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Extension of landscape-based population viability models to ecoregional scales for conservation planning

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ABSTRACT

Landscape-based population models are potentially valuable tools in facilitating conservation planning and actions at large scales. However, such models have rarely been applied at ecoregional scales. We extended landscape-based population models to ecoregional scales for three species of concern in the Central Hardwoods Bird Conservation Region and compared model projections against long-term trend data from the North American Breeding Bird Survey. We used a spatially-explicit demographic model and structured the regional population into ecological subsections on the basis of habitat, landscape patterns, and demographic rates to assess species viability. Our model projections were within 2% of the Breeding Bird Survey trends over the last 40 years for each species. Wood thrush (*Hylocichla mustelina*) populations remained relatively stable over the simulation and worm-eating warbler (*Helmitheros vermivorus*) abundance increased throughout most of the time period until reaching carrying capacity. In contrast, the prairie warbler (*Dendroica discolor*) population steadily declined by 0.59% annually. The combination of habitat and demographic modeling allowed us to create models that address processes driving these populations at all scales, which is critical to understanding how regional populations respond to landscape processes such as habitat loss and fragmentation. Therefore, because it is spatially explicit and directly addresses population growth and viability, this approach provides a valuable foundation to planning conservation strategies, offering the ability to identify the most salient risks to viability and explore ways to address them.

1. Introduction

The ability of populations to sustain themselves in the face of global change and habitat fragmentation and loss depends on population processes that occur over large scales. As a result, avian conservation efforts increasingly target larger spatial scales (Boyd et al., 2008; Millspaugh and Thompson, 2009). Recognition that successful wildlife conservation and natural resources planning must consider more than just site-level management has led to collaboration across agency and ownership boundaries. The North American Bird Conservation Initiative plans and implements bird conservation in ecologically distinct Bird Conservation Regions (BCR) with similar bird communities, habitats, and resource management issues (US North American Bird Conservation Initiative Committee, 2000). Within each BCR federal, state, and local government agencies and non-government organizations form joint ventures that work to step down continental or national population goals to ecoregional scales and to implement conservation (Fitzgerald et al., 2009). Joint ventures use a conservation design approach to assess the current capability of landscapes to support species and to plan conservation actions to sustain species at desired levels (Fitzgerald et al., 2009; Will et al., 2005). Integral to this process is the development of landscape to regional-scale models to assess habitat availability, bird-species abundance, and population growth and viability under current and future conditions.

Landscape-scale population viability models are potentially valuable tools for conservation design because they integrate habitat- and demographic-modeling approaches at a relevant scale. Habitat suitability index (HSI) models can incorporate species' habitat requirements and landscape processes to assess habitat quality across a landscape (Dijak and Rittenhouse, 2009), or even BCRs (Tirpak et al., 2009a,b), but by themselves do not directly address abundance or growth. However, HSI models can identify suitability of habitat patches that can be used to spatially structure demographic models that project population growth (Akçakaya and Brook, 2009; Larson et al., 2004). Including environmental

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and demographic stochasticity in demographic models puts predictions in a probabilistic framework with which we can more realistically assess viability (Burgman et al., 1993; Lande, 2002). By implicitly considering risk, viability measures derived from these models are fundamental to making sound decisions when assessing and designing alternative management strategies (Millspaugh et al., 2009; Morris and Doak, 2002).

Landscape-based demographic models have rarely been applied at the scale of BCRs (but see Fitzgerald et al., 2009; Tirpak et al., 2009b). Estimating population growth at this scale requires models to consider large scale processes that are poorly understood. For example, source-sink dynamics are regarded as important drivers of populations (Faaborg et al., 2010a; Pulliam, 1988); however, we still lack complete understanding of these dynamics in regional populations (Faaborg et al., 2010b). Furthermore, integration of fine scale habitat data across extents as large as BCRs results in populations with spatial structures beyond the computational limits of many population modeling programs. Last, when developing models at the scale of BCRs, lack of comparable long-term datasets from similar scales has limited opportunities to verify that ecological processes are correctly and sufficiently embodied in models (i.e., do models behave in a realistic way) (Rykiel, 1996; Shifley et al., 2009), and validate the accuracy of their predictions against empirical observations (Beissinger, 2002). Therefore, an approach that can address important processes while avoiding these constraints is needed so that populations can be effectively modeled at ecoregional scales.

Our objective was to extend landscape-scale demographic models to an ecoregional scale for conservation planning. Implicit in this approach is our belief that models such as those developed here are useful for conservation even when based on imprecise parameters or assumptions about processes because they synthesize current knowledge in a transparent way, can be used to quantify uncertainty, and are required to assess viability at meaningful scales (Burgman and Possingham, 2000; Millspaugh et al., 2009). We developed and evaluated models for three priority species of breeding landbirds, wood thrush (*Hylocichla mustelina*), prairie warblers (*Dendroica discolor*), and worm-eating warblers (*Helmitheros vermivorus*), in the Central Hardwoods Bird Conservation Region (CHBCR). We selected the three species because of their priority in regional conservation and because they represent a variation in suitable habitats and life history strategies. We compared model projections to long-term trends from the North American Breeding Bird Survey (BBS) data to verify each model's results.

2. Study area

The CHBCR covers portions of 10 states that straddle the Mississippi River in the center of the conterminous United States (Fig. 1). Located between the 83 and 94 west longitudes and the 34 and 40 north latitudes this region is approximately 33-million ha in size. The entire area is dominated by oak (Quercus spp.)–hickory (Carya spp.) forests that provide habitat for many high-priority bird species (US North American Bird Conservation Initiative Committee, 2000). While much of the land that was forested historically remains so today—the region includes some of the most extensive forests in the middle of the continent—woodlands and other communities have been dramatically altered by wide-spread logging in the early part of the 20th century and fire suppression in subsequent decades (Fitzgerald et al., 2005). Glades, barrens, and extensive pine woodlands have largely converted to oak or oak-pine forests but are conservation priorities (US North American Bird Conservation Initiative Committee, 2000). Threats to the habitats of the region include agricultural conversion of floodplain habitats and urbanization.

Wood thrush, prairie warblers, and worm-eating warblers in the region are all regarded with conservation concern by Partners in Flight (Panjabi et al., 2005) or the US Fish and Wildlife Service (US Department of the Interior Fish and Wildlife Service, 2002). Declines in Midwestern populations of wood thrush and prairie warblers are linked to fragmenting landscapes (Robinson et al., 1995; Sauer et al., 2008) and loss of early-successional habitat (Nolan, 1978), respectively. As a result of the worm-eating warbler's area sensitivity when using forest interiors, Partners in Flight designates it as a management attention priority in the CHBCR (Panjabi et al., 2005).

3. Model development

We used a spatially-explicit demographic modeling approach (Beissinger et al., 2009) in which we treated ecological subsections as patches in our models. While these patches were not isolated patches of habitat in the typical metapopulation sense, they allowed for spatial structure based on ecologically relevant units while maintaining a reasonable number of patches (Fig. 1). Each patch represented a sub-population in the model and demographic parameters for that sub-population were derived from habitat attributes of the patch, using spatially-explicit suitability models. Key in this approach was summarizing cell level demographics in each patch to obtain patch level parameters for input into the demographic model (Fig. 2). The CHBCR is composed of 59 ecological subsections (Bailey et al., 1994) representing areas of similar landform and vegetation that occur in 145 distinct patches. We dropped 24 patches from consideration because of their small size (<1 ha), which was a result of intersecting the BCR boundaries with ecological subsection boundaries. The size of the remaining 121 patches ranged from 26.09 ha to >2.6 million ha (average patch size = 250 204.13 ha SD (399840.35).

