EVALUATING HABITAT AS A SURROGATE FOR POPULATION VIABILITY USING A SPATIALLY EXPLICIT POPULATION MODEL

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Abstract. Because data for conservation planning are always limited, surrogates are often substituted for intractable measurements such as species richness or population viability. We examined the ability of habitat quality to act as a surrogate for population performance for both Red-shouldered Hawks (*Buteo lineatus*) and Northern Goshawks (*Accipiter gentilis*). We compared simple measures of habitat quality to estimates of population growth rates obtained from a spatially explicit model of population dynamics. We found that habitat quality was a relatively poor predictor of simulated population growth rates for several reasons. First, a relatively small proportion of the potential habitat for each species served as population sources in our simulations —15% for Red-shouldered Hawks and 2% for Goshawks. Second, when habitat quality correctly predicted demographic sources on the landscape, it consistently underestimated the contribution of these areas to the population. In areas where habitat quality correctly anticipated the presence of demographic sinks, we found no useful quantitative relationship between the two measures. Our simulation model captured the influence of habitat quality on the hawk populations, but it also incorporated interactions between dispersing individuals and landscape patterns. Thus, the discrepancies we observed likely reflected the influence of forest fragmentation and the spatial arrangement of forest patches on the populations. We conclude that simple measures of habitat quality will often be poor surrogates for population persistence, but that spatially explicit population models can help inform the development of better indices.

Keywords: eastern United States, habitat, landscape pattern, Mid-Atlantic, Northern Goshawk, PATCH, population dynamics, Red-shouldered Hawk, ReVA**,** spatially explicit population models

1. Introduction

Nature reserves are one of the most effective tools for conserving biodiversity. The systematic selection of reserves has predominantly been focused on maximizing the biodiversity (often species richness) protected within a reserve network (Margules et al., 1988). However, in addition to containing a diverse set of species, a successful reserve network must also be capable of supporting viable populations (Margules and Pressey, 2000). Although the need for estimating population viability is widely recognized, assessing the probability of persistence for populations of all species within a potential reserve network is a Herculean task that has yet to be attempted (Cabeza and Moilanen, 2001). Tractable approaches that have been implemented include addressing persistence by manipulating a single component of reserve design (e.g., reserve shape, size, or

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connectivity), or developing easily measured surrogates for species viability.

Habitat quality may be the most commonly used surrogate for population persistence at large spatial scales. However, because population dynamics are clearly influenced by habitat pattern, as well as type (Hansson et al., 1995), assessments based on simple measures of habitat quality that do not take the effects of landscape pattern into account are unlikely to provide accurate estimates of population persistence for many species. The spatial configuration of habitat has the potential to influence dispersal, survival, and reproduction (Hansson et al., 1995). The natures of these influences are in part determined by both species-area requirements and species dispersal abilities. For example, habitat pattern can affect habitat quality by determining the distribution of resources within the potential home range or territory of an organism. In an extreme case, a highly fragmented habitat may not contain adequate resources within the search radius of an individual. Habitat pattern can also affect population dynamics by limiting dispersal and hence the colonization of isolated habitats.

We used a spatially explicit population model (SEPM) (Dunning et al., 1995) to assess the ability of habitat quality to predict persistence in Red-shouldered Hawk (*Buteo lineatus*) and Northern Goshawk (*Accipiter gentilis*) populations. Our measure of habitat quality was a combined measure of both the type and amount of habitat within a potential territory. Thus, habitat quality took into account some aspects of landscape pattern. However, this static measure did not reflect the effects of dispersal and thus additional effects of landscape pattern. We compared maps of predicted habitat quality to maps of observed demographic sources and sinks (described below) resulting from computer simulations of hawk populations in the Mid-Atlantic Region of the United States. Our models allowed us to indirectly assess the influence of landscape pattern on population dynamics. Furthermore, by comparing predicted habitat quality and SEPM projections, we were able to evaluate habitat quality as a surrogate for population persistence. Any failure of habitat quality to predict population performance in our analyses presumably reflected the metric's inability to capture the effects of habitat pattern on dispersal within simulated hawk populations.

