow for optimizing allocation of management resources among habitats and pathways. Furthermore, many managers are faced with optimizing management decisions for a wide array of species. Application of graph-, occupancy-, and demographic-based metrics to multispecies arrangements seems essential. Some efforts have been made in riparian settings (e.g., Perkin & Gido, 2012), but conservation-guided research for highly mobile species seems lacking. Graph theory giving rise to the graph-based metrics we described, however, provides a sufficient framework for representing the topological space of interspecific relationships (Jordan & Scheuring, 2004). The important step is to represent the spatial arrangement of each member of a community and the interaction among them. This insight would allow waterfowl managers, for instance, to move beyond seeing dabbling ducks as mallard-like animals (*sensu* Lonsdorf et al., 2016) and instead examine the place-specific community-level constraints each dabbling duck faces. In addition, a dynamical depiction of the network changing in step with a changing landscape, climate or in the face of competition, coupled with the response of populations to those changes, will provide a more realistic decision context for managers (e.g., Wimberly, 2006).

4 | CONCLUSION

Our descriptions and comparisons of diverse habitat-quality metrics provide means for practitioners to overcome the modeling challenges associated with management or conservation of highly mobile species. Whereas previous guidance for applying habitat-quality metrics has been scattered in diversified tracks of literature, we have brought this information together into a user-friendly format including accessible descriptions and computer code for a case study example. As with many migratory, or partially migratory species, managing elk at a population scale presents an enormous challenge due to the multiple jurisdictions involved and uncertainties about population-level responses to management actions. This work gives conservation professionals a foundation for metrics that they can adapt for their own decision contexts and focal populations.



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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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APPENDIX A

A.1 Table of mathematical symbols

TABLE A1 Mathematical symbols and notation

Variable	Definition
a^{oid} and j^{oid}	Class-specific migratory path contributions where a denotes adult and j denotes juvenile
A_i	Area of habitat i
A	Subelements for the metapopulation landscape matrix, bold face capital letters generally represent matrices
B and W	As subscripts represent parameter values for the breeding and nonbreeding seasons, respectively
\mathbf{B}_\star^i	$k \times k$ demographic matrix for season \star and node or habitat i
\mathbb{B}_\star	$nk \times nk$ block diagonal matrix containing demographic matrices for season \star
C_i	Colonization rate for habitat i , in general it is a function of occupancy probabilities $C_i = C_i(\mathbf{p}(t))$
c	Species-specific colonization rate
C^o	Per capita contribution of an individual at origin habitat o
C^{oi}	Per capita contribution from a subannual pathway
C^{oid}	Migratory path contribution for $(o, i, d) = (\text{origin, intermediate, destination})$ habitats
D_{ij}	Shortest migratory path distance from habitat i to habitat j —measured by summing pathway weights along the migratory path
d_{ij}	Distance between habitats i and j , could represent migration difficulty or Euclidean distance
$deg(i)$	Degree of habitat i
E_i	Extinction rate for habitat i
e	Species-specific extinction rate
$f_i^\star(t)$	Time-dependent habitat update function for dynamic model
$g(i)$	Betweenness of habitat i
H_i	Connectivity of habitat i as defined in occupancy-based metrics
i, j	Represents habitats (or nodes)
$indeg(i)$ and $outdeg(i)$	Indegree and outdegree of habitat i
J_i	Incidence of occupancy
k	Total number of species classes
L	Population projection matrix for transitioning from 1 year to the next
\mathbf{L}_\star	Season-specific population projection matrix
M	Metapopulation landscape (dispersal) matrix, described here for a seasonally migrating species
\mathbf{M}_\star	$n \times n$ dispersal matrix for season \star and class \bullet
\mathbb{M}_\star	$nk \times nk$ block diagonal matrix containing dispersal matrices for season \star
n	Total number of habitats in the network
n_B and n_W	Represent the number of breeding and nonbreeding habitats respectively such that $n = n_B + n_W$

(Continued)



TABLE A1 (Continued)