3.1. Carrying capacity and initial abundances

We determined an initial abundance and carrying capacity (K) for a species in each patch using HSI models previously developed specifically for the CHBCR (Tirpak et al., 2009a,b). Tirpak et al. (2009a) developed the HSI models with knowledge from published studies and then verified and validated them with data from the BBS. The HSI models predict a value between 0 and 1 for each 30 × 30-m cell in the CHBCR where 0 represented non-habitat and 1 optimal habitat. Habitat suitability index values for each cell were based on the attributes of that cell which included landform, land cover, and forest successional stage and of the surrounding landscape such as patch size, interspersion and distance to edge (Tirpak et al., 2009b).

To calculate K of each patch (K_{patch})we first calculated K of each 30 × 30-m cell (K_{cell}) as the product of cell area (0.09 ha), bird density (pairs/ha) in optimal habitat, and the cell HSI value; we assumed bird density reached its maximum where HSI = 1 and declined linearly to zero pairs/ha where HSI = 0. We derived bird densities for optimal habitat from available literature (Appendix). To estimate K_{patch}, we used the Zonal Statistics in ArcGIS 9.3 to sum K_{cell} of each species across grid cells within each of 121 patches (Fig. 2). We calculated initial abundances as a percentage of K_{patch} based on current knowledge of the status of each species' population in relation to carrying capacity.

3.2. Stage-based matrix models

We used a Lefkovitch matrix model that included only females in two stages as

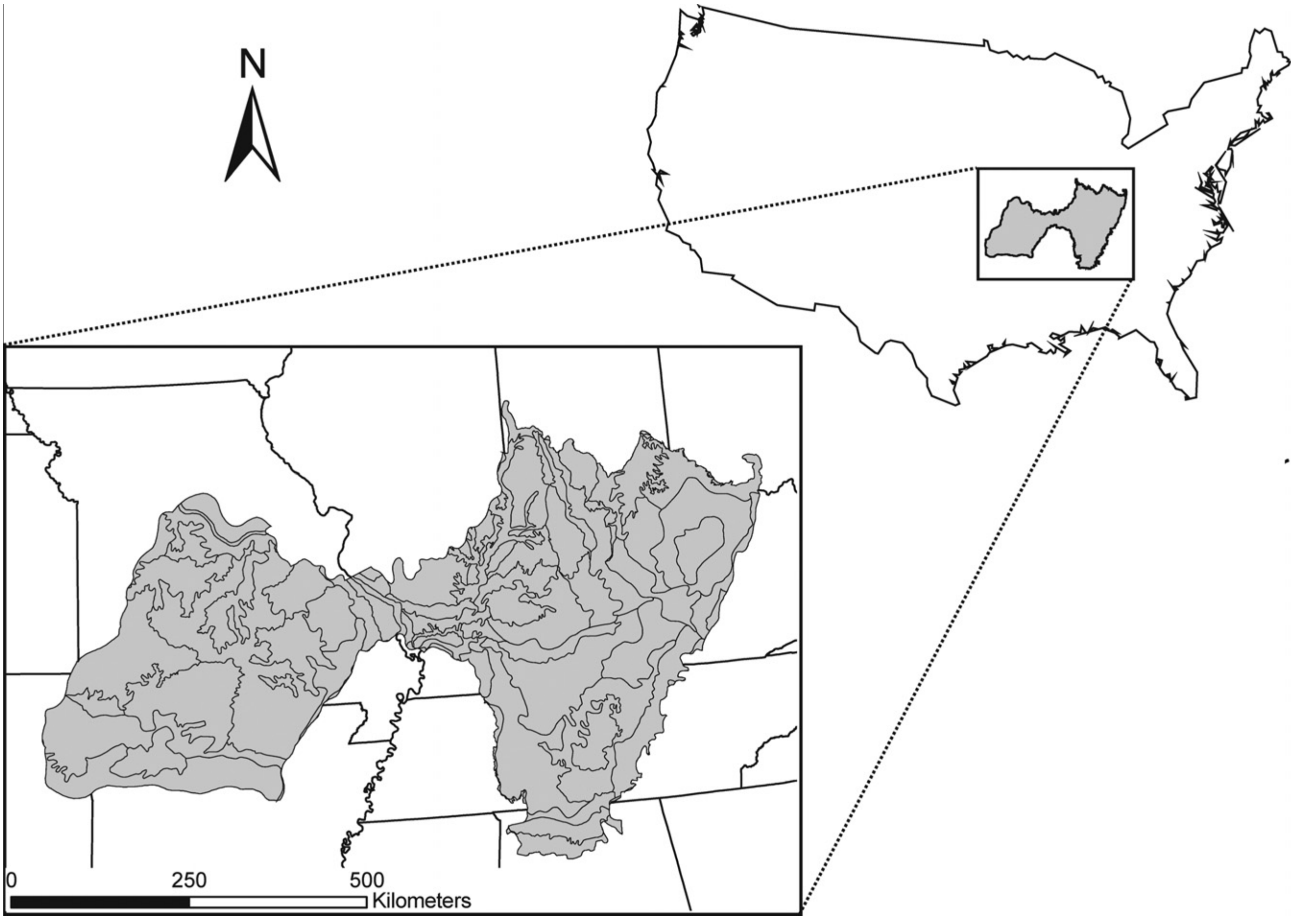

Fig. 1. Location of the Central Hardwoods Bird Conservation Region within the USA. Located between the 83 and 94 west longitudes and the 34 and 40 north latitudes, this 33 million ha region includes some of the most extensive forests in the middle of the continent. This region comprises 59 ecological subsection that occur in 145 separate patches.

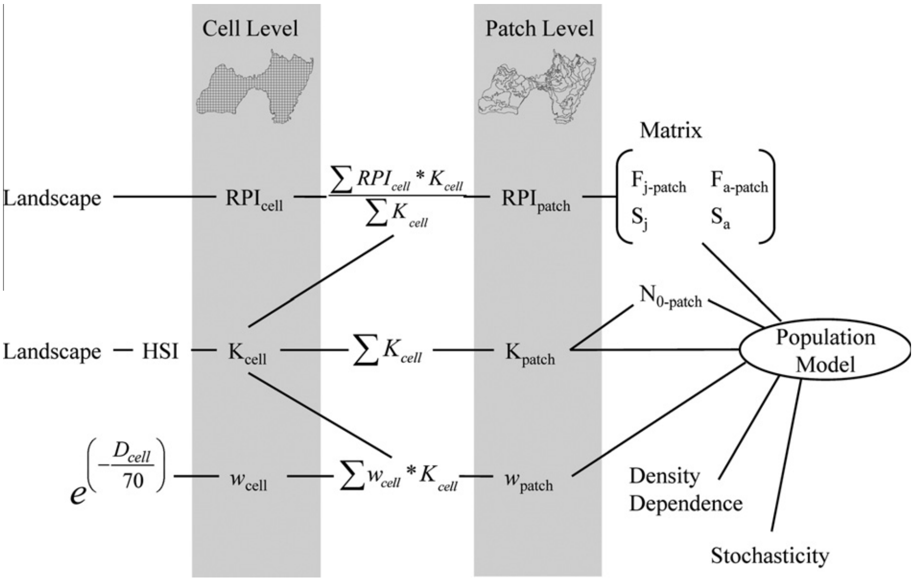

Fig. 2. Flowchart of steps involved in the parameterization of population viability models for 3 species of breeding birds in the Central Hardwoods Bird Conservation Region, USA. Inputs into the model include patch-level demographic rates such as carrying capacities (K), initial abundances (N_0), survival rates for adults (S_a) and juveniles (S_j), and fecundity rates for adults (F_a) and juveniles (F_j). Patch-level demographics, in addition to relative rates of dispersal among patches (w) were based on cell-level patterns in the relative productivity index (RPI), K, and the distance between cells (D).