2. Methods

2.1 Study Site

We conducted our analyses in the eastern United States in an area encompassing the states of Pennsylvania, Maryland, Delaware, West Virginia, and Virginia, as well as portions of the surrounding states (Figure 1). The region is dominated by deciduous forests and agriculture. The Appalachian Mountains run northeast-southwest through the region, separating the Western Allegheny Plateau from the Piedmont Plains. These mountains are composed of a series of forested ridges and agricultural valleys. In addition, several areas of intense residential and commercial development are concentrated in the eastern portion of the region, centered on the cities of Baltimore, Washington DC, and Philadelphia.

2.2 Study Species

Red-shouldered Hawks and Northern Goshawks are forest dwelling species. The U.S. Department of Agriculture Forest Service lists the Goshawk as a “sensitive species” in the western U.S. and describes it as a potential “management indicator” due to its sensitivity to changes in habitat (Squires and Reynolds, 1997; Kennedy, 2003). Red-shouldered Hawk populations have experienced dramatic declines in the Midwest and eastern U.S. including the states of Pennsylvania and Maryland. In addition, Red-shouldered Hawks have been listed as endangered in New Jersey and threatened in New York. Both Red-shouldered Hawks and Northern Goshawks are large-bodied birds with relatively large area requirements. Collectively, these two species require a variety of forest types to persist, and as such they may function as good indicators of viability for a broad array of forest faunal communities.

The Goshawk, at 630–1,360 g, is the larger of the two species and it defends territories of approximately 170 ha (Kennedy et al., 1994). Goshawks inhabit coniferous, mixed, and deciduous forests in the eastern U.S. Although Pennsylvania partly marks the southern extent of their range in the eastern U.S., they occur in the Appalachians south into Virginia and West Virginia. At roughly 550–700 g, Red-shouldered Hawks generally defend territories ranging from 30 ha to at least 200 ha (Crocoll, 1994; Dykstra et al., 2001). These birds also inhabit a broad range of forest types. In addition to coniferous, deciduous, and mixed forests, they also tend to inhabit wooded wetlands or areas with access to small wetlands