Variable	Definition
$N_i^*(t)$	Population at habitat i for class \bullet at time t
$\mathbf{N}(t)$	Vector containing population for each habitat and class at time t
o	Used to denote a focal habitat for which a calculation is being considered, for example, removal of habitat o or the per capita contribution of o
p_i	Occupancy probability for habitat i
p_{ij}	Pathway transition probability where subscripts denote origin and destination of the pathway
$p_{ij}^*(t)$	Time-dependent pathway transition probability for dynamic model
\mathbf{p}	Vector of occupancy probabilities for all n habitats
\mathbf{P}	Vec-permutation matrix
q_i	Occupancy probability for nonbreeding habitats when seasonally migratory species are being considered. When q_i is defined, p_i represents breeding habitats
\mathcal{Q}	The set of all habitats in the network
r_i	Reproductive rate at habitat i
S_B and S_W	Breeding and nonbreeding season metapopulation size
s_i	Survival rate at habitat i
s_{ij}	Survival rate along a pathway where subscripts denote origin and destination of the pathway
$s_{ij}^*(t)$	Time-dependent pathway survival function for dynamic model
t	Time for temporal networks or dynamics metrics
$U_{B,o}^L$ and $U_{W,o}^L$	Contribution of habitat o to overall metapopulation size
V_o^- and V_o^+	Relative patch value for long-term persistence under habitat removal R or habitat addition A
ws_i	Weight used in metapopulation size calculation
w_o	Proportion of the total population residing in habitat o
λ_{MM}	The metapopulation persistence capacity as defined for a seasonally migratory species
λ	Population growth rate at the network level
τ	Total number of steps in a full annual cycle
θ	Vector containing input parameters
ξ	Vector containing output variables
ζ_{em} and ζ_{ex}	Emigration and extinction by area scaling factors, respectively
*	As a superscript represents equilibrium values
\bullet	As a superscript represents class type, e.g., $\bullet = a, j$ for adults and juveniles
\star	As a subscript represents seasons

A.2 Elk network population model formulation and parameterization

A.2.1 General parameter description

Approximate areas of each of the habitats are estimated from GPS locations in Middleton et al. (2013) where the breeding-only habitat is approximately 718 km², the nonbreeding-only range is approximately 315 km², and year-round only habitat is approximately 1093 km². Distances between

**TABLE A2** Demography without dispersal for each season within 1 year

	Winter-Spring Season	Summer-Fall Season
Breeding-only	$\mathbf{B}_w^1 = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}$	$\mathbf{B}_s^1 = \begin{pmatrix} 0 & r_1 s_1^a \\ s_1^j & s_1^a \end{pmatrix}$
Nonbreeding-only	$\mathbf{B}_w^2 = \begin{pmatrix} s_2^j & 0 \\ 0 & s_2^a \end{pmatrix}$	$\mathbf{B}_s^2 = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}$
Year-round	$\mathbf{B}_w^3 = \begin{pmatrix} s_3^j & 0 \\ 0 & s_3^a \end{pmatrix}$	$\mathbf{B}_s^3 = \begin{pmatrix} 0 & r_3 s_3^a \\ s_3^j & s_3^a \end{pmatrix}$

Notes: The entries b_{ij} represent the transition from stage j to stage i , where juvenile stage is enumerated 1 and adult stage is 2. Matrix superscripts represent node number and the subscripts w and s stand for winter and summer, respectively. Note that \mathbf{B}_w^1 and \mathbf{B}_s^2 are identity matrices to indicate that everything stays the same; there are no individuals in these habitats during the indicated season.

habitats are also estimated using a center-to-center measurement, which results in a pathway distance of 40 km between the breeding-only and nonbreeding-only habitats and a pathway distance of 60 km between the breeding-only and year-round habitats.

Movement probabilities are season-dependent. Middleton et al. (2013) determined that resident elk and about 10–15% of migratory elk spend their winters in the year-round habitat. Therefore, about 85–90% of elk in the breeding-only habitat migrate to the nonbreeding-only habitat during fall migration. Furthermore, during fall migration 100% of the resident population remains in the year-round habitat. Data from 2005 to 2009 indicate that about 47.5% of elk are currently migratory (Middleton et al., 2013). To calculate the proportion that remain in the year-round habitat for spring migration, we note that the year-round habitat contains all resident elk and about 13% of the migratory elk during the winter. The proportion that remain in the year-round habitat for spring migration (that is, the proportion of resident elk) is calculated as $(0.525 N_{tot}) / (0.525 N_{tot} + (0.13)(0.475 N_{tot}))$, or about 89%. Thus, only about 11% of the population in the year-round habitat migrate to the breeding-only habitat and 100% of the population at the nonbreeding-only habitat move to the breeding-only habitat during spring migration.

