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AN ASSESSMENT OF BIRD HABITAT QUALITY USING POPULATION GROWTH RATES

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Abstract. Survival and reproduction directly affect population growth rate (λ), making λ a fundamental parameter for assessing habitat quality. We used field data, literature review, and a computer simulation to predict annual productivity and λ for several species of landbirds breeding in floodplain and upland forests in the Midwestern United States. We monitored 1735 nests of 27 species; 760 nests were in the uplands and 975 were in the floodplain. Each type of forest habitat (upland and floodplain) was a source habitat for some species. Despite a relatively low proportion of regional forest cover, the majority of species had stable or increasing populations in all or some habitats, including six species of conservation concern. In our search for a simple analog for λ, we found that only adult apparent survival, juvenile survival, and annual productivity were correlated with λ; daily nest survival and relative abundance estimated from point counts were not. Survival and annual productivity are among the most costly demographic parameters to measure and there does not seem to be a low-cost alternative. In addition, our literature search revealed that the demographic parameters needed to model annual productivity and λ were unavailable for several species. More collective effort across North America is needed to fill the gaps in our knowledge of demographic parameters necessary to model both annual productivity and λ. Managers can use habitat-specific predictions of annual productivity to compare habitat quality among species and habitats for purposes of evaluating management plans.

Key words: Driftless Area, floodplain forest, habitat quality, population growth rate, population model, upland forest.

Determinación de Calidad del Hábitat para Aves Utilizando Tasas de Crecimiento Poblacional

Resumen. La supervivencia y la reproducción afectan directamente a la tasa de crecimiento poblacional (λ), lo cual hace que λ sea un parámetro fundamental para determinar la calidad del hábitat. Utilizamos datos de campo, una revisión de la literatura y una simulación computacional para predecir la productividad anual y λ para varias especies de aves terrestres que se reproducen en los bosques de planicies de inundación y de tierras altas en el centro-oeste de Estados Unidos. Monitoreamos 1735 nidos pertenecientes a 27 especies; 760 nidos estuvieron en las tierras altas y 975 en las planicies de inundación. Cada tipo de hábitat de bosque (tierras altas y planicies de inundación) fue un hábitat fuente para algunas especies. A pesar de una proporción de cobertura de bosque relativamente baja a nivel regional, la mayoría de las especies (incluyendo seis con problemas de conservación) tuvieron poblaciones estables o en crecimiento en todos o algunos hábitats. En nuestra búsqueda de un análogo simple de λ, encontramos que sólo la supervivencia aparente de los adultos, la supervivencia de los juveniles y la productividad anual se correlacionaron con λ, mientras que la supervivencia diaria de los nidos y la abundancia relativa estimada a través de puntos de conteo no se correlacionaron con λ. La supervivencia y la productividad anual son unos de los parámetros demográficos más costosos de medir y no parece existir una alternativa de bajo costo. Además, nuestra búsqueda en la literatura reveló que los parámetros demográficos necesarios para modelar productividad anual y λ no se encuentran disponibles para varias especies. Se requiere un esfuerzo colectivo mayor a través de

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toda Norte América para poder llenar los vacíos en nuestro conocimiento acerca de los parámetros demográficos necesarios para modelar la productividad anual y λ. Es posible utilizar predicciones hábitat-específicas de la productividad anual para comparar la calidad del hábitat entre especies y hábitats con el propósito de evaluar planes de manejo.

INTRODUCTION

Assessing habitat quality for breeding birds is a major concern for many land managers (Marzluff et al. 2000). Managers want to know what species are reproducing successfully on their management units and they want to predict what species will benefit (or suffer) from predicted habitat change or planned management actions. Several types of data have been used to assess habitat quality, including estimates of abundance (Best et al. 1997), food availability (Burke and Nol 1998), nest survival (Knutson et al. 2004), annual productivity (Holmes et al. 1996), and annual survival (Chase et al. 1997, Rosenberg et al. 1999). Survival and reproduction directly affect population growth rate (λ), making λ a fundamental parameter for assessing habitat quality (Sæther and Bakke 2000). References to population "sources" and "sinks," sensu Pulliam (1988), have become widespread in the avian literature. Sources are habitat areas in which per capita annual growth rate is above replacement ($\lambda >> 1.0$), whereas sinks are areas in which local populations are not replacing themselves ($\lambda << 1.0$). In stable populations, $\lambda \approx 1$. Variability in this parameter is useful for modeling metapopulation dynamics across landscapes (Hanski et al. 1996).

Demographic rates such as nest survival and annual productivity (fledglings per female) have been used to assess habitat quality for single species and are useful for exploring the causes of population trends (Williams et al. 2002). However, estimates of density, nest survival, and annual productivity have limitations when there is a need to compare location-specific habitat quality among species. For example, nest survival is not a direct analog of annual productivity because productivity is also influenced by breeding strategies such as multibrooding (Thompson et al. 2001). Furthermore, a species with relatively low annual productivity but a long life span (higher annual survival rate) may have the same λ as a species with high annual productivity but a short life span (Sæther and Bakke 2000). Therefore, direct comparisons of nest survival or annual productivity among species are misleading. Population models that incorporate breeding strategies and adult and juvenile survival are required to compare λ among habitats (Powell et al. 2000), and predictions of λ allow comparisons of habitat quality among species.

Land managers are in the position of managing habitats occupied by assemblages of bird species; thus, they often need to make management decisions that affect multiple species. Predictions of λ that allow direct comparisons among habitats for multiple species are useful in this context. Models are now available to predict annual productivity from variables that can be measured by field studies, including nest survival (Pease and Grzybowski 1995, Powell et al. 1999). Population growth can then be modeled using estimates of annual productivity and survival. These models incorporate error estimates that are needed to simulate realistic variability in annual productivity and λ over time (Powell and Knutson 2006).