$$\begin{bmatrix} f_j & f_a \\ s_j & s_a \end{bmatrix},$$

where f_j and f_a are stage-specific fecundity values of juveniles (young of the year) and adults ($\geqslant$1-year-old), respectively, and s_j and s_a are the annual survival rates for juveniles and adults. We assumed annual time steps in which "birth-pulse" breeding occurs followed by a post-breeding census (Caswell, 2001). Though the model outputs the number of adults and juveniles at each time step, we report only the adult population size as a chief model output to simulate survey methods for breeding birds (Akçakaya, 2002; Larson et al., 2004). The stage-specific fecundity values are a function of maternity (number of female fledglings per female per season) and survival (Caswell, 2001). Because our models consider only two stages and assume a post-birth census, we calculated fecundity rates in each species' matrix by multiplying estimates of maternity derived from the literature by juvenile and adult survival rates. Because productivity of migratory songbirds in the Midwestern US is related to landscape level forest fragmentation and edge effects (Donovan et al., 1997; Hoover et al., 1995; Robinson et al., 1995) we modified the matrix to incorporate patch-specific maternity values:

$$\begin{bmatrix} m_{ai} \cdot s_j & m_{ai} \cdot s_a \\ s_j & s_a \end{bmatrix},$$

where m_{ai} is the maternity of an adult female breeding in patch i in the CHBCR. Because we assumed juveniles from the previous year breed as adults (Noon and Sauer, 1992), we used adult maternity to estimate fecundity for both stages.We calculated patch-specific maternities using a relative productivity index (RPI) developed by Farrand-Jones, Tirpak, Thompson, Twedt (personal communication). We calculated RPI for each 30 × 30-m cell (RPI_{cell}) as:

$$\text{RPI}_{\text{cell}} = \frac{2}{3}[1.017(1 - e^{(-0.041c)})] + \frac{1}{3}\left[\frac{1.012}{1.0 + (102.151e^{(-0.184p)})}\right]$$

where c = the percent of forest cover in a 10-km radius and p = the number of forest cells in a 7 × 7 cell window (Fig. 3). The terms in brackets address landscape-scale processes that act on reproduction. Each term results in a number between 0 and 1, which are then weighted before averaging (Fig. 2). The quantity on the left side of the equation represents 2/3 of the RPI and is a landcover (amount) effect based on average nesting success of the species studied by Robinson et al. (1995). The quantity on the right side of the equation is 1/3 of the RPI and represents a fragmentation effect based on the amount of forest/non-forest edge nearby (Fig. 3). While this function is not validated, it represents the fragmentation paradigm that reproductive success is lower in fragmented landscapes and proximate to edge, and that landscape scale fragmentation effects have a greater effect than local edge effects (Chalfoun et al., 2002; Donovan et al., 1997; Robinson et al., 1995; Stephens et al., 2004; Thompson et al., 2002).

We calculated the RPI for each patch ($\text{RPI}_{\text{patch}}$) by averaging RPI_{cell} values across all cells in each patch weighted by the density of pairs they contain, because we assumed that the effect relative productivity of an area has on the entire patch is conditional on the proportion of breeding that occurs in that area (Fig. 2). Due to their proportional nature (i.e., a patch with a value of 0.9 implies that maternity is 90% of what would be expected given optimal habitat) $\text{RPI}_{\text{patch}}$ values can be incorporated into maternity estimates if the maximum possible productivity for each species is known. Therefore we reviewed the literature to identify ranges of maternities or other reproductive rates from studies where maximum productivity could reasonably be assumed because the study occurred in contiguous forest habitat with little edge (Appendix).

3.3. Dispersal

Although the CHBCR populations of the three species considered here do not resemble classic metapopulations because of the lack of isolation (Harrison and Taylor, 1997; With, 2004), the size of the landscape necessitates the assumption that not all areas are available to individuals at any point. Thus, we modeled dispersal as a function of distance. To model dispersal we combined assumptions about the proportion of the population in each patch that dispersed with relative estimates of the cell-based movements of those dispersers to the surrounding landscape. To begin, we assumed dispersal in these birds was not a function of density dependence, but stage related behavior [e.g., juveniles are more likely to disperse than adults (Greenwood and Harvey, 1982)]. We assumed that dispersal rates are stage specific with juveniles dispersing at higher rates (90%) than adults [10%, 10%, and 20% for wood thrush, worm-eating warblers, and prairie warblers, respectively (Hanners and Patton, 1998; Nolan et al., 1999; Roth et al., 1996)]. We multiplied each patch's stage abundances by their respective dispersal rates to identify the proportion of that patch's population dispersing each year.

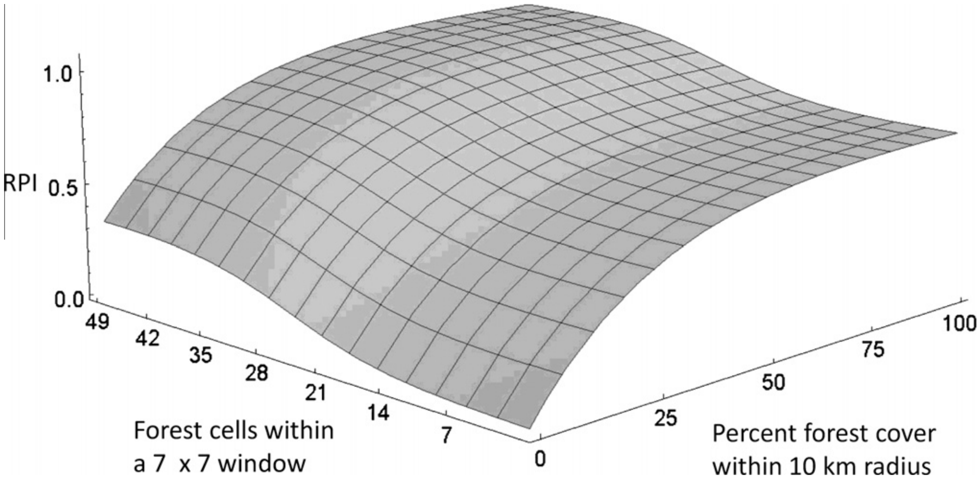

Fig. 3. Influence of landcover and edge, resulting from fragmentation, on the relative productivity of breeding birds throughout the Central Hardwoods Bird Conservation Region. Relative Productivity Index (RPI) values for each cell are based on the percent of forest cover within 10 km and the amount of nearby edge, characterized by the number of forest cells within a surrounding 7 × 7 window. Values were used to set patch-specific maternities.

We modeled dispersal movements for all three species at a 900 m × 900 m cell scale based on the assumption that movements of dispersers occurred at a scale smaller than patches, thus allowing individuals to disperse and yet, potentially remain within the same patch. We estimated the rate of movement from each cell in the CHBCR landscape to all other cells as a function of distances to and carrying capacities of destination cells. Dispersal to surrounding cells decreased with distance according to a negative exponential function (Akcakaya, 2002):

$$\begin{aligned} w &= e^{(-D/b)}, && \text{if } D \leqslant D_{max} \\ 0, & && \text{if } D > D_{max} \end{aligned}$$

where w is the rate of dispersal, b is a constant representing the average dispersal range observed for the species, D is the distance between cells, and D_{max} is the maximum dispersal distance allowed. We set $b = 70$ km based on the distance at which Tittler et al. (2006) observed one-year time-lagged correlations between pairs of populations, suggesting wood thrush frequently disperse over such a range. We arbitrarily assumed D_{max} to be twice that of b to permit some larger dispersal movements that seemed reasonable for a migratory songbird. Those values were then weighted by K_{cell} for each species to account for the quality and availability of habitat in the cell. Because patches at K could still receive immigrants, this weighting added a density (or K) dependent component to dispersal which made models more realistic. Lastly, dispersal rates were summarized by patches and standardized to obtain relative rates of dispersal from each patch to surrounding patches (Fig. 2).