To estimate per capita growth rates in each habitat, we use the density-dependent expression for annual adult survival proposed by Taper and Gogan (2002) and juvenile (<1-year old) survival proposed by Singer et al. (1997) to calculate seasonal survival rates. For simplicity, we assume that the population is at carrying capacity to estimate adult seasonal survival rate as 0.90 for both seasons, and juvenile seasonal survival rate as 0.65 in the summer and 0.72 in the winter (Singer et al., 1997). Reproduction occurs in the summer and the rate is higher for the residents of the year-round habitat (0.86) than for the migratory subpopulation of the breeding-only habitat (0.68), these numbers are estimated by the proportion of pregnant elk, using a weighted average for the different age classes (Middleton et al., 2013). By assuming a 1.5:1 ratio of female juveniles to male juveniles (Houston, 1982) and a female calf:cow ratio of 0.3 in the year-round habitat and 0.2 in the other habitats (Middleton et al., 2013), we estimate a habitat-specific growth rate when the patch populations are at carrying capacity by using a weighted average of survival and reproductive rates. In the winter/spring, the nonbreeding-only habitat has growth rate of $(0.8)(0.9) + (0.2)(0.72) = 0.86$ and the year-round habitat has growth rate $(0.7)(0.9) + (0.3)(0.72) = 0.85$, respectively. In the summer/fall, the breeding-only habitat has growth rate $(0.8)(0.9)(1.68) + (0.2)(0.65) = 1.34$, and for the year-round habitat, $(0.7)(0.9)(1.86) + (0.3)(0.65) = 1.37$. See Sample et al. (In Review) for details on parameterization and for examples when the population is not at carrying capacity. Figure A1 summarizes the parameterization results.

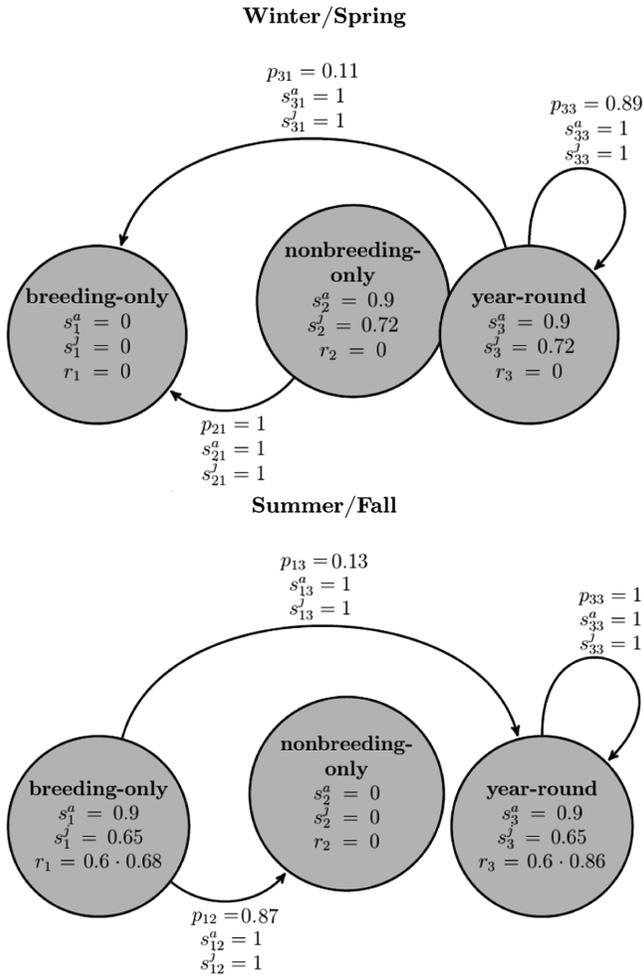


FIGURE A1 Network structure and parameter values used in C^o snapshot and sensitivity calculations. Superscripts a and j reference values specific to adults and juveniles, respectively. Survival rates are denoted s_i and s_{ij} at the habitats and along the pathways, respectively, transition probabilities along the pathways are denoted as p_{ij} , and reproductive rates at the habitats are denoted r_i

A.2.2 Vec-permutation matrix model

We applied the approach in Hunter and Caswell (2005) and Caswell and Shyu (2012) to our elk example to have a matrix model that accounts for different stages, spatial structure, and migration. As we did for the previous models, we considered two stages of females (juveniles and adults), three habitats and two seasons. To formulate the spatial model with two stages, we need to specify the demographic characteristics of each habitat, and the dispersal of individuals among them.