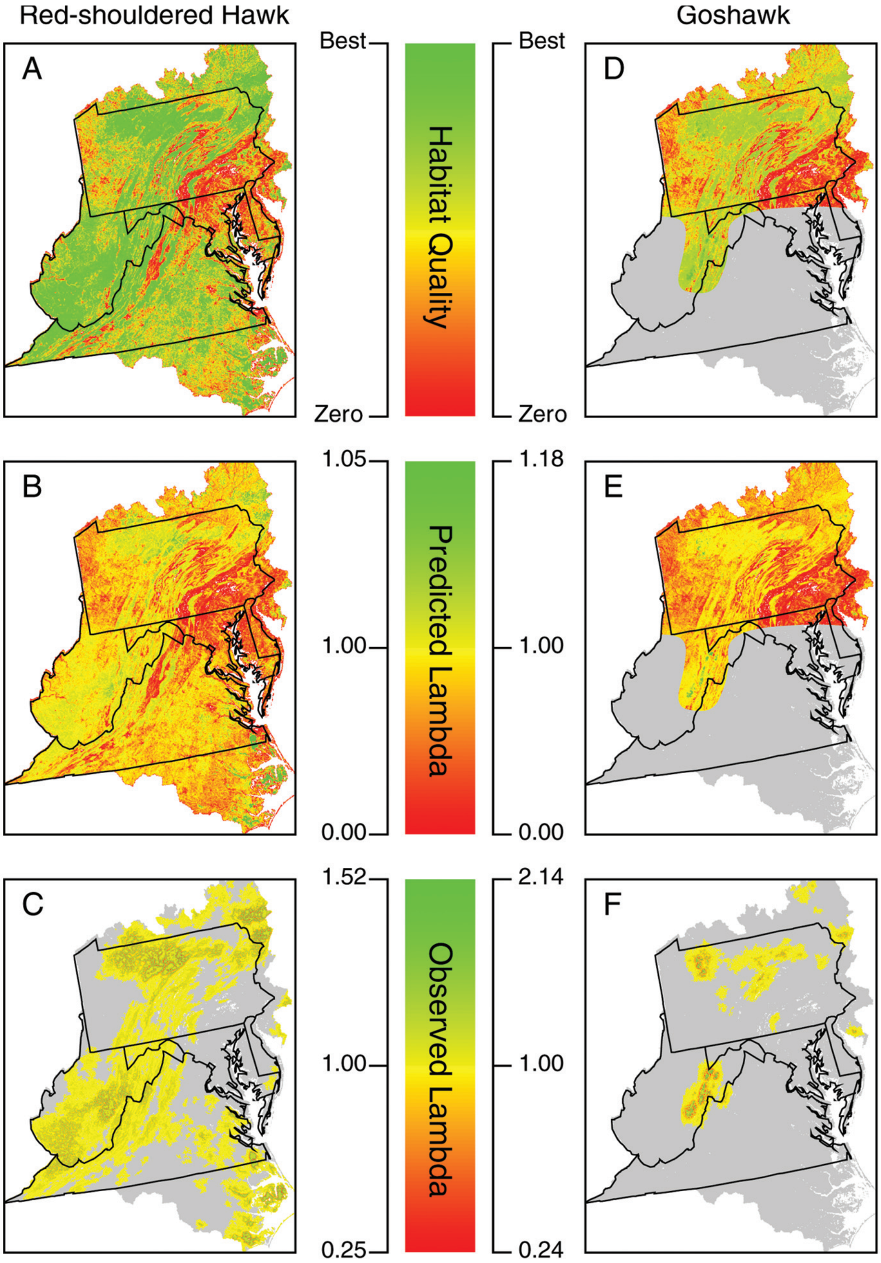

Figure 1. Maps showing the habitat quality in each PATCH model hexagon (A, D), the hexagon's predicted lambda values (B, E), and their observed lambda values (C, F). Maps A, B, and C display results for the Red-shouldered Hawk. Maps D, E, and F, display results for the Goshawk. The colored areas in D and E represent the extent of the Goshawk's geographic range within the region.

(Crocoll, 1994). A few populations of Red-shouldered Hawks have been found nesting in residential areas with low to moderate densities of houses (Dykstra et al., 2000; Dykstra et al., 2001). However, the selection of urban habitats does not appear to be consistent throughout the Red-shouldered Hawk's range, and the different habitat preferences and other observed behaviors of the forest vs. suburban birds have led some to suggest that they are potentially two types of birds, a wild type and a suburban type (C. Dykstra, personal communication). Assuming this distinction is valid, we modeled only the "wild-type" and thus did not consider residential areas as potential habitat.

2.3 Model Design, Parameterization, and Calibration

We used PATCH (Program to Assist in Tracking Critical Habitat) (Schumaker, 1998) to model population dynamics of both hawk species. PATCH is a stochastic females-only model that generates simulations driven by spatial geographic information systems (GIS) data, species-habitat preferences and territory sizes, estimates of dispersal frequency and distance, and estimated survival and fecundity values in the form of population projection matrices (Leslie, 1945; Lefkovitch, 1965; Caswell, 1989; Gotelli, 1995). The model produces measures of population size, habitat occupancy, movement patterns, and estimates of the importance of each territory-sized parcel of habitat for the modeled population.

The first step in running a PATCH simulation involves dividing a landscape into territory-sized units specific to the species of interest. This is accomplished by sampling the GIS data into a grid of hexagonal cells for which the hexagon size is set to the average size of an individual territory. Each hexagon then receives a score equal to the arithmetic average of the species-habitat preferences associated with each of the data pixels it contains. All hexagons with non-zero scores have the potential to function as breeding sites. Each model year begins with simultaneous survival and breeding events (emulating matrix multiplication), followed by the potential movements of adult animals (adult breeders typically remain in good breeding habitats), the mandatory dispersal of the juveniles, and finally a population census. This cycle of events is repeated for each year of a simulation.

Survival and reproductive rates are supplied to PATCH as a population projection matrix. The user must also associate this matrix with a specific hexagon score and select interpolation functions that allow PATCH to assign new matrices to hexagons with different scores. Typically, these interpolation functions ensure that hexagons with higher scores are assigned better matrices (larger survival and reproductive rates) and those with lower scores receive poorer matrices. We used a linear interpolation function to relate fecundity to habitat quality, but specified that the relationship between habitat and survival was mildly convex. Thus, as habitat quality increased, survival values reached their maximum more quickly than fecundities. The survival and reproductive rates actually experienced by an individual changed as it moved from hexagon to hexagon. We fit the interpolation function as part of the calibration process described below. Based on its projection matrix, a lambda-value (λ) can be calculated for each hexagon. Lambda, a matrix's dominant eigenvalue (Caswell, 1989; Gotelli, 1995), determines whether a site can be expected to function as a demographic sink ($\lambda < 1.0$) or source ($\lambda > 1.0$) (Pulliam, 1988; Pulliam and Danielson, 1991).