We used field data (Gustafson et al. 2002, Knutson et al. 2004), literature review, and a computer simulation to predict annual productivity and λ for several species of landbirds breeding in floodplain and upland forests of the Driftless Area, the unglaciated portions of Minnesota, Wisconsin, and Iowa in the Midwestern United States. For each species, we tested the null hypothesis that the modeled $\lambda = 1$ over a simulated 200-year time span (stable population). This information will help land managers assess the conservation value of these habitats for focal species and plan future land management. Our predictions also provide baseline reproductive parameters for comparison with future predictions from the same or other regions.

METHODS

STUDY AREA

Our field study was conducted in the Driftless Area, including portions of the states of Iowa, Minnesota, and Wisconsin (McNab and Avers 1994; Fig. 1). The landforms in the region are

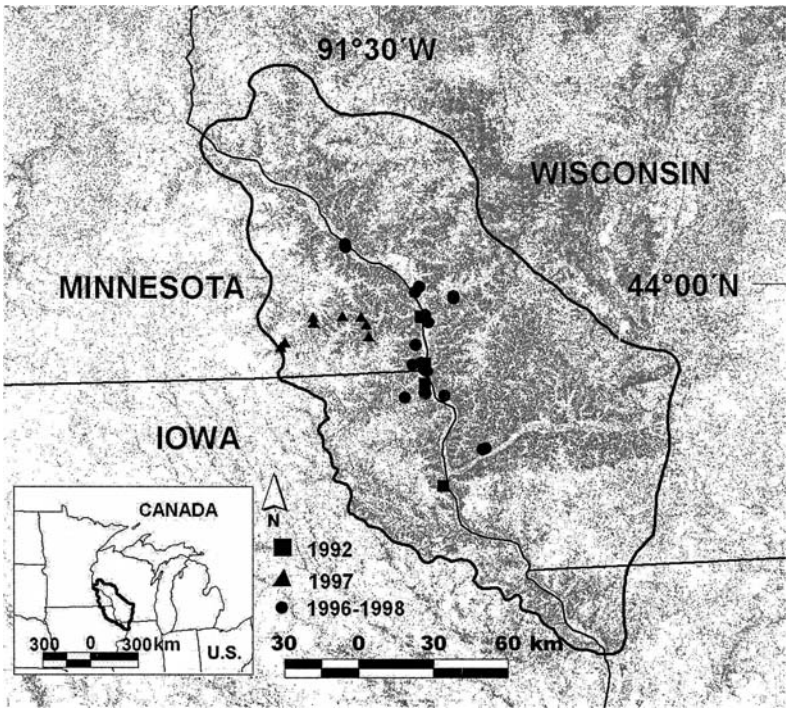

FIGURE 1. Study sites in the Driftless Area of North America. Squares, triangles, and circles indicate the location of plots studied in 1992, 1997, and 1996–1998, respectively. Heavier shading represents forested land cover.

characterized by dissected, upland plateaus with steep bedrock ridges descending to river drainages that ultimately flow to the Mississippi River. Upland forests of the Driftless Area were historically a transition zone between forest and grassland habitats. Before European settlement, the ecoregion was covered by an oak savanna complex of mixed grasslands with upland forests dominated by oaks (*Quercus* spp.), sugar maple (*Acer saccharum*), and basswood (*Tilia americana*, Curtis 1959, Cahayla-Wynne and Glenn-Lewin 1978). Under fire suppression and modern agricultural practices, these oak savanna forests have become closed-canopy woodlands within a matrix of row and forage crops (Glenn-Lewin et al. 1984, Leach and Givnish 1999). Forests are confined to steep slopes adjacent to streams and rivers and form a connected, dendritic pattern. Complex topography and erosive soils support a less intensive agriculture than in many parts of the Midwest, with agriculture replacing the grasslands and comprising 30%–40% of the landscape (McNab and Avers 1994).

The Mississippi River floodplain in this region is unrestricted by levees; forests dominate most islands and main channel borders within the floodplain (Knutson et al. 1996). The plant community of floodplain forests is dominated by silver maple (*Acer saccharinum*), with elm (*Ulmus* spp.), green ash (*Fraxinus pennsylvanica*), swamp white oak (*Quercus bicolor*), cottonwood (*Populus deltoides*), hackberry (*Celtis occidentalis*), and river birch (*Betula nigra*) as subdominants (Knutson and Klaas 1997).

We previously reported that nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) in the study area was relatively low (14% of vulnerable nests; Gustafson et al. 2002), and there were only small differences in upland nest survival among sites in more forested compared with less forested landscapes (Knutson et al. 2004). Forests comprised between 13% and 53% of the landscape within a 10-km radius surrounding our study sites. Predation was the primary cause of nest failure in the region (Knutson et al. 2004).

FIELD METHODS

We monitored landbird nests from May to August in upland (n = 18) and floodplain (n = 15) forest sites located in southeastern Minnesota, northeastern Iowa, and western Wisconsin (Fig. 1). We studied five floodplain sites in 1992, 10 floodplain and 10 upland sites from 1996 to 1998, and an additional eight upland sites in 1997 (Gustafson et al. 2002, Knutson et al. 2004). We selected our upland sites from state forests that were not recently logged or grazed. We used a stratified random design to select sites from federal land in the Upper Mississippi River floodplain, based on forest inventory data (U.S. Army Corps of Engineers 1990–1997). We stratified forest units among three floodplain stand types: mature silver maple forest (n = 9), mature, mast-producing bottomland forest (n = 3), and young forest stands (n = 3). The mature silver maple forest had dominant tree genera of *Acer*, *Ulmus*, and *Fraxinus*, with a mean dbh >25 cm and fewer than two mast trees per plot within a stand. The mature, mast-producing bottomland forest was dominated by *Acer*, mixed with *Quercus*, walnut (*Juglans* spp.), and hickory (*Carya* spp.), with mean dbh >25 cm, and ≥2 mast trees per plot within a stand. The young forests stands had trees with mean dbh ≤25 cm. Sites were approximately 40 ha in the uplands and 20 ha in the floodplain, but monitoring effort was similar among all sites.