Using the notation and constant parameter values in Figure A1, we defined the matrices that account for the demographic changes (reproduction and survival) and migration given in Tables A2 and A3 , respectively.



TABLE A3 Dispersal without demographic changes for each season and class

	Winter-Spring Season	Summer-Fall Season
Stage 1 (Juveniles)	$\mathbf{M}_w^1 = \begin{pmatrix} 0 & p_{21}^j s_{21}^j & p_{31}^j s_{31}^j \\ 0 & 0 & 0 \\ 0 & 0 & p_{33}^j s_{33}^j \end{pmatrix}$	$\mathbf{M}_s^1 = \begin{pmatrix} 0 & 0 & 0 \\ p_{12}^j s_{12}^j & 0 & 0 \\ p_{13}^j s_{13}^j & 0 & p_{33}^j s_{33}^j \end{pmatrix}$
Stage 2 (adults)	$\mathbf{M}_w^2 = \begin{pmatrix} 0 & p_{21}^a s_{21}^a & p_{31}^a s_{31}^a \\ 0 & 0 & 0 \\ 0 & 0 & p_{33}^a s_{33}^a \end{pmatrix}$	$\mathbf{M}_s^2 = \begin{pmatrix} 0 & 0 & 0 \\ p_{12}^a s_{12}^a & 0 & 0 \\ p_{13}^a s_{13}^a & 0 & p_{33}^a s_{33}^a \end{pmatrix}$

Notes: The entries m_{ij} represents the transition from habitat j to habitat i . Matrix subscripts indicate season and superscripts indicate class number.

To model demographic changes for a given season, a population vector is organized by habitats and the projection is represented as

$$\begin{pmatrix} N_1^j(t + \Delta t) \\ N_1^a(t + \Delta t) \\ N_2^j(t + \Delta t) \\ N_2^a(t + \Delta t) \\ N_3^j(t + \Delta t) \\ N_3^a(t + \Delta t) \end{pmatrix} = \underbrace{\begin{pmatrix} \mathbf{B}_\star^1 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{B}_\star^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{B}_\star^3 \end{pmatrix}}_{\mathbb{B}_\star} \begin{pmatrix} N_1^j(t) \\ N_1^a(t) \\ N_2^j(t) \\ N_2^a(t) \\ N_3^j(t) \\ N_3^a(t) \end{pmatrix},$$

where Δt is portion of the length of one season and \star is a placeholder for w or s representing winter and summer seasons. Then to model population dispersal, a population vector is organized by classes and the projection is represented as

$$\begin{pmatrix} N_1^j(t + 1) \\ N_2^j(t + 1) \\ N_3^j(t + 1) \\ N_1^a(t + 1) \\ N_2^a(t + 1) \\ N_3^a(t + 1) \end{pmatrix} = \underbrace{\begin{pmatrix} \mathbf{M}_\star^1 & \mathbf{0} \\ \mathbf{0} & \mathbf{M}_\star^2 \end{pmatrix}}_{\mathbb{M}_\star} \begin{pmatrix} N_1^j(t + \Delta t) \\ N_2^j(t + \Delta t) \\ N_3^j(t + \Delta t) \\ N_1^a(t + \Delta t) \\ N_2^a(t + \Delta t) \\ N_3^a(t + \Delta t) \end{pmatrix}.$$

To write model equation (6) so that matrix \mathbf{L} includes both dispersal and demography, Hunter and Caswell (2005) defined a vec-permutation matrix, $\mathbf{P} = \sum_{i=1}^k \sum_{j=1}^n E_{ij} \otimes E_{ij}^T$, where k is the number of stages, n is the number of habitats, E_{ij} is an $k \times n$ matrix with a 1 in the (i, j) position and zeros elsewhere, and \otimes is the Kronecker matrix product, so that

$$\mathbf{L}_\star = \mathbf{P}^T \mathbb{M}_\star \mathbf{P} \mathbb{B}_\star.$$