Movement in PATCH is the process through which individuals locate and claim unoccupied breeding sites. Our model parameterization specified that adult animals would abandon territories that could be expected to behave as demographic sinks, and retain sites that functioned as sources. In contrast, juveniles always dispersed (unless adult mortality made their natal site available). Only one breeder could occupy a hexagon in a given year. All movement was modeled as a biased random walk in which individuals tended to gravitate towards areas of higher habitat quality. PATCH requires that a maximum dispersal distance be specified, but individuals are not required to move that distance in a given dispersal event. Instead, the selection of available breeding sites is influenced by habitat quality. The aggregate distribution of movement distances typically displays a relatively short mode and a long tail approaching the specified maximum value.

Before running the models for use in our analyses, we calibrated them by comparing the predicted distributions of the two species produced by the PATCH model to estimated distributions from the Breeding Bird Survey (BBS) (Sauer et al., 2003). We made adjustments to the interpolation function that related the population projection matrix values to the habitat types until the distributions predicted by PATCH resembled those predicted by BBS sampling. In the absence of data on regional population sizes, these comparisons provided adequate calibration criteria for the purpose of our analyses.

Having calibrated the models, our subsequent analyses focused principally on a comparison of individual hexagon scores, hexagon lambda values, and measures of immigration and emigration events tallied on a hexagon-by-hexagon basis. Over the period of a simulation, immigration was calculated as the sum of all movements into a hexagon, whereas emigration was calculated as the sum of all movements out of the hexagon. For example, an *emigration minus immigration* tally kept for a hexagon would increase by one if a hawk fledged from the site, would decrease by one if a hawk settled the site and died, and would remain unchanged if a hawk simply passed through the site. As described below, we compiled the immigration and emigration data only after the model had achieved steady-state.

For each hexagon in a territory map, we focused our attention on three specific model outputs: the hexagon scores, their "predicted" lambda values, and their "observed" lambda values. As described above, a hexagon's score is the arithmetic average of the numerical habitat quality values (derived from species habitat preferences) associated with each of the data pixels it contains. A hexagon's predicted lambda value indicates whether it should behave as a demographic source or sink. We measured each hexagon's observed lambda value using the relationship:

$$\text{observed lambda} = 1.0 + \left(\frac{\text{emigration} - \text{immigration}}{R \times N} \right) \qquad (1)$$

where emigration and immigration are per-hexagon tallies, R is the total number of replicate simulations conducted, N is the number of years (per replicate) for which emigration and immigration data were collected, and the addition of 1.0 simply shifts the metric's scale so that it coincides with the predicted lambda values. Generation of the observed lambda metric requires running a PATCH simulation, and it indicates whether a hexagon actually performed as a demographic sink or source in the experiment.

The hexagon scores functioned as our simplest predictor of habitat quality. These scores accounted for vegetation type and interactions between landscape pattern and species-area requirements, but did not take into account the effects of landscape pattern on dispersal. The predicted lambda metric served as a more complex static measure of performance that introduced information on species vital rates. Our dynamic measure of hexagon performance, the observed lambda value, resulted from running

PATCH simulations and thus reflected the effects of landscape pattern and dispersal on the population.

The habitat maps were derived from a 30-m resolution land-cover map compiled from the Multi Resolution Land Characterization Consortium's National Land-Cover Data (NLCD) (Vogelmann et al., 2001). We smoothed the data with a moving window and then aggregated the pixels to 90-m resolution to reduce some of the inaccuracies in the land-cover assignments. The final map contained sixteen land-cover classes. We assigned habitat quality values to the land-cover types based on species preferences reported in the literature (Crocoll, 1994; Squires and Reynolds, 1997). For the Red-shouldered Hawk, deciduous, coniferous, transitional, and mixed forests, as well as wooded wetlands were all considered to be potential breeding habitat. We ranked wooded wetlands and mixed forests slightly higher (values of 8) than the other classes (values of 7) on a scale of 0–8. For the Goshawk, we considered deciduous, coniferous and mixed forest to be habitat, ranking coniferous forest (a values of 3) slightly above the other two forest types (values of 2) on a scale of 0–3. All other vegetation types in the models received values of 0. The scores we selected are estimates but are based on the best data we could find. We limited our analyses for the Goshawk to the area of the region within the species' geographic range (Figure 1d and 1e). We set the hexagon size to 219 ha for both species. Because of a current constraint of the PATCH model, we were unable to more closely match the upper bound of the two estimated territory sizes.