We located nests using standard protocols (Martin and Geupel 1993, Martin et al. 1997). All active nests were monitored every two to four days until fledging or failure. The sum of the laying, incubation, and nestling periods was used as the observation period for each nest. Observation days began with the first day a nest was observed and ended with the last observed active date for successful nests and nests with uncertain fate; observation days ended with the midpoint between the last active visit and the first inactive visit for failed nests ("Last Active A", Manolis et al. 2000). Nests were considered successful if they fledged at least one host young. We used the Mayfield method (Mayfield 1961, Johnson 1979) to estimate daily nest survival by species for all sites and for upland sites, floodplain sites, and the three types of floodplain sites.

To correlate λ with species abundances, we counted birds on each plot between 20 May and 30 June at 6–12 points spaced ≥200 m apart during the same years that nests were monitored. We recorded all birds observed during a 10-min point count (Ralph et al. 1993). We estimated the overall relative abundance of each species by estimating the mean number of birds per point, across all sites and years. We identified the species of highest conservation concern based on the Partners in Flight North American landbird conservation plan (Rich et al. 2004).

PRODUCTIVITY MODEL

We used a modification of Powell et al.'s (1999) model to provide predictions of annual productivity for multibrooded songbirds that experience Brown-headed Cowbird parasitism (Powell and Knutson 2006). We used our field data to parameterize the annual productivity model (daily nest survival, number of fledglings produced, probability of parasitism, and cowbird effects such as abandonment or reduction and loss of host nestlings). Our field study, however, was not designed to estimate other demographic parameters necessary to calculate annual productivity and λ. We used a literature review to obtain estimates of adult and juvenile apparent survival, length of the breeding season, duration of nest building and fledgling care periods, and likelihood of renesting. Parameter estimates obtained from field data and the literature, and additional constraints imposed on the model, are presented in Appendices A, B, and C, respectively, published online at http://www.umesc.usgs.gov/staff/bios/mgk0.html. The model used estimates and variances of the above parameters in a stochastic simulation.

The productivity model was structured as a dynamic, stochastic, individual-based model of reproduction, and simulated a female songbird and her offspring on a random walk through the breeding season (Powell et al. 1999). The female, her nest, and her offspring were at constant risk of mortality (Powell and Knutson 2006), based on species-specific, daily estimates of nest survival, adult survival, and fledgling survival (Appendix A, B). The simulated female began the breeding season by building a nest for a species-specific period (Appendix B). If the simulated nest failed during the nesting period (Appendix B), the female built another nest (unless limited by

species-specific life history; Appendix C). If the simulated nest was successful, the female cared for the simulated offspring for a species-specific period (Appendix B); the offspring were produced stochastically using estimates of the mean clutch size for the species (Appendix A). After fledgling care, the simulated female could renest if time and life history traits allowed (Appendix B, C). At the end of the season, the model provided the number of attempted nests, number of nests parasitized, number of successful nests, and number of fledglings produced by the simulated female.

Our modification of Powell et al.'s (1999) model allowed nests to be parasitized by Brown-headed Cowbirds. Nests were randomly assigned parasitism status based on our species- and habitat-specific field estimates of the probability of parasitism (Powell and Knutson 2006; Appendix A). Our data indicated that some songbirds showed high rates of abandonment after nest parasitism. Other species commonly incubated only cowbird eggs, while some continued to care for their mixed host and parasite clutches with normal behavior. Thus, our model accounted for all three possibilities, based on species- and habitat-specific probabilities calculated from our data (Powell and Knutson 2006; Appendix A).

The model incorporated several stochastic components, and our goal was to use the model to make predictions regarding annual productivity of the population of birds in our study area. Thus, we performed 200 simulations to obtain mean and variance estimates for the model outputs (Powell et al. 1999). A detailed explanation of the model is found in Powell and Knutson (2006).

Model outputs for breeding season productivity were the average number of: nests initiated per female during a breeding season, successful nests per female during a breeding season, fledglings produced per female that survived to the end of a breeding season (annual productivity, p), and parasitized nests per female during the breeding season. The model also provided estimates of variance for these predictions.

POPULATION GROWTH MODEL

Discrete population growth (λ) is a function of annual adult survival (S_A), fecundity (the number of females produced per female, alive at the end of the breeding season, B), and the survival of juveniles from the end of the breeding season to the next breeding season (S_J). Thus, we used our predictions of annual productivity (p) to calculate annual population growth rate (λ) as defined by Pulliam (1988) using a dynamic, stochastic simulation based on the equation: $\lambda = S_A + BS_J$ (Powell et al. 2000).

We obtained estimates of adult survival from the literature in the form of apparent annual survival rates from band return data (DeSante et al. 1998). No estimates of S_J (first winter survival) exist for most species; we followed the methods of Temple and Cary (1988) and Donovan et al. (1995) by using a value of 50% of the adult apparent survival rate over an identical time interval. We predicted fecundity using our results from the annual productivity model. To obtain B (female offspring per female), we divided the number of fledglings produced per female (p) in our annual productivity model by 2.