To model population dynamics over one annual cycle, we recognize that the elk go through two demographic/dispersal events. Thus, when starting in the beginning of the winter season of 1 year, the projection matrix is $\mathbf{L} = \mathbf{L}_s \mathbf{L}_w$ and the population in the beginning of the winter/spring season of the next year is calculated as

$$\mathbf{N}(t + 2) = \mathbf{L}_s \mathbf{L}_w \mathbf{N}(t). \tag{A1}$$



A.2.3 Sensitivity analysis

In the following analysis, we will consider a linear model such that \mathbf{L} of equation (A1) is constant and not density-dependent. Given population dynamics described by equation (A1), we follow the work of Hunter and Caswell (2005) and Caswell and Shyu (2012) to calculate sensitivity of population growth rate, λ , with respect to habitat- and season-specific survival rates, given by the following derivative:

$$\frac{d\lambda}{d\theta^T} = \frac{d\lambda}{d\text{vec}^T \mathbf{L}} \frac{d\text{vec} \mathbf{L}}{d\theta^T}, \quad (\text{A2})$$

where the vec operator stacks the columns of a matrix into a column vector and the parameter vector is chosen to be $\theta = (s_1^j \ s_1^a \ s_2^j \ s_2^a \ s_{3,w}^j \ s_{3,w}^a \ s_{3,s}^j \ s_{3,s}^a)^T$. The derivative of λ with respect to the matrix \mathbf{L} is given by

$$\frac{d\lambda}{d\text{vec}^T \mathbf{L}} = \frac{(\mathbf{w}^T \otimes \mathbf{v}^T)}{\langle \mathbf{w}, \mathbf{v} \rangle}, \quad (\text{A3})$$

where \mathbf{w} and \mathbf{v} are the right and left eigenvectors associated with λ . This gives the sensitivity with respect to the parameters for the full annual population projection matrix.

Following Hunter and Caswell (2005), we can calculate the sensitivity of lambda with respect to the demographic parameters. Recall that the demographic parameters are stored in the demography block diagonal matrix \mathbb{B}_* . To calculate the sensitivity of λ with respect to the winter demographic parameters, we write the full annual population projection matrix as

$$\mathbf{L} = \underbrace{\mathbf{P}^T \mathbb{M}_s \mathbf{P} \mathbb{B}_s \mathbf{P}^T \mathbb{M}_w \mathbf{P}}_{\mathbf{F}_w} \underbrace{\mathbb{B}_w \mathbf{I}}_{\mathbf{G}_w} = \mathbf{F}_w \mathbb{B}_w \mathbf{G}_w.$$

Then the sensitivity matrix is given by

$$\text{SEN}_{\mathbb{B}_w} = \mathbf{F}_w^T \left(\frac{d\lambda}{d\text{vec}^T \mathbf{L}} \right) \mathbf{G}_w^T,$$

where we use the sensitivity matrix calculated in equation (A3). The ij th entry of $\text{SEN}_{\mathbb{B}_w}$ corresponds to the sensitivity of λ to the ij th entry of the winter demography matrix \mathbb{B}_w . So to calculate the sensitivity with respect to juvenile survival in habitat 2 we look to the $i = 3, j = 3$ entry of $\text{SEN}_{\mathbb{B}_w}$. Similarly, we can calculate the sensitivity with respect to the summer demography:

$$\mathbf{L} = \underbrace{\mathbf{P}^T \mathbb{M}_s \mathbf{P}}_{\mathbf{F}_s} \mathbb{B}_s \underbrace{\mathbf{P}^T \mathbb{M}_w \mathbf{P}}_{\mathbf{G}_s} \mathbb{B}_w = \mathbf{F}_s \mathbb{B}_s \mathbf{G}_s.$$

Then the sensitivity matrix is given by

$$\text{SEN}_{\mathbb{B}_s} = \mathbf{F}_s^T \left(\frac{d\lambda}{d\text{vec}^T \mathbf{L}} \right) \mathbf{G}_s^T,$$

where the ij th entry of this matrix corresponds to the sensitivity of λ to the ij th entry of the summer demography matrix \mathbb{B}_s . When parameter values appear in multiple entries of the matrix \mathbb{B}_s , e.g., adult survival affects both adult and juvenile demography, then the sensitivity effects would be weighted. To calculate the sensitivity with respect to adult survival at Habitat 1 in the summer, we find sensitivity values in both the $i = 1, j = 2$ and the $i = 2, j = 2$ entries of matrix $\text{SEN}_{\mathbb{B}_s}$ and calculate the



sensitivity with respect to adult survival as

$$0.6 \cdot 0.68 \cdot \text{SEN}_{\mathbb{B}_s}[1, 2] + \text{SEN}_{\mathbb{B}_s}[2, 2],$$

here we note that with respect to adult survival, the reproductive and sex ratio parameters, 0.6 and 0.68, would be constants in the partial derivative.