3.4. Density dependence and stochasticity

We used the metapopulation program within RAMAS GIS 4.0 (Akçakaya, 2002) to model density dependence and stochasticity in our populations. We assumed ceiling-type density dependence, which is appropriate for territorial songbirds whose breeding is relatively unaffected by density at abundances below K (Akçakaya, 2002; but see Sherry and Holmes, 1995). However, when abundances of territories increased above K, they were reduced to K.

We included both demographic and environmental stochasticity in each model. We included demographic stochasticity by drawing the number of survivors and the number of young produced in each stage each year from binomial and Poisson distributions, respectively (Akçakaya, 2002). We incorporated environmental stochasticity by selecting, annually, survival and fecundity rates from a lognormal distribution defined by a mean, which was the matrix value for the given rate, and a standard deviation, which we based on the amount of temporal variation empirically observed in survival or reproduction or what could be expected based on differences in site fidelity between stages (Table 1, also see Appendix). We assumed that patterns in survival and fecundity rates were correlated among patches at a rate:

$$\rho_{ij} = e^{\left(\frac{-D_{ij}}{140}\right)}$$

based on the distance between them (D_{ij}), but that these rates were not correlated with each other or K within a patch (Akçakaya, 2002). We modeled populations over a 100 year period using 1000 simulations. We chose to not incorporate catastrophes (see Lande, 2002) into model projections due to the lack of sufficient knowledge to accurately quantify the effects of large Midwestern catastrophes on migrant songbird vital rates (Rotenberry et al., 1995).

Table 1
Parameters used to develop landscape population viability models for three species of breeding birds in the Central Hardwoods Bird Conservation Region in the Midwestern United States.

Parameter	Wood thrush	Worm-eating warbler	Prairie warbler
Carrying capacity (pairs/ha) @ HSI = 1	0.50	0.86	1.00
Initial abundance (% of carrying capacity)	0.12	0.20	0.50
Maximum maternity (fem/fem/year)	1.49	1.58	1.42
Adult survival	0.61	0.60	0.60
Juvenile survival	0.29	0.30	0.31
Environmental stochasticity (CV)			
Maternity	0.27	0.27	0.27
Juvenile survival	0.25	0.15	0.15
Adult survival	0.10	0.10	0.10
Demographic stochasticity	Yes	Yes	Yes
Density dependence	Ceiling type	Ceiling type	Ceiling type
Juvenile dispersal rate	90%	90%	90%
Adult dispersal rate	10%	10%	20%

4. Model evaluation

4.1. Verification

We verified each model's projection of population growth by comparing it to empirical trends of growth estimated from the BBS for the CHBCR for 1966–2007 (Sauer et al., 2008). The BBS dataset was the best available data for verification because of its large geographic and temporal scale and it was largely independent of our modeling efforts (i.e., only the mean dispersal distance was based on BBS data; demographic and habitat inputs to the models were not derived from BBS data). We did not consider such comparisons validation because the period of BBS data did not match the period of our models projections (i.e., we were not predicting growth from 1966–2007). However, the BBS trends were relevant to verify if our models captured the important processes governing these populations. Given the lack of substantial changes (<15%) in the amount of total forest cover in the CHBCR during 1966–2007 (USDA, 2010), we expected model projected trends to resemble those reported by BBS. However, because specific forest components or conditions (i.e., succession stages) are important to these birds, any specific changes to them could cause discrepancies between the two estimates.

4.2. Sensitivity

We used both analytical and simulation-based methods to analyze the sensitivity of models to various parameters and assumptions. Given that population growth for each species varies among patches, we calculated elasticities for vital rates under deterministic conditions (Caswell, 2001; Mills and Lindberg, 2002) to evaluate the relative importance of survival and fecundity rates in population growth across the landscape. We also conducted conventional sensitivity analyses to explore the impacts that management targeting habitat suitability for occupancy or productivity can have on population growth relative to basic life history traits. Parameters included adult and juvenile survival rates, maternity rates, K, initial abundance, relative productivity, and the CV in vital rates, all of which were changed by 10% in both directions. We also investigated each model's sensitivity to estimates of dispersal distance by changing the maximum and mean distances specified in the dispersal function to half- and twice that of the original estimates (e.g., $b_{\mathrm{reduced}} = 35$ km and $D_{\max(\mathrm{reduced})} =$ 70 km) and recalculating relative dispersal rates between patches. Sensitivity of viability results were evaluated by the change in the median abundance in year 100 and the median quasi-extinction threshold [abundance below which 50% of simulated populations fall during the 100 year simulation (Larson et al., 2004)].

5. Results

5.1. Deterministic results

We parameterized models for each species and used them to project populations deterministically and stochastically for the CHBCR. Estimates of K and deterministic growth, obtained from running models without stochasticity, dispersal and density dependence, varied across the landscape for each species. We estimated overall carrying capacities (K) at 2968120; 7 188065; and 305952 pairs for wood thrush, worm-eating warbler, and prairie warbler, respectively. Applying $\mathrm{RPI}_{\mathrm{patch}}$ to maternity resulted in a large range of patch fecundities and deterministic growth rates (λ_d) based on the patch-level stage matrices for each species (Fig. 4). Although the same RPI model was used for all 3 species, weighting the averages by K_{cell} caused relative productivity to differ between species on the basis of their abundance patterns within the patch. Deterministic growth rates ranged from <1 to >1 for all three species (Figs. 4 and 5). The maximum $\lambda_d = 1.04$, 1.07, 1.07 for wood thrush, worm-eating warblers, and prairie warblers, respectively, but on average λ_d was greatest for worm-eating warblers (Fig. 4). Largely due to habitat influences, only 38% of the patches that support breeding prairie warblers had growth rates of $\lambda_d > 1.00$ (Fig. 4c).

5.2. Stochastic results

Simulations with dispersal, stochasticity, and density dependence resulted in a narrower range of stochastic growth rates (λ_s) than when based on matrices alone (Fig. 4); nevertheless some patches had increasing populations and others decreasing populations (Fig. 6). Dispersal enabled persistence of some populations