To calculate λ_i, we randomly selected survival rates from a beta distribution to ensure parameter values between 0.0 and 1.0, and we randomly selected fecundity rates from a normal distribution. Each distribution was shaped by the variance estimate of the given parameter estimate. To characterize the growth rate of the population under a specific set of model parameter values, we calculated the geometric mean $\overline{\lambda}$ as suggested by Pulliam (1996) for n = 200 (Powell et al. 2000) simulations of λ_i as:

$$\overline{\lambda} = anti\log\left[\frac{1}{n}\sum_{i=1}^{n}\log(\overline{\lambda}_i)\right],$$

and computed a 95% CI for the geometric mean (Sokal and Rohlf 1981:421) as

$$anti\log\left[\overline{\log\lambda} \pm 1.96\sqrt{\frac{1}{n}\mathrm{var}(\log\overline{\lambda})}\right].$$

DEMOGRAPHIC PARAMETERS AND POPULATION GROWTH RATE

We explored associations between λ and other demographic parameters in hopes of finding an analog for λ that is simple to measure. We plotted the association between λ and daily nest survival, annual productivity, probability of parasitism, mean clutch size, length of the breeding season (days), maximum successful

TABLE 1. Mean annual productivity (fledglings per female) ± SD simulated (n = 200 replications) from landbird nesting data collected in the Driftless Area of Iowa, Minnesota, and Wisconsin from 1992 to 1998 and demographic data reported in the literature for 27 species, under six model structures: all study sites, upland sites, all floodplain sites, maple-dominated floodplain sites, mast-producing tree-dominated floodplain sites, and young forest floodplain sites. Missing data indicates there were too few nests in the sample.

Species	All sites	Upland	Floodplain, all	Floodplain, maple	Floodplain, mast	Floodplain, young
Ruby-throated Hummingbird (*Archilochus colubris*)	1.64 ± 1.24	1.64 ± 1.24	—	—	—	—
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	3.10 ± 1.40	—	3.10 ± 1.40	—	2.78 ± 1.56	—
Red-bellied Woodpecker (*Melanerpes carolinus*)	2.97 ± 1.42	2.93 ± 1.36	2.81 ± 1.61	—	—	—
Hairy Woodpecker (*Picoides villosus*)	2.56 ± 1.55	2.58 ± 1.41	2.20 ± 1.64	1.97 ± 1.58	—	—
Eastern Wood-Pewee (*Contopus virens*)	1.99 ± 1.52	1.81 ± 1.59	1.97 ± 1.74	2.11 ± 1.57	2.56 ± 1.74	2.66 ± 1.71
Acadian Flycatcher (*Empidonax virescens*)	1.98 ± 1.03	1.98 ± 1.03	—	—	—	—
Great Crested Flycatcher (*Myiarchus crinitus*)	3.01 ± 1.38	—	2.89 ± 1.43	2.66 ± 1.56	2.95 ± 1.32	3.03 ± 1.34
Warbling Vireo (*Vireo gilvus*)	2.25 ± 1.93	—	2.25 ± 1.93	3.21 ± 2.00	2.38 ± 1.86	2.01 ± 1.93
Red-eyed Vireo (*Vireo olivaceus*)	1.70 ± 1.71	1.70 ± 1.71	—	—	—	—
Blue Jay (*Cyanocitta cristata*)	3.35 ± 2.58	2.96 ± 2.31	4.08 ± 2.74	—	4.08 ± 2.74	—
Tree Swallow (*Tachycineta bicolor*)	2.82 ± 1.45	—	2.82 ± 1.45	3.06 ± 1.16	2.00 ± 1.77	2.85 ± 1.40
Black-capped Chickadee (*Poecile atricapillus*)	3.44 ± 1.60	3.50 ± 1.47	3.31 ± 1.51	3.45 ± 1.47	3.53 ± 1.39	—
House Wren (*Troglodytes aedon*)	4.96 ± 3.11	4.80 ± 3.15	4.96 ± 3.11	4.76 ± 3.04	5.17 ± 3.36	—
Blue-gray Gnatcatcher (*Polioptila caerulea*)	1.53 ± 1.18	1.50 ± 1.21	1.54 ± 1.22	1.43 ± 1.28	1.34 ± 1.20	1.52 ± 1.22
Wood Thrush (*Hylocichla mustelina*)	2.03 ± 1.60	2.03 ± 1.60	—	—	—	—
American Robin (*Turdus migratorius*)	3.50 ± 2.09	3.28 ± 1.99	3.61 ± 2.10	3.84 ± 1.86	3.55 ± 2.06	3.55 ± 2.06
Gray Catbird (*Dumetella carolinensis*)	2.76 ± 2.05	2.81 ± 1.93	2.83 ± 1.99	2.75 ± 1.90	3.20 ± 2.05	3.32 ± 1.92
Brown Thrasher (*Toxostoma rufum*)	2.23 ± 1.20	—	2.23 ± 1.20	—	—	—
Yellow Warbler (*Dendroica petechia*)	2.41 ± 1.26	—	2.31 ± 1.23	2.30 ± 1.28	—	2.11 ± 1.40
American Redstart (*Setophaga ruticilla*)	1.56 ± 1.31	1.60 ± 1.27	1.71 ± 1.33	1.57 ± 1.24	1.52 ± 1.27	1.37 ± 1.22
Prothonotary Warbler (*Protonotaria citrea*)	1.26 ± 1.53	—	1.26 ± 1.53	1.32 ± 1.65	1.37 ± 1.59	0.98 ± 1.47
Ovenbird (*Seiurus aurocapillus*)	1.30 ± 1.22	1.30 ± 1.22	—	—	—	—

TABLE 1. Continued.