A.2.4 Dynamic model formulation

We consider a female-only model with two stages, juveniles and adults, and recall the general form of the network model

$$N_i^*(t+1) = \sum_{j=1}^n s_{ji}^*(t) p_{ji}^*(t) f_j^*(t),$$

where the superscript $\bullet = \{a, j\}$ denotes adults and juveniles. We assume that our initial population consists of only adult females, with $t = 0$ corresponding to the winter/spring season. There are ~ 4500 elk between the nonbreeding-only and year-round habitats in the winter (Middleton et al., 2013) and given a male:female sex ratio of 1:4 (Cook, 1993), we begin simulations in with 3600 female adults. We assume that carrying capacity is proportional to area, which gives an initial population distribution of $N_2^a(t=0) = 1427$ and $N_s^a(t=0) = 2173$ at the nonbreeding-only and year-round habitats, respectively. All other population counts start at zero. The main challenge comes in identifying the form and assumptions for the update function, $f_i(t)$, the proportional movement function, $p_{ij}(t)$, and the pathway survival function, $s_{ij}(t)$.

We specify the adult update function for each habitat by identifying two processes: adult survival and juveniles transitioning to adults. Adult survival is density-dependent during both seasons (Taper & Gogan, 2002), and the functional dependence is assumed to take the form

$$s_{i,t}^a = \sqrt{e^{-0.219 \left(\frac{N_{i,t}^a + N_{i,t}^j}{K_i} \right)^{3.77}}},$$

where K_i is the total habitat carrying capacity (summing adults and juveniles) estimated using data from (Middleton et al., 2013) as $K_1 = 1886$, $K_2 = 1641$, and $K_3 = 2694$. Juveniles transitioning to adults depends on juvenile survival rates, which are density-dependent in the summer/spring, and the functional dependence is assumed to take the form

$$s_{i,t}^j = 0.65e^{\left(1 - \frac{N_{i,t}^a + N_{i,t}^j}{K_i} \right)}.$$

Juveniles transition to adults every year (in the summer). From these assumptions, we specify the update function for adults in each season as

$$f_{i,t}^a = \begin{cases} s_{i,t}^a N_{i,t}^a + s_{i,t}^j N_{i,t}^j & t = \text{summer/fall,} \\ s_{i,t}^a N_{i,t}^a & t = \text{winter/spring.} \end{cases}$$

The two processes that can change juvenile populations within a given habitat include juvenile survival and reproduction by adults. Juvenile survival is not assumed density-dependent in the winter/fall and a baseline survival rate of $s_{i,t}^j = 0.72$ is used (Singer et al., 1997). We note that any juveniles that



survive in the summer/spring transition to adults and thus are not part of the juvenile update function. Reproduction happens only in the summer/spring and survival of immature calves depends on the survival of the adult females. These assumptions lead to the full update function for juveniles

$$f_{i,t}^j = \begin{cases} 0.6r_i s_{i,t}^a N_{i,t}^a & t = \text{summer/fall}, \\ 0.72N_{i,t}^j & t = \text{winter/spring}. \end{cases}$$

The coefficient 0.6 represents the proportion of female offspring.