We parameterized the simulation model with estimates of demographic rates and dispersal distances from the literature. Available data permitted the construction of a two stage-class Leslie matrix for the Red-shouldered Hawk (juveniles and adults) and a three stage-class matrix for the Goshawk (juveniles, sub-adults, and adults). For the Red-shouldered Hawk, we used a probability of juvenile survival of 0.41 and adult survival of 0.70. Red-shouldered Hawk juvenile fecundity was zero, and adult fecundity was set to 0.72 female offspring per female per year (Crocoll, 1994). For the Goshawk, we used a probability of 0.33 for juvenile survival, 0.68 for sub-adult survival, and 0.81 for adult survival (Squires and Reynolds, 1997). Juvenile fecundity was set to zero, sub-adult fecundity was estimated at 0.55 and adult fecundity at 1.15 (Reynolds et al., 1994). Dispersal distances are generally poorly known for most bird species. The few estimates of dispersal distances for Goshawks and Red-shouldered Hawks varied greatly by study and region (Squires and Reynolds, 1997; Jacobs and Jacobs, 2002). For inputs into PATCH, we used maximum dispersal distances of 75 km for Red-shouldered Hawks and 100 km for Goshawks, both of which reflected upper limits of dispersal estimates in the literature.

We initialized the PATCH model by filling all potential breeding sites (155,555 sites for the Red-shouldered Hawk, and 56,173 sites for the Goshawk) with hawks and running the models for 500 years. Comparisons of PATCH output maps for each species to maps of estimated abundance produced by the BBS indicated that our models adequately predicted the species' distributions. Thus, while we believe that these projections are reasonable, we are less concerned with the degree to which the simulated population sizes approximated real population sizes in the region because the aim of the study was not to assess population size, but rather to compare the distribution of potential habitat to the use of the landscape by simulated populations. We ran the models for 500 years and recorded results from year 400 through year 500. We used this lag period because it generally took at least 200 years for populations to reach a relatively stable size after adjusting to the initial conditions of the model. We performed 100 replicate runs for each species and used the mean of the results in our comparisons.

3. Results

Our principle results are represented by the six maps shown in Figure 1. These maps depict measures of each hawk territory's habitat quality (Figure 1a and 1d), its predicted lambda value (Figure 1b and 1e), and its observed lambda value (Figure 1c and 1f). The extent to which the three maps for each species differ illustrates the degree to which habitat quality failed to anticipate simulated population dynamics and the use of space. The maps of habitat quality revealed that a large area of the region contained territories that included habitat for the two species (401,422 km^2 for the Red-shouldered Hawk and 194,043 km^2 for the Goshawk) (Figure 1a and 1d). This potential habitat was distributed throughout the region for both species, but tended to be more concentrated in the west.

It is clear from Figure 1 that, for both species, the large quantity of available habitat does not guarantee an abundance of demographic source areas. For the Red-shouldered Hawk, 15% of the territories containing habitat had predicted lambda values exceeding 1.0. Likewise, for the

Goshawk, only 2% of the territories with habitat had predicted lambda values exceeding 1.0. The majority of the habitats were predicted to behave as population sinks, where on average mortality should exceed reproduction. For the Red-shouldered Hawk, even the best available habitats produced predicted lambda values just slightly exceeding 1.0. The maximum predicted lambda values for the Goshawk were considerably higher, but most of the landscape was of a lesser quality.