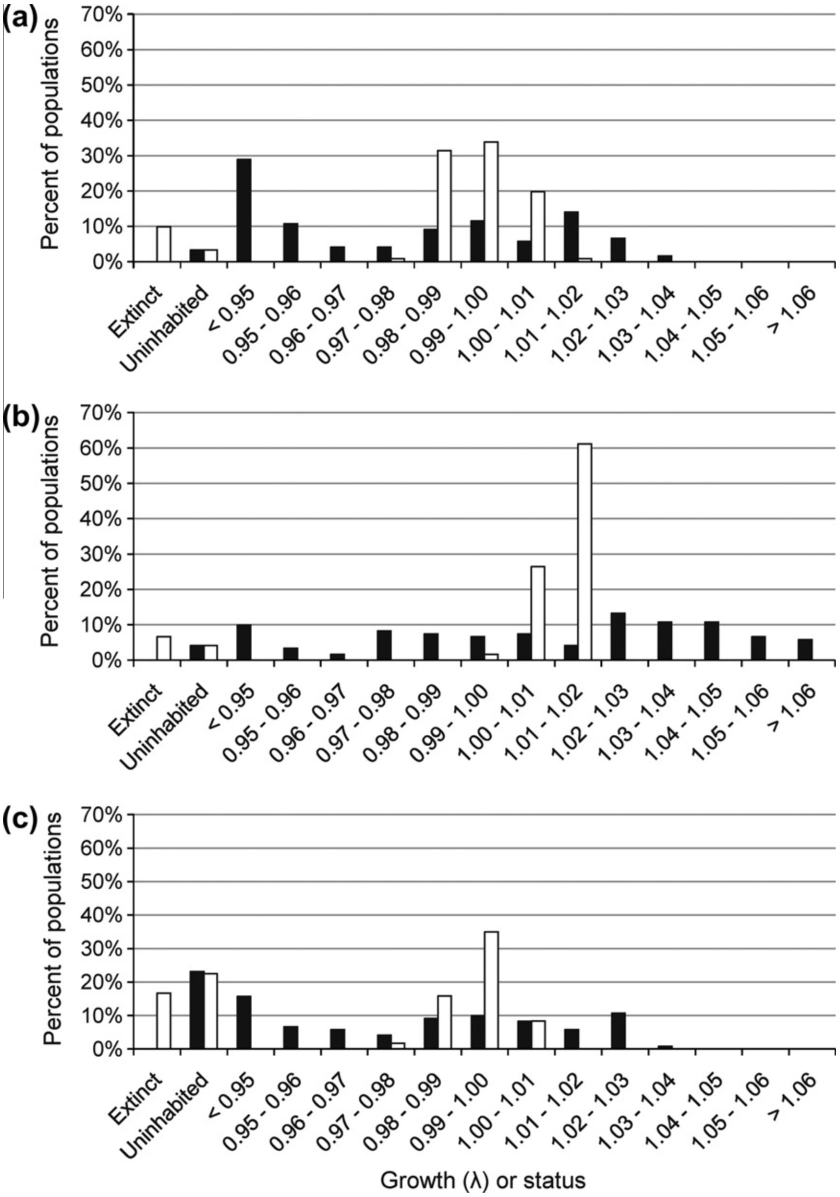

Fig. 4. Distribution of deterministic (does not include stochasticity, density dependence, and dispersal) (black bars) and stochastic (white bars) growth rates for populations of wood thrush (a), worm-eating warblers (b), and prairie warblers (c) in the Central Hardwoods Bird Conservation Region. The vertical axis indicates the percentage of populations/patches in the region having specific deterministic and stochastic growth.

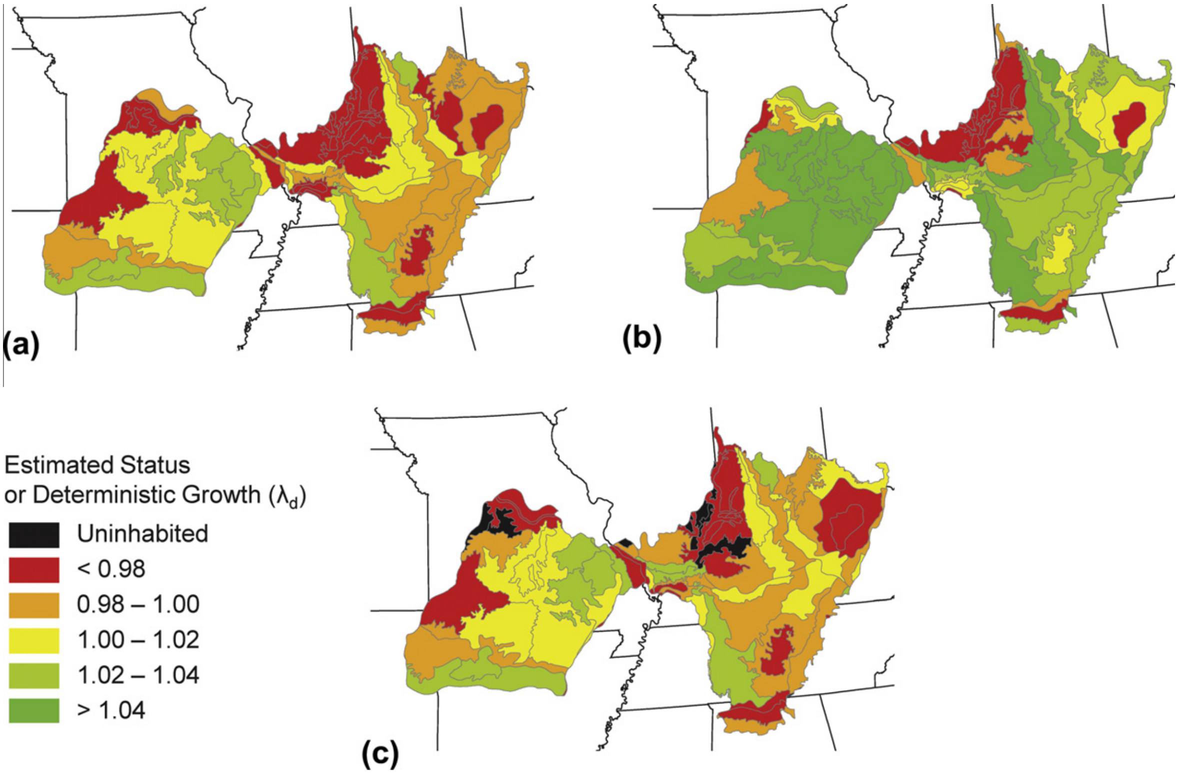

Fig. 5. Deterministic growth estimates (λ_d) of wood thrush (a), worm-eating warbler (b), and prairie warbler (c) populations within in individual patches in the Central Hardwoods Bird Conservation Region. Estimates of λ_d are based solely on patch-specific matrices and do not include stochasticity, density dependence, and dispersal.