Species	All sites	Upland	Floodplain, all	Floodplain, maple	Floodplain, mast	Floodplain, young
Scarlet Tanager (*Piranga olivacea*)	1.77 ± 1.58	1.77 ± 1.58	—	—	—	—
Northern Cardinal (*Cardinalis cardinalis*)	2.82 ± 1.77	2.66 ± 1.65	2.92 ± 1.83	3.19 ± 1.91	3.38 ± 1.71	—
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	1.53 ± 1.30	1.45 ± 1.26	1.59 ± 1.26	1.52 ± 1.27	1.92 ± 1.10	1.60 ± 1.21
Indigo Bunting (*Passerina cyanea*)	2.74 ± 2.31	2.74 ± 2.31	—	—	—	—
Baltimore Oriole (*Icterus galbula*)	2.36 ± 1.36	—	2.36 ± 1.36	2.36 ± 1.50	2.27 ± 1.46	2.28 ± 1.36

broods, relative abundance, adult daily survival, and juvenile daily survival; each data point represented one species. We calculated the coefficient of determination (r^2) between a pair of parameter estimates and the significance of the association (Zar 1999).

RESULTS

We counted 5237 total birds distributed among 27 species during 514 point counts and monitored 1735 nests; 760 nests were in the uplands and 975 were in the floodplain (Appendix A). Annual productivity predictions (fledglings per female) for all sites ranged from a high of 4.96 ± 3.11 SD fledglings per female for House Wrens (*Troglodytes aedon*) to a low of 1.26 ± 1.53 for Prothonotary Warblers (*Protonotaria citrea*, Table 1).

Population growth rate predictions varied among both species and habitat types (Table 2), and ranged from a high of $\lambda = 1.71$ (95% CI: 1.62–1.80) for the Red-headed Woodpecker (*Melanerpes erythrocephalus*) to a low of $\lambda = 0.54$ (0.47–0.61) for the Scarlet Tanager (*Piranga olivacea*) over all sites. Over all habitats, 20 species had $\lambda \geq 1$ and seven species had $\lambda < 1$ (Table 2); the latter were all Neotropical migrants. All habitats were sinks for the Ruby-throated Hummingbird (*Archilochus colubris*), Blue-gray Gnatcatcher (*Polioptila caerulea*), Prothonotary Warbler (*Protonotaria citrea*), Scarlet Tanager, and Baltimore Oriole (*Icterus galbula*, Table 2). Among the species of conservation concern (Rich et al. 2004), the Red-headed Woodpecker, Red-bellied Woodpecker (*Melanerpes carolinus*), Acadian Flycatcher (*Empidonax virescens*), Wood Thrush (*Hylocichla mustelina*), Brown Thrasher (*Toxostoma rufum*), and Indigo Bunting (*Passerina cyanea*) had stable or increasing populations in all or some habitats.

In upland forests, $\lambda \geq 1$ for 14 species (Table 2), including four species of conservation concern (Red-bellied Woodpecker, Acadian Flycatcher, Wood Thrush, and Indigo Bunting). Sixteen species of landbirds (Table 2), including three species of conservation concern (Red-headed Woodpecker, Red-bellied Woodpecker, and Brown Thrasher), had a $\lambda \geq 1$ in Mississippi floodplain forests. Among the floodplain forest types, $\lambda \geq 1$ for 11 species (Table 2), including one species of conservation concern (Red-headed Woodpecker), in stands

that included mast trees. In the maple-dominated stands, which comprised the large majority of the floodplain (Yin et al. 1997, Knutson and Klaas 1998), $\lambda \geq 1$ for 11 landbird species; the Warbling Vireo (*Vireo gilvus*), Tree Swallow (*Tachycineta bicolor*), American Robin (*Turdus migratorius*), Yellow Warbler (*Dendroica petechia*) and American Redstart (*Setophaga ruticilla*) fared best in this habitat (Table 2). The Eastern Wood-Pewee (*Contopus virens*) and Great Crested Flycatcher (*Myiarchus crinitus*) fared best in young floodplain stands compared with all other habitat types.

There was a positive association between λ and annual productivity ($r^2 = 0.48$, $P < 0.001$), juvenile survival ($r^2 = 0.54$, $P < 0.001$), and adult survival ($r^2 = 0.36$, $P < 0.001$; Fig. 2). No other demographic parameter had a significant association with λ.

DISCUSSION

FOREST FRAGMENTATION AND LAND MANAGEMENT

We observed relatively strong reproductive performance of forest birds in the Driftless Area, given that our forests are on the low end of the range of forest cover (13%–53%) studied by Robinson et al. (1995). Their model would predict that the Driftless Area is a sink for the Acadian Flycatcher, Red-eyed Vireo (*Vireo olivaceus*), Wood Thrush, Ovenbird (*Seiurus aurocapillus*), Scarlet Tanager, Northern Cardinal (*Cardinalis cardinalis*), and Indigo Bunting. Of this group, we found that only the Scarlet Tanager experienced sink habitat, although $\lambda \approx 1$ for the Red-eyed Vireo, Ovenbird, and Indigo Bunting.