In general, the results of our simulation runs indicated that individuals of both species avoided the majority of the areas predicted to be demographic sinks—i.e., most of the red-shaded hexagons in the predicted lambda maps (Figure 1b and 1e) were unused (after the population reached a steady-state) and thus are represented in gray on the observed lambda maps (Figure 1c and 1f). Closer inspection reveals that the areas that were observed to be strong sinks were not necessarily predicted to be strong sinks. In contrast, many of the hexagons that were predicted to be sources (green areas in Figures 1b and 1e) were observed to be sources (green areas in Figures 1c and 1f).

A more quantitative analysis of these results supports the notion that habitat quality performed poorly as a predictor of per-hexagon observed lambda values (Figure 2). The curved lines in Figure 2 depict the relationships between habitat quality and predicted lambda, while the individual points display each territory's score and its observed lambda value. Observed lambda values frequently deviated from the predicted values because the mean occupancy rates for any given hexagon did not necessarily match the stage class distribution present in the population as a whole, which itself will likely differ from the steady-state stage class distribution that would be derived mathematically from the projection matrices. But understanding the details of such deviations is central to the development of useful surrogates for population viability. Figure 2 provides some initial insights into this process. For example, for territories that served as habitat sources, habitat quality under-predicted observed lambda. That is, most of the points in the upper right quadrants of the plots in Figure 2 fall above the curved lines.

In the case of the Goshawk, territories for which habitat quality correctly predicted demographic sources (upper right quadrant of the lower plot in Figure 2) showed a potentially bimodal positive relationship between habitat quality and observed lambda. In contrast, there was no clear relationship between habitat quality and observed lambda for the correctly predicted Red-shouldered Hawk demographic sources. For both species, territories that were correctly predicted to be population sinks (lower left quadrants of Figure 2) had a very different distribution. Most points in the lower left quadrants of the plots in Figure 2 are clustered close to the axes. Thus demographic sinks (both predicted and observed) with lower habitat quality appeared to have little negative impact on the populations. In contrast, territories predicted to be weak sinks were broadly distributed among a wide range of observed lambda values, and hence played a more complex role in the overall population dynamics. The latter statement applies more strongly to the Red-shouldered Hawk than for the Goshawk which potentially showed a positive relationship between overall habitat quality and observed lambda (Figure 2).

4. Discussion

Ecological processes are influenced by landscape patterns (Hansen and Urban, 1992; Schumaker, 1993; Lichstein et al., 2002). For example, habitat fragmentation can produce effects on population dynamics above and beyond those predicted solely by the corresponding habitat loss (Fahrig and Merriam, 1985; Saunders et al., 1991). Thus, as our results demonstrate, measures of habitat quality that do not take landscape pattern into account will likely be poor surrogates for population persistence for some species (Schumaker et al., in press).

One of the ways that landscape pattern influences population dynamics is through effects on dispersal behavior (Cooper et al., 2002). The under-prediction of observed lambda values by habitat quality in our analyses likely reflects the spatial aggregation of habitat. Habitat patches that are clustered are more likely to be encountered than are highly isolated patches (MacArthur and Wilson, 1967). When habitat patches that function as population sources are aggregated, they will tend to be occupied frequently and consequently produce more offspring than isolated source patches that receive dispersers less frequently.

The spatial aggregation of habitat patches may also explain the relationship we found between habitat quality and observed lambda in correctly predicted population sinks (lower left quadrants of Figure 2). The clustering of territories close to the axes in Figure 2 indicates that patches with extremely poor habitat quality likely received few dispersers and thus only appeared to be weak population sinks. Thus, it is likely that these areas with extremely poor habitats were isolated from the majority of the source habitats. In contrast, areas with marginally poor habitat (those