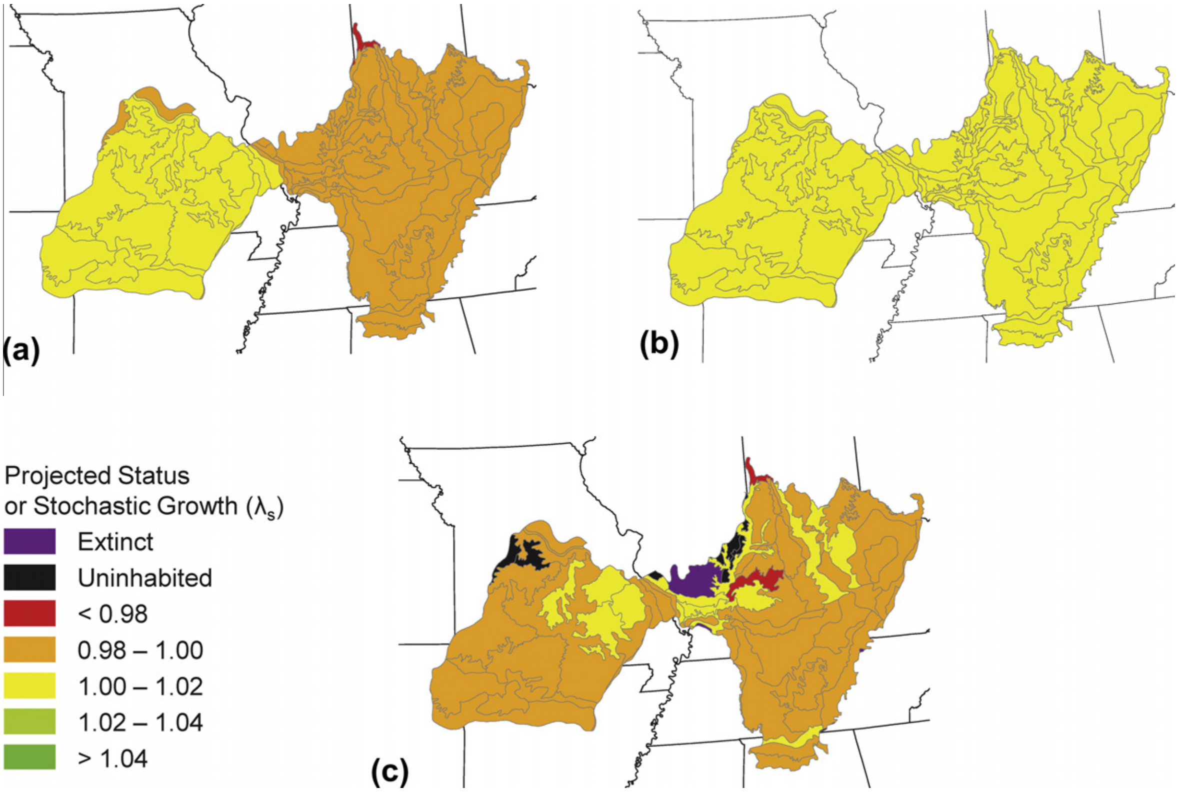

Fig. 6. Stochastic growth rates (λ_s) growth rates of wood thrush (a), worm-eating warbler (b), and prairie warbler (c) populations in patches throughout the Central Hardwoods Bird Conservation region from landscape population models. Estimates of λ_s are based on change in the median abundance of each patch after 1000–100 year simulations that considered stochasticity, density dependence, and dispersal among patches.

with $\lambda_d < 1$, thus the regional population consisted of sources and sinks, which together with density dependence, mediated some variation in λ_d. Furthermore, as is thought to occur in source-sink interactions, reduced reproduction and a lack of immigration into smaller populations ($K_{\text{patch}} < 25$ pairs) led to declines and eventually extinction (Fig. 6). Overall, these processes produced different population trajectories for the three species. There was a small annual decrease of 0.03% in the median abundance of wood thrush (Fig. 7a). Worm-eating warbler numbers initially increased 4% annually then stabilized just below K for an average 1.47% growth annually (Fig. 7b). The prairie warbler population declined 0.50% annually (Fig. 7c).

Population growth projections were similar to BBS trends for the last 40 years. The predicted annual decline in wood thrush and prairie warblers differed from BBS estimates by less than 1% and 2%, respectively (BBS estimates of growth: wood thrush = −0.7%, $P < 0.05$; prairie warbler = −2.5%, $P < 0.05$). Growth in the worm-eating warbler population estimated from the BBS was 1.9% ($P = 0.12$) compared to 1.47% for our modeled population. Furthermore, the gradual decrease in growth of the worm-eating warbler population we predicted is similar to the estimates from early (3.5% annual increase from 1966 to 1979, $P = 0.39$) and more recent time periods (1.3% annual increase from 1980 to 2007, $P = 0.35$) from the BBS.

Models were highly sensitive to life history traits, particularly survival. However, populations were also affected by habitat-influenced productivity and dispersal. Adult survival had the largest proportional impact on λ_d across all populations for each species, especially when relative productivity was low. However, elasticities of survival and fecundity rates on λ_d varied across the landscape and the relative sensitivity to survival versus fecundity decreased for patches with higher productivity (e.g., >80%) (Fig. 8). In general, we observed similar results between elasticities and the conventional sensitivity analyses in that viability estimates from our models were most sensitive to adult survival for each species (Table 2). Beyond adult survival, decreasing the relative productivity of a patch based on its habitat had similar or slightly greater effects on viability than either juvenile survival or maternity rates in all three species (Table 2). Carrying capacity had relatively small impacts except for worm-eating warblers, whose population was limited by K, in which case median quasi-extinction threshold was less affected than the abundance at the end of

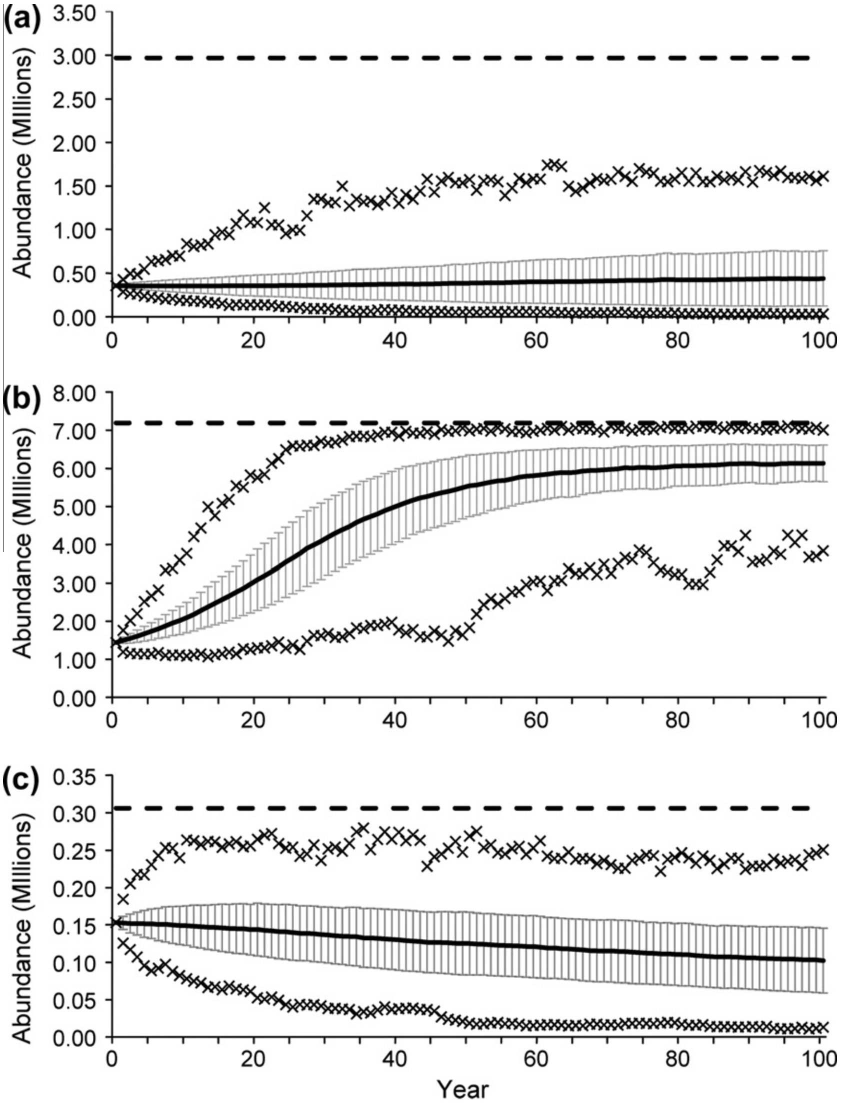

Fig. 7. Estimated carrying capacities (dotted lines) and projected abundances of wood thrush (a), worm-eating warblers (b), and prairie warblers (c) in the Central Hardwoods Bird Conservation Region. Solid lines are mean abundances ±1 SD and are bracketed by minimum and maximum values (x) observed over 1000 simulations. Note: actual growth and trend estimates are based on median abundance rather than mean abundance therefore, trajectories of graphs may not accurately convey population trends.