From a theoretical perspective, populations of forest-dependent wildlife are predicted to decline when regional forest cover falls below a threshold, usually estimated at 20% to 30%, although this hypothesis lacks empirical testing (Fahrig 2003). If this were true, we might expect the most area-sensitive species to decline first when forest cover approximates this threshold. Our predictions of λ for five area-sensitive species showed a sink for the Blue-gray Gnatcatcher, Ovenbird, and Scarlet Tanager, and a source for the Acadian Flycatcher and Wood Thrush (Robbins et al. 1989, Best et al. 1996), which may be an indication that our study area is near the threshold of forest cover needed to sustain most forest bird populations. Possibly, the Blue-gray Gnatcatcher, Ovenbird, and Scarlet Tanager are more sensitive to low forest cover than either the Acadian Flycatcher or Wood Thrush (Porneluzi et al. 1993, Roberts and Norment 1999, Donovan and Flather 2002). However, since the Ovenbird is a ground-nester whereas the Blue-gray Gnatcatcher and Scarlet Tanager nest in the mid to upper tree canopy, different nest predators are probably responsible for their reproductive failures. We note that area-sensitive species were found primarily in the uplands.

Despite a relatively low proportion of forest cover, our simulations suggest that populations in the Driftless Area are stable or increasing for the majority of birds we studied, including six species of conservation concern. In addition, because our model incorporated apparent survival rates, our estimates of population growth rate are probably conservative (Anders and Marshall 2005). Hanski et al. (1996), using simulation models, showed that even if habitat patches only intermittently function as sources they can contribute to population stability. If λ occasionally exceeds 1, and there is movement among sites, metapopulations tend to persist. It is even possible for metapopulations consisting only of sink populations to persist (Hanski et al. 1996).

MISSING DEMOGRAPHIC PARAMETERS

Our modeling exercise demonstrates the importance of collecting and reporting demographic data for a wide variety of species in multiple habitats and across the geographic range of the species. Appendix A provides a summary of the parameters from our field data that were used to model seasonal productivity and annual population growth rates; these are the parameters that nesting studies should strive to estimate as accurately as possible. They include nest survival, number of fledglings produced, probability of parasitism, and effects of parasitism (proportion of nests that are abandoned, have reduced nestlings, raise cowbirds only, and no effect). While national protocols for nesting studies support the collection of these data (Martin et al. 1997), our modeling exercise demonstrates the value of these specific parameters.

One limitation of our models was the lack of habitat-specific adult and juvenile survival

TABLE 2. Predicted mean annual population growth rate (λ) and 95% CIs, derived from landbird nesting data collected in the Driftless Area of Iowa, Minnesota, and Wisconsin from 1992–1998 and demographic data reported in the literature for 27 species. Growth rates are predicted under six potential productivity model structures: all study sites, upland sites, all floodplain sites, maple-dominated floodplain sites, mast-producing tree-dominated floodplain sites, and young forest floodplain sites. Mean growth rate shown is the geometric mean of 200 simulated years. Missing data indicates there were too few nests in the sample; statistical sink populations ($\lambda << 1.0$) are denoted by ‡ and statistical source populations ($\lambda >> 1.0$) are denoted by †. See Table 1 for Latin names of species.

Species	All sites	Upland	Floodplain, all	Floodplain, maple	Floodplain, mast	Floodplain, young
Ruby-throated Hummingbird	0.84 (0.80–0.88)‡	0.84 (0.80–0.88)‡	—	—	—	—
Red-headed Woodpecker[a]	1.71 (1.62–1.80)†	—	1.71 (1.62–1.80)†	—	1.65 (1.55–1.75)†	—
Red-bellied Woodpecker[a]	1.58 (1.49–1.67)†	1.66 (1.57–1.75)†	1.57 (1.47–1.67)†	—	—	—
Hairy Woodpecker	1.05 (0.96–1.14)	1.02 (0.93–1.11)	0.95 (0.87–1.03)	0.89 (0.81–0.97)‡	—	—
Eastern Wood-Pewee	0.76 (0.71–0.81)‡	0.76 (0.70–0.82)‡	0.82 (0.76–0.88)‡	0.82 (0.76–0.88)‡	0.90 (0.84–0.96)‡	0.96 (0.89–1.03)
Acadian Flycatcher[a]	1.11 (1.06–1.16)†	1.11 (1.06–1.16)†	—	—	—	—
Great Crested Flycatcher	1.06 (0.99–1.13)	—	1.03 (0.95–1.11)	0.97 (0.90–1.04)	0.99 (0.92–1.06)	1.19 (1.09–1.29)†
Warbling Vireo	1.22 (1.16–1.28)†	—	1.22 (1.16–1.28)†	1.46 (1.39–1.53)†	1.24 (1.18–1.30)†	1.17 (1.12–1.22)†
Red-eyed Vireo	1.00 (0.95–1.05)	1.00 (0.95–1.05)	—	—	—	—
Blue Jay	1.61 (1.50–1.72)†	1.45 (1.36–1.54)†	1.80 (1.68–1.92)†	—	1.80 (1.68–1.72)†	—
Tree Swallow	1.17 (1.06–1.28)†	—	1.17 (1.06–1.28)†	1.24 (1.14–1.34)†	1.18 (1.09–1.27)†	1.19 (1.09–1.29)†
Black-capped Chickadee	1.65 (1.58–1.72)†	1.67 (1.58–1.72)†	1.66 (1.59–1.73)†	1.64 (1.57–1.71)†	1.72 (1.66–1.78)†	—
House Wren	1.40 (1.31–1.49)†	1.42 (1.33–1.51)†	1.40 (1.31–1.49)†	1.43 (1.34–1.52)†	1.47 (1.37–1.67)†	—
Blue-gray Gnatcatcher	0.82 (0.78–0.86)‡	0.81 (0.78–0.84)‡	0.82 (0.79–0.85)‡	0.79 (0.76–0.82)‡	0.80 (0.76–0.84)‡	0.79 (0.76–0.82)‡
Wood Thrush[a]	1.08 (1.03–1.13)†	1.08 (1.03–1.13)†	—	—	—	—
American Robin	1.51 (1.43–1.59)†	1.44 (1.36–1.52)†	1.53 (1.45–1.61)†	1.59 (1.51–1.67)†	1.53 (1.45–1.61)†	1.53 (1.45–1.61)†
Gray Catbird	1.18 (1.12–1.24)†	1.17 (1.12–1.22)†	1.13 (1.07–1.19)†	1.19 (1.14–1.24)†	1.29 (1.23–1.35)†	1.29 (1.23–1.35)†
Brown Thrasher[a]	1.01 (0.97–1.05)	—	1.01 (0.97–1.05)	—	—	—
Yellow Warbler	1.15 (1.11–1.19)†	—	1.09 (1.05–1.13)†	1.11 (1.07–1.15)†	—	1.06 (1.02–1.10)†
American Redstart	0.95 (0.92–0.98)‡	0.96 (0.93–0.99)‡	0.97 (0.94–1.00)	0.98 (0.95–1.01)	0.94 (0.91–0.97)‡	0.93 (0.90–0.96)‡
Prothonotary Warbler[a]	0.85 (0.81–0.89)‡	—	0.85 (0.81–0.89)‡	0.86 (0.82–0.90)‡	0.89 (0.85–0.93)‡	0.87 (0.83–0.91)‡
Ovenbird	0.97 (0.92–1.02)	0.97 (0.92–1.02)	—	—	—	—
Scarlet Tanager	0.54 (0.47–0.61)‡	0.54 (0.47–0.61)‡	—	—	—	—
Northern Cardinal	1.26 (1.20–1.32)†	1.24 (1.20–1.28)†	1.30 (1.24–1.36)†	1.44 (1.37–1.51)†	1.45 (1.39–1.51)†	—
Rose-breasted Grosbeak	1.32 (1.25–1.39)†	1.23 (1.16–1.30)†	1.22 (1.16–1.28)†	1.26 (1.19–1.33)†	1.32 (1.25–1.39)†	1.26 (1.19–1.33)†
Indigo Bunting[a]	1.02 (0.96–1.08)	1.02 (0.96–1.08)	—	—	—	—
Baltimore Oriole	0.70 (0.65–0.75)‡	—	0.70 (0.65–0.75)‡	0.71 (0.66–0.76)‡	0.64 (0.59–0.69)‡	0.67 (0.62–0.72)‡