Next we consider pathway transitions, which requires identifying the proportional movement function, $p_{ij,t}$ and the pathway survival function, $s_{ij,t}$. Here we assume that adults and juveniles have identical transition probabilities and pathway survival rates. We also assume that an individual inherits its movement pathway in that a resident elk will likely remain a resident and a migratory elk will likely remain migratory. This means that the pathway transitions from the year-round habitat, p_{31} and p_{33} , during the summer/fall are dependent on the proportions of migrants using the pathway in the previous step:

$$Z_t^* = \frac{s_{33,t-1} p_{33,t-1} f_{3,t-1}^*}{N_{3,t}^*}.$$

For both adults and juveniles, we assign these probabilities using the functions

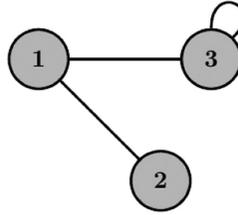
$$p_{31,t}^* = \begin{cases} 0 & t = \text{summer/fall}, \\ 1 - Z_t^* & t = \text{winter/spring}, \end{cases}$$

$$p_{33,t}^* = \begin{cases} 1 & t = \text{summer/fall}, \\ Z_t^* & t = \text{winter/spring}. \end{cases}$$

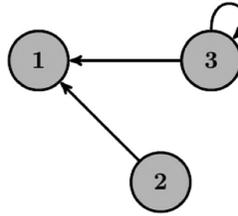
Here, we note that transition probabilities leaving a habitat sum to one, since every individual must choose at least one available pathway. All other pathway transitions in the network are assumed constant. We assume that all pathway survival probabilities are one, as we account for mortality of individuals from counts within the habitats, making $s_{ij,t}^* = 1$. Figure A3 shows the network and transition probabilities for the iterative model. Equations (7) are computationally simulated until an equilibrium solution is reached (see code provided in supplementary material). At equilibrium, we find that the total population values are $N_{\text{winter/spring}} = 4825$ and $N_{\text{summer/fall}} = 3917$.

A.3 Example of graph types and structure

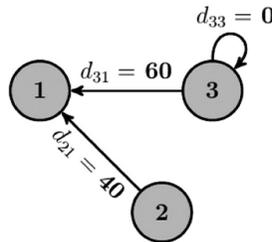
(a) Unweighted Undirected Graph



(b) Unweighted Directed Graph



(c) Weighted Directed Graph



Pathways weighted by distance between nodes

(d) Temporal Unweighted Directed Graph

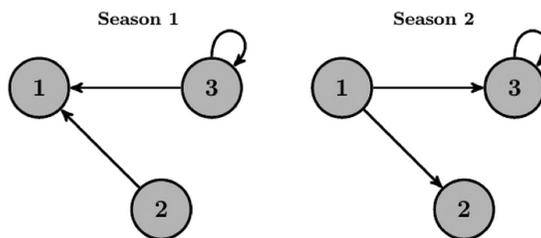


FIGURE A2 Example network structure for a variety of graph types. (a) Unweighted undirected graph, note no direction is assigned to pathways. (b) Unweighted directed graph, pathways now have a direction but remain unweighted. (c) Weighted directed graph, pathways have both a direction and a weight, here assumed to be pathway distances between habitats. (d) Temporal unweighted directed graph, seasons have different directions for the paths and graph measures take into account the sequential seasons when considering pathway availability

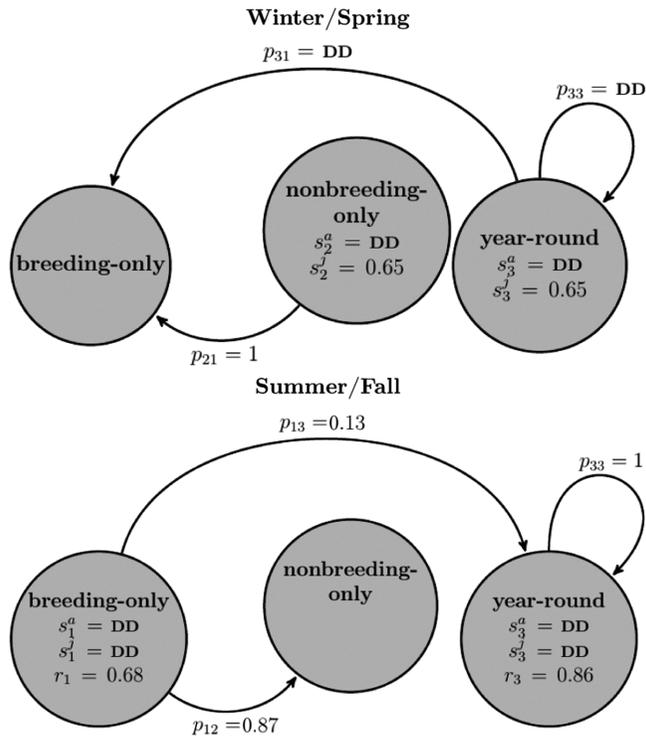


FIGURE A3 Network structure and density dependence for the demographic-based iterative network model. Survival rates along pathways are all assumed to be one. Here *DD* denotes a value that is density-dependent