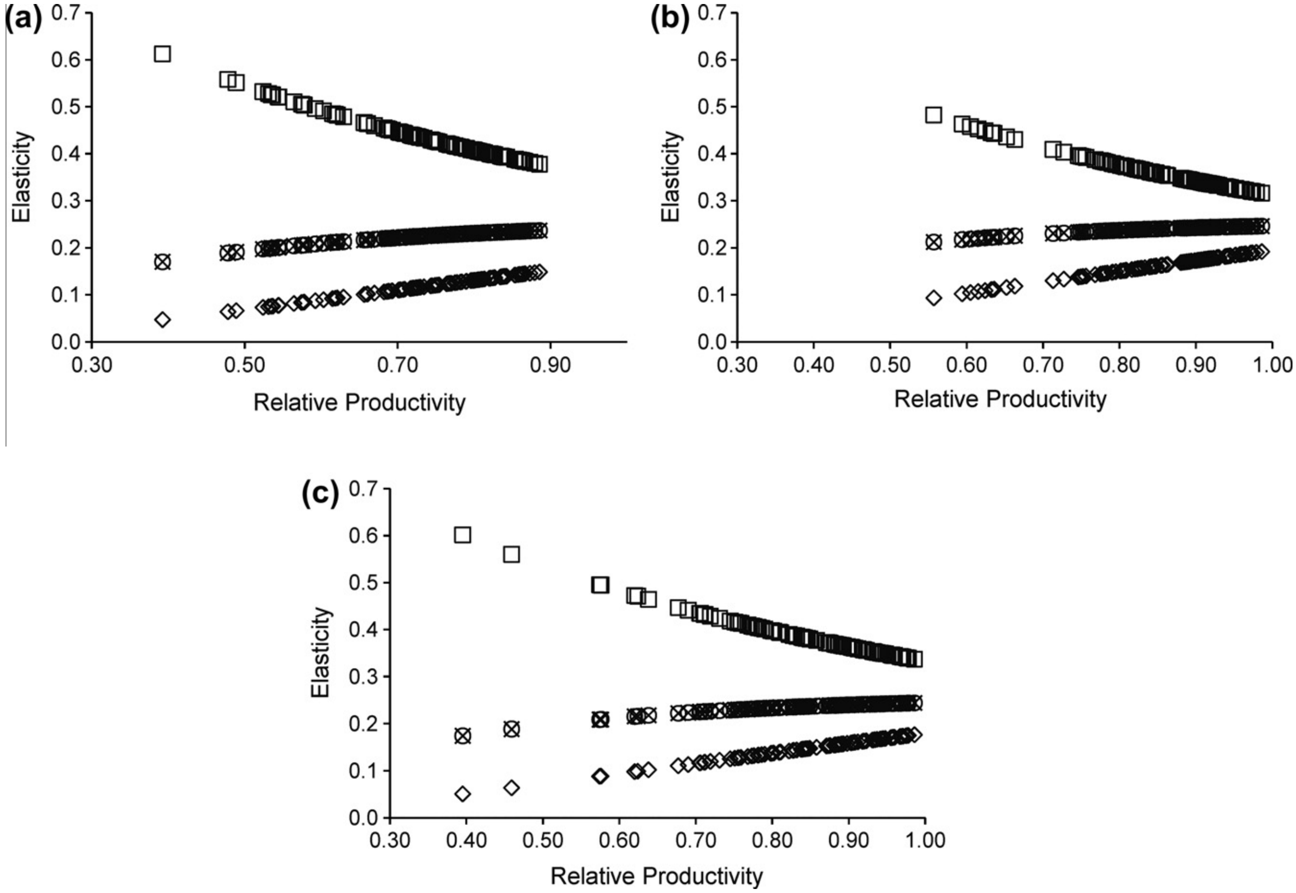

Fig. 8. Elasticities of survival rates (adult – □, juvenile – *x*) and fecundity rates (adult – ○, juvenile – ◇) from populations of wood thrush (a), worm-eating warblers (b), and prairie warblers (c) within the Central Hardwoods Bird Conservation Region. Elasticities for each population are plotted according to the relative productivity of the patch containing that population.

the simulation. However, because of *K* constraints on the worm-eating warbler population, this scenario reversed when changing initial abundance; the end abundance of the worm-eating warbler population was less affected than its viability. Wood thrush and prairie warbler populations exhibited greater sensitivity to initial abundance than *K*, probably because their populations were declining. Reducing dispersal range increased viability and increasing dispersal range decreased viability for wood thrush and prairie warbler, however, this pattern was reversed for worm-eating warbler (Table 2).

6. Discussion

The combination of habitat and demographic modeling allowed us to reasonably extend landscape-based population models to ecoregional scales, consequently providing a powerful approach to conservation planning at large scales. Modeled-based estimates of future growth departed little from past BBS trends, suggesting they effectively captured the effects of landscape patterns on populations. Furthermore, the differences between model and BBS estimates are readily explained by the specific changes in habitat that did occur. For example, forest inventory and analysis data show moderate change (<15%) in the amount of forest cover in the region (USDA, 2010), which explains the small differences (<1%) between modeled and observed trends for wood thrush and worm-eating warblers. However, the early successional component of forests ($\leqslant$20 years old) has declined >40% during the last 20 years (USDA, 2010). Therefore, we would expect estimates of declines in prairie warblers from BBS data to be greater than those from our model which was based on a static landscape or constant *K*. To begin at a scale as small as 30 m and see credible results at the regional scale implies that combining habitat and demographic modeling can address processes that drive these populations across all scales (e.g., from linking suitability indices to demographic rates in cells to replicating source-sink dynamics across patches). Furthermore, it enables assessment of populations in ways that habitat-based approaches alone cannot; HSI models may not identify the risk to a population if that population is below *K*, as we predicted for the wood thrush and prairie warbler. This approach provides a tool to assess bird species viability at the scale of bird conservation regions. For example, based on model projections for the CHBCR there is less call for concern for worm-eating warblers than the wood thrush population, which appear stable but sensitive to changes in productivity, while prairie warblers may require active steps to meet regional population goals. Although, we acknowledge the need for and welcome continuous evaluation and refinement, our models offer a foundation to identifying the most salient risks to viability and exploring ways to address them.

The effectiveness of these models at a regional scale is in part due to our ability to use ecological subsections to represent population patches for which we could summarize spatially-explicit habitat suitability data for modeling the effects of landscape patterns on abundance and growth in populations. Given hypotheses of habitat loss and fragmentation and the variation in landscape pattern across the BCR, it was realistic to spatially structure the population into subsections with different population parameters.

Table 2
Proportional changes in viability and abundance for three populations of breeding birds over 100 years in the Central Hardwoods Bird Conservation Region to a 10% decrease or increase in vital rates and model parameters and 50% decrease or 200% increase in the range of dispersal.

Parameter/assumption	Median quasi-extinction threshold (N)[a]		Median abundance (N) in year 100	
	Decrease	Increase	Decrease	Increase
Wood thrush				
Base[b]	205,667		346,407	
Adult survival	−99.7%	79.2%	−99.8%	672.2%
Juvenile survival	−96.8%	70.9%	−97.9%	590.4%
Maternity	−96.9%	72.4%	−98.0%	591.2%
Relative productivity	−97.1%	66.9%	-98.2%	525.6%
Carrying capacity	2.9%	3.0%	4.7%	5.7%
Initial abundance	−11.2%	14.1%	−14.2%	13.8%
CV[c] survival	4.4%	−2.9%	6.2%	3.1%
CV fecundity	3.2%	−2.7%	3.4%	3.4%
Dispersal	12.1%	−4.7%	23.2%	−13.3%
Worm-eating warbler				
Base[b]	14,53,329		62,14,559	
Adult survival	−89.9%	8.5%	−97.3%	12.3%
Juvenile survival	−55.0%	5.9%	−86.2%	10.4%
Maternity	−54.5%	5.3%	−86.1%	10.2%
Relative productivity	−57.2%	4.1%	−86.2%	9.1%
Carrying capacity	−0.5%	−1.2%	−10.3%	9.3%
Initial abundance	−10.0%	8.7%	−0.3%	0.3%
CV survival	−0.2%	−0.9%	1.5%	−0.9%
CV fecundity	−0.3%	−1.0%	0.6%	−0.9%
Dispersal	−0.2%	−0.3%	−0.8%	2.5%
Prairie warbler				
Base[b]	74,004		97,709	
Adult survival	−99.7%	98.1%	−99.7%	156.8%
Juvenile survival	−97.4%	105.8%	−98.0%	166.1%
Maternity	−97.4%	106.4%	−97.9%	168.7%
Relative productivity	−97.6%	101.1%	−98.1%	155.5%
Carrying capacity	−2.5%	2.2%	−2.5%	2.8%
Initial abundance	−3.1%	8.0%	−6.4%	4.4%
CV survival	10.1%	0.9%	6.9%	2.3%
CV fecundity	6.1%	−6.2%	1.9%	−6.7%
Dispersal	4.8%	−7.4%	5.2%	−8.9%

[a] Abundance (adult females) below which 50% of simulated populations fell during the 100-year period.
[b] Absolute abundance value based on original models with unchanged parameters and assumptions.
[c] CV stands for coefficient of variation.