[a] Species of conservation concern (Rich et al. 2004).

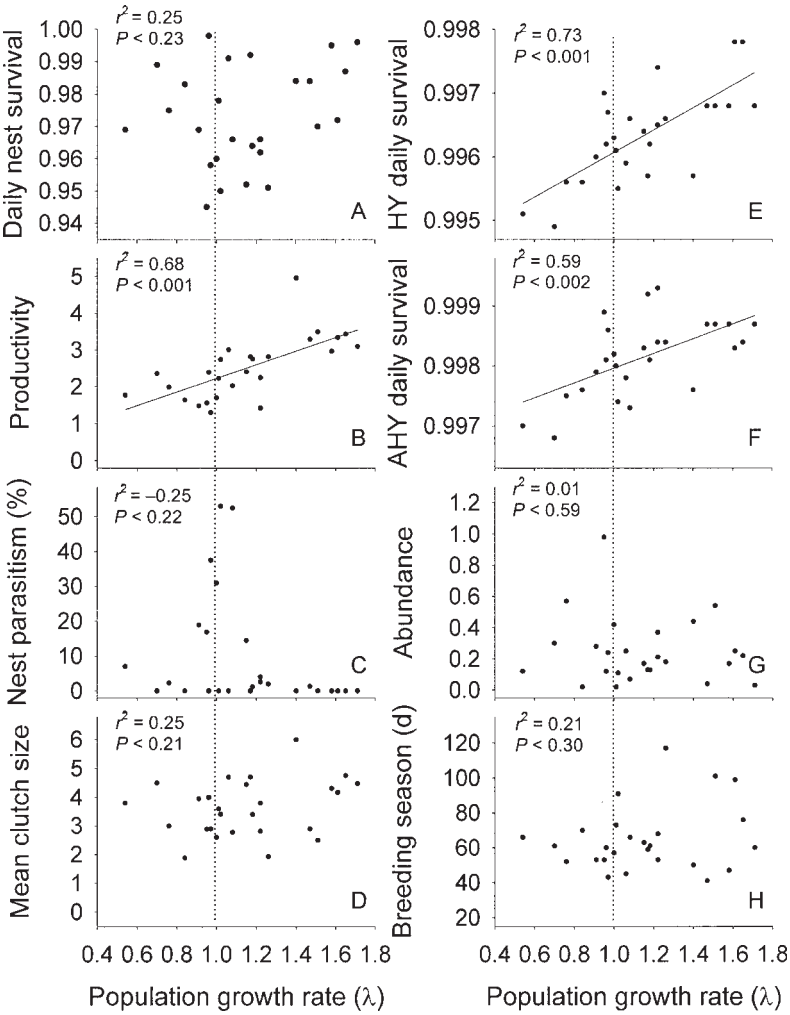

FIGURE 2. Association between annual population growth rate (λ) and several demographic parameters for 27 species, including daily nest survival (A), annual productivity (fledglings per female; B), nest parasitism (percentage of nests parasitized; C), mean clutch size (D), juvenile (hatch-year, HY) daily survival (E), adult (after-hatch-year, AHY) daily survival (F), relative abundance (birds per 10 ha; G), and length of the breeding season (days; H). Vertical dotted lines indicate stable populations (λ = 1.0).

estimates. Variation in these parameters could strongly affect our predictions of λ (Sæther and Bakke 2000, Sæther and Engen 2002, Reid et al. 2004), however, it is a major challenge to measure habitat-specific survival for even a few species because long-term data sets are required (Murphy 2001). From a management perspective, our results provide the best possible predictions of annual productivity and population growth rates using our large, habitat-specific nesting data set and the best survival information available at this time. As habitat-specific survival estimates become available our results could be updated, and habitat-specific comparisons of population growth would be possible. Currently, our results are most valuable for comparing general trends in annual productivity or population growth among species.