A.4 Summary of case study results

A.4.1 Habitat-specific comparisons

A.4.2 Pathway-specific comparisons



TABLE A4 Habitat-specific comparisons

	Breeding-Only Habitat	Nonbreeding-Only Habitat	Year-Round Habitat
Graph-based metrics	Results indicate that the year-round habitat is most important to the overall population while the breeding-only habitat is most important for providing a central hub for migration.	Results indicate that the year-round habitat is most important to the overall population while the breeding-only habitat is most important for providing a central hub for migration.	Results indicate that the year-round habitat is most important to the overall population while the breeding-only habitat is most important for providing a central hub for migration.
	Highest betweenness.	Generally lower measures of degree (in/out) and betweenness imply lower importance.	Highest degree in undirected case.
	Ties year-round habitat in measures of in/out degree in the directed case.	Ties year-round habitat in measures of in/out degree in the directed case.	Ties breeding-only habitat in measures of in/out degree in the directed case.
Occupancy-based metrics	Results are limited—metapopulation assumptions are weak for this model.	Removal decreases persistence probability in the breeding-only.	During nonbreeding season has the highest occupancy probability.
	Removal causes habitat isolation.		Has the largest impact on the metapopulation persistence capacity.
			Has the highest relative value and largest contribution to metapopulation size.
Demographic-based metrics	Results indicate that the year-round habitat is most important to the overall population. It has the highest per capita contribution and perturbations to this habitat cause the largest changes in equilibrium population size even when density-dependent effects are considered.	Results indicate that the year-round habitat is most important to the overall population. It has the highest per capita contribution and perturbations to this habitat cause the largest changes in equilibrium population size even when density-dependent effects are considered.	Results indicate that the year-round habitat is most important to the overall population. It has the highest per capita contribution and perturbations to this habitat cause the largest changes in equilibrium population size even when density-dependent effects are considered.
	Perturbations have relatively small effects on the entire population.	Perturbations have relatively small effects on the entire population.	Has the highest C^0 values among habitats for both anniversary dates.
			Highest sensitivity of growth rate to changes in adult survival.
			Compared to other habitats, perturbations have greatest population-level effects.
			Habitat degradation has the larger effect than habitat enhancement.



TABLE A5 Pathway-specific comparisons

	Pathway 1-2 Connecting breeding-only and nonbreeding-only habitats	Pathway 1-3 Connecting breeding-only and year-round habitats	Pathway 3-3 Representing the resident population remaining in year-round habitat
Graph-based metrics	<p>Results indicate that both of the migratory pathways are important to the connectivity of the graph.</p> <p>If pathway 1-2 is removed the graph becomes disconnected with the nonbreeding-only habitat becoming unreachable.</p>	<p>Longest distance.</p> <p>If pathway 1-3 is removed the graph becomes disconnected with migrating populations no longer using the year-round habitat.</p>	<p>Shortest distance—nonmigratory.</p> <p>If pathway 3-3 is removed then the whole population must become migratory. Average migration pathway length increases.</p>
Occupancy-based metrics	<p>Results are limited—metapopulation assumptions are weak for this model. Complete removal of pathways would disconnect habitats making occupancy-based metrics incompatible.</p>	<p>Degradation (doubling length) causes a decrease in population persistence in the nonbreeding-only habitat.</p>	<p>Is robust to pathway perturbations along the migratory routes.</p>
Demographic-based metrics	<p>Results indicate that the pathway allowing for a resident population is most important to equilibrium population size and has the highest per capita value. The pathway between breeding-only and year-round habitats has the least effect on equilibrium population size.</p> <p>Reduction of 20% in survival along pathway causes a greater than 15% reduction in equilibrium population.</p>	<p>Reduction of 20% in survival along pathway has the least effect on equilibrium population (less than 2%).</p>	<p>Has the highest average flux and highest C^{oi} per capita contribution values.</p>
			<p>Reduction of 20% in survival causes a greater than 50% decrease in equilibrium population.</p>