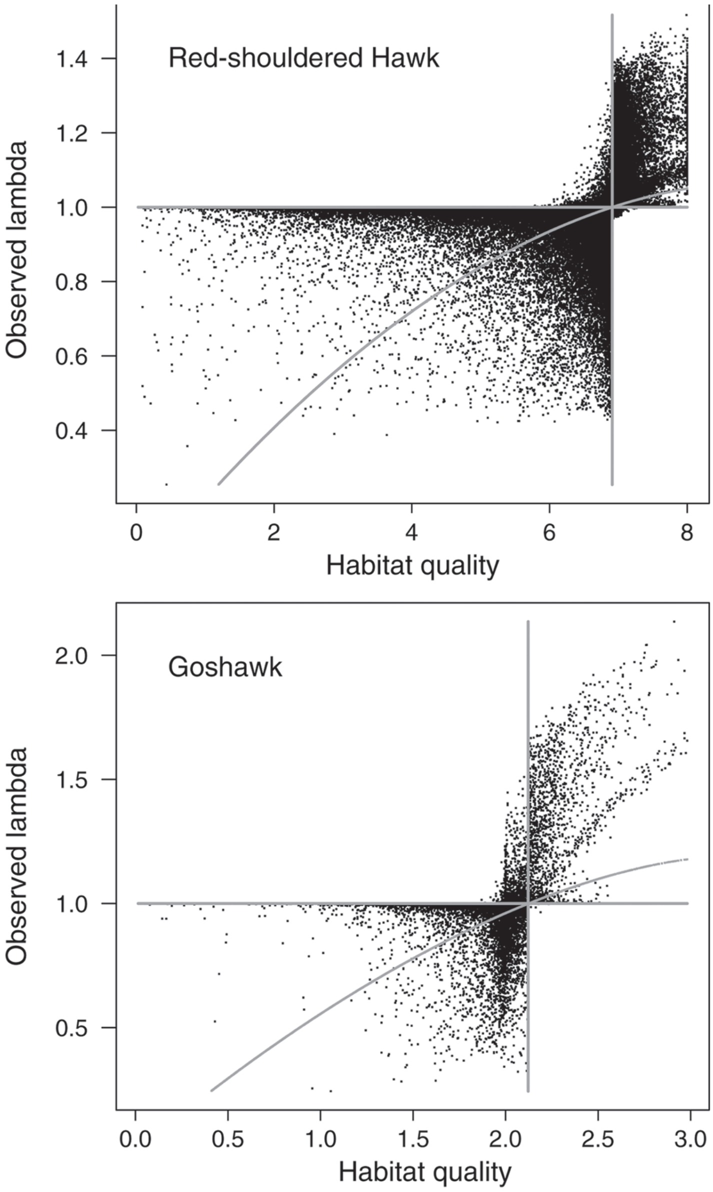

Figure 2. The relationship between habitat quality and observed lambda values for territories of Red-shouldered Hawks and Northern Goshawks in the Mid-Atlantic Region of the United States. The horizontal and vertical gray lines indicate observed lambda values of one, and the quality of habitat that equated to predicted lambdas of one, respectively. The curved lines depict the predicted lambda values as a function of habitat.

territories close to the vertical gray lines in Figure 2) were potentially more evenly dispersed among source and sink patches. Those that were closer to aggregations of source habitat received more dispersers and were observed to be stronger sinks whereas those that were more isolated from population sources received few dispersers and served as weak sinks.

Assessing population viability is a key aspect of both conservation planning efforts and regional environmental assessments. The U.S. Environmental Protection Agency's Regional Vulnerability Assessment (ReVA) program is designed to integrate information about environmental condition, resource availability, biodiversity, and potential stressors to both human and natural systems (Bradley and Smith, 2004). Assessing simple measures of habitat quality provides an estimate of which species potentially occupy a given site. By incorporating ecologically meaningful measures of landscape pattern derived from spatially explicit population analyses, regional assessments such as ReVA can provide an estimate of whether populations of a given species would be able to persist at a given site. In addition, regional, spatially explicit population viability analyses like those conducted here can provide a means of prioritizing areas for restoration, conservation, or development based in part on their contribution to population or metapopulation dynamics.

Because species respond to landscape patterns in different ways, building estimates of population viability into regional environmental assessments and conservation planning tools is a daunting task (Norton and Lord, 1990; Opdam et al., 1993). There are, however, at least two promising approaches to facilitate such an integration. First, the development of meaningful indices based on general population responses to landscape pattern will allow planners to predict the persistence of populations over large areas with minimal effort. Spatially explicit population models can play an important role in investigating how meaningful and how general these indices are likely to be (Schumaker, 1993; Vos et al., 2001). Second, reserve selection and conservation planning can integrate population persistence estimates for a small set of focal species of particular interest or whose habitat requirements are assumed to be representative of the wildlife in the region (Carroll et al., 2003). We conclude that simple measures of habitat quality will not always provide adequate surrogates for population persistence. However, spatially explicit population models can aid in the development of methods for incorporating more informed estimates of population persistence into conservation planning approaches.

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