Because we lacked several habitat-specific demographic parameters, we needed regional or continental estimates by species, including adult and juvenile daily survival, length of the breeding season, and duration of the nest

building, nesting, and postfledging care periods (Appendix B). The value of comprehensive species accounts that report these parameters, such as the *Birds of North America* series (Poole and Gill 1992–2004), was evident. However, for many species, some parameters did not exist or were unavailable from the published literature. For these species, we were forced to substitute values from a closely related species. For example, we could find no reported adult or juvenile survival estimates for the Blue-gray Gnatcatcher, and instead used estimates for the Common Yellowthroat (*Geothlypis trichas*), which is similar in size and migrates a similar distance (Appendix B). Juvenile survival was missing for nearly all species. Estimates of the number of successfully fledged young and the fledgling care interval were either missing or derived from sparse data for many species. More collective effort across North America should be directed toward obtaining better estimates of both adult and juvenile annual survival and filling in the gaps in our knowledge of other demographic parameters necessary for modeling annual productivity and λ. We suspect that the missing demographic parameters for some species may be buried in unpublished data sets or 'gray' literature, and the availability of such data could improve predictions of annual productivity and λ. We urge ornithologists to make this descriptive information widely available by publishing short communications or notes when a more lengthy publication is not warranted. A demographic database for North America birds could also be developed to store this information and make it widely available.

DEMOGRAPHIC INDICATORS OF SOURCES AND SINKS

Many field studies conduct counts of birds and monitor their nests for purposes of assessing habitat quality. Density or relative abundance and nest survival rates are relatively simple to estimate, although consideration of detection probabilities complicates even density estimates (Royle and Nichols 2003). Designating source and sink habitats for landbirds could be simplified if density or nest survival were analogs for λ. Unfortunately, we found that only adult survival, juvenile survival, and annual productivity were correlated with λ; daily nest survival and relative abundance estimated from point counts were not. Survival and annual productivity are among the most costly demographic parameters to measure and there does not seem to be a simple, low-cost alternative.

Our finding that density was not related to λ supports the assertion made by Van Horne (1983) more than 20 years ago. Since then, many investigators have found little correlation between bird density and annual productivity (Purcell and Verner 1998, Roberts and Norment 1999, Rangen et al. 2000, Underwood and Roth 2002). Our finding that Mayfield nest survival was also uncorrelated with λ is in agreement with the findings of Underwood and Roth (2002), probably because of the variable effects of cowbird parasitism, breeding season length, and the tendency of some species to renest within a season. Rangen et al. (2000) also found that behavioral observations of reproductive success were weakly associated with density for most species. However, annual productivity in our study was correlated with λ. This supports the value of annual productivity models such as Pease and Grzybowski (1995) and Powell et al. (1999) for assessing habitat quality. Because predictions of annual productivity and λ are sensitive to survival rates, long-term capture-mark-recapture data sets such as those generated by the MAPS program (Institute for Bird Populations, Point Reyes Station, CA) remain critical for obtaining survival rate estimates (DeSante et al. 1998).

MANAGEMENT APPLICATIONS

How will managers use habitat- and species-specific predictions of annual productivity and population growth? Managers can use predictions of λ to compare habitat quality among species or among habitats. They can identify which species are benefiting from present habitat conditions and which species might benefit from habitat change. For example, our four warbler species, Yellow Warbler, American Redstart, Prothonotary Warbler, and Ovenbird, vary in annual productivity and λ among habitat types. It is difficult for a manager to interpret annual productivity data among species; all four species could be experiencing source habitat in all forest types where they are found or the converse or some combination. However, predictions of λ indicate that the Yellow Warbler is doing well in all habitats

where it is found, but the other three species are barely maintaining stable populations. Nest survival estimates were also misleading indicators of habitat quality; among these four species, Prothonotary Warblers had the highest overall daily nest survival, but the lowest λ. Managers will observe that these four species require conservation of both upland forests and maple-dominated floodplain forests; a goal might be to improve floodplain habitat quality for the Prothonotary Warbler, a species of conservation concern.

Managers may also evaluate habitat-specific λ in light of historical or other information about habitat quality. Mississippi River forest managers are considering silvicultural prescriptions designed to diversify tree stand age and increase the number of tree species in the floodplain (Urich et al. 2002); both habitat diversity measures have declined over the last 50 years (Knutson and Klaas 1998, Yin 1998). The variation in λ among the floodplain forest types for several species suggests that population growth is related in part to forest composition and structure.

In our study area, different agencies are responsible for managing upland forests (states) vs. floodplain forests (U.S. Fish and Wildlife Service and U.S. Army Corps of Engineers). Management agencies can better evaluate their respective responsibilities for managing habitat for different species using our models. A modeling approach for estimating annual productivity and λ will help bird conservation move beyond the nearly exclusive reliance on counts, density, and nest survival as indicators of habitat quality. We acknowledge that ornithologists have much work ahead to make predictions of λ more precise, especially with regard to survival estimates. At a minimum, our models help identify which demographic parameters are most in need of tenacious pursuit.

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