For example, wood thrush breeding within patches occurring in the heavily forested Ozarks, where there is relatively little fragmentation, had > 90% of the maximum possible productivity and $\lambda_d > 1.02$ (Fig. 5a). This is consistent with other studies that considered these forests as self sustaining based on local estimates of survival and reproduction (Anders et al., 1997; Donovan et al., 1995). In contrast, wood thrush in southern Illinois had some of the lowest rates of reproduction in the CHBCR and in the absence of immigration declined by >2% annually (Fig. 5a). This result for southern Illinois is consistent with Trine's (1998) conclusion that several large forest fragments in that region acted as sinks due to suppressed reproduction from parasitism.

By combining demographic and habitat-based approaches our models appeared to effectively address population level processes that are critical to modeling populations at an ecoregional scale. Source-sink dynamics (sensu Pulliam, 1988) are thought to greatly influence the persistence of regional bird populations (Freemark et al., 1995). However, conclusive evidence of how these interactions occur remains missing (Faaborg et al., 2010b). In our approach, the spatial structure of the CHBCR determined by HSI and RPI models created the potential for source-sink interactions, and the demographic model that included dispersal predicted population impacts. Source-sink interactions were most evident in the wood thrush model, which is fitting given that this species has been cited in many source-sink studies (e.g., Anders et al., 1997; Donovan et al., 1995; Duguay et al., 2001; Fauth, 2000, 2001; Tittler et al., 2006; Weinberg and Roth, 1998). For wood thrush, patches in the western and eastern portions of the CHBCR experienced moderate growth and decline, respectively, depending on the number of nearby patches experiencing high growth, for example the Ozarks in south-central and south-eastern Missouri (Figs. 3 and 4). Although, the interactions replicated in our model are simplistic, their contribution to our effectively modeling CHBCR populations provides circumstantial evidence for the long standing views of the importance of source-sinks dynamics in sustaining regional populations of these birds (Freemark et al., 1995).

Sensitivity and elasticity analyses not only highlighted parameters to which models are sensitive and thus require accurate estimates, but they also demonstrated the relative responsiveness of populations to certain aspects of management. Both elasticity and conventional sensitivity results showed adult survival to have the largest proportional impact on growth for each species (Table 2, Fig. 8). Thus, there is clearly a need for accurate estimates of adult survival when projecting population growth. However, Mills and Lindberg (2002) point out the need to consider elasticity or importance of vital rates in the context of their natural range of variation. Therefore, given adult survival is likely less variable through management, just as it is naturally (Sæther and Bakke, 2000), parameters with high levels of variation such as those associated with reproduction may be of equal interest. The relative increase in the importance of fecundity rates in populations experiencing higher productivities (Fig. 8), leads us to consider whether adult survival or productivity is the most effective approach to maintaining viability in these species. Similar comparisons exist between aspects of management that target productivity vs. *K*. Changes in *K* had relatively small impacts on the three populations except when a population was limited by *K* (Table 2). We do not imply that *K* is unimportant to species viability; obviously continued declines in *K* would be detrimental to populations. Rather, we suggest that to restore populations which are not limited by *K*, effort would be better focused on attributes of habitat that affect productivity or survival. For species with populations near *K* (e.g., worm-eating warblers), *K* might be the most efficient demographic to target to increase abundance or viability through habitat management or restoration.

Model sensitivities to changes in dispersal range also provided insight into interdependency of processes that drive populations at large scales. The negative response by wood thrush and prairie warblers to increasing dispersal range contrasted the response by worm-eating warbler, which responded positively to such increases. These types of results have been observed by others (Akçakaya and Atwood, 1997) and may seem counterintuitive, but can be explained by source-sink dynamics and whether the population was limited by density dependence or productivity. In the wood thrush and prairie warbler populations an increase in dispersal range meant more individuals dispersed from source patches into patches with low productivity (sinks), so the population declined more rapidly. However, for the worm-eating warbler, increased emigration from patches with high productivity meant fewer individuals were affected by density dependent factors.

Although, we take some consolation that projected trends compared well with observed trends, we realize the uncertainties in our approach. While based on the best available knowledge of demographic rates and habitat relationships for the region, many of these values and functions are uncertain. Despite these uncertainties, a strength of the modeling approach is its transparency. Models require assigning values and specifying functions so assumptions are transparent and testable (Burgman and Possingham, 2000). Therefore, these models can continually be refined as new information becomes available. Also, future efforts to verify spatial patterns in growth across populations within the region will provide more insight into the use of this approach. Where predictions deviate from observed patterns, assumptions can be investigated by further research and monitoring.

Until future research reduces the uncertainties involved in these models, conservation decisions resulting from their output would benefit from directly considering uncertainty. The implications of basing management on incorrect population projections can be great (Patterson and Murray 2008). Therefore, integrating uncertainty in specific parameters or assumptions with the model's sensitivity to them can help quantify the effects of uncertainty on model-based decisions (Burgman et al., 2005; Halpern et al., 2006). Inherent in such an approach is the need for formal, comprehensive sensitivity analyses, such as those reviewed by Cross and Beissinger (2001) and Cariboni et al. (2007) on all model components. Our limited analyses demonstrated great sensitivity of model projections to certain model parameters (e.g., adult survival), but we did not test sensitivity to other major components such as the RPI and HSI models. Other approaches have been presented for considering uncertainty. Fuller et al. (2008) quantified the relative impacts of uncertainty on scenario rankings to assess the robustness of management decisions. McGowan et al. (2010) fully accounted for risk in management and decision contexts by explicitly incorporating uncertainty into the dynamics of population models.

Ecoregional-scale population viability models such as those presented here have numerous applications to conservation design. The spatially-explicit nature of landscape-based population models allows systematic conservation planning (Margules and Pressey, 2000; Turner and Pressey, 2009). The ability to model regional population processes such as dispersal and source-sink interactions enables conservation planners to assess how growth in specific geographies (patches) contributes to the overall CHBCR population. Furthermore, because each model is based on habitat suitability, attributes that can be addressed by habitat management can be directly related to population viability as in Duca et al. (2009). Thus, multiple scenarios that strategically call for management in different areas can be created and their impacts on viability evaluated in a decision analysis framework (Maguire, 1986; McCarthy et al., 2010). Although our application of these models was static (used only current conditions), they can be made dynamic by incorporating estimates of future landscape conditions (Akçakaya and Brook, 2009; He, 2009; Wintle et al., 2005). For example, projections of future urbanization can be used to forecast new threats to viability from further habitat loss and fragmentation (Hepinstall et al., 2009).

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