Assessing Ecoregional-Scale Habitat Suitability Index Models for Priority Landbirds

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ABSTRACT Emerging methods in habitat and wildlife population modeling promise new horizons in conservation but only if these methods provide robust population–habitat linkages. We used Breeding Bird Survey (BBS) data to verify and validate newly developed habitat suitability index (HSI) models for 40 priority landbird species in the Central Hardwoods and West Gulf Coastal Plain/Ouachitas Bird Conservation Regions. We considered a species' HSI model verified if there was a significant rank correlation between mean predicted HSI score and mean observed BBS abundance across the 88 ecological subsections within these Bird Conservation Regions. When we included all subsections, correlations verified 37 models. Models for 3 species were unverified. Rank correlations for an additional 5 species were not significant when analyses included only subsections with BBS abundance >0. To validate models, we developed generalized linear models with mean observed BBS abundance as the response variable and mean HSI score and Bird Conservation Region as predictor variables. We considered verified models validated if the overall model was an improvement over an intercept-only null model and the coefficient on the HSI variable in the model was >0. Validation provided a more rigorous assessment of model performance than verification, and models for 12 species that we verified failed validation. Species whose models failed validation were either poorly sampled by BBS protocols or associated with woodland and shrubland habitats embedded within predominantly open landscapes. We validated models for 25 species. Habitat specialists and species reaching their highest densities in predominantly forested landscapes were more likely to have validated models. In their current form, validated models are useful for conservation planning of priority landbirds and offer both insight into limiting factors at ecoregional scales and a framework for monitoring priority landbird populations from readily available national data sets. (JOURNAL OF WILDLIFE MANAGEMENT 73(8):1307–1315; 2009)

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The North American Landbird Conservation Plan recommends creation of landscapes capable of sustaining bird populations range-wide at prescribed levels (Rich et al. 2004). To achieve this goal, the Conservation Plan sets continental population objectives and recommends establishing regional objectives that reflect these continental numbers. Bird–habitat models that assess current regional conditions can characterize the capacity of these landscapes to support and sustain bird populations at prescribed levels and ultimately guide on-the-ground conservation actions (Will et al. 2005). Thus, implementation of the Conservation Plan has created a demand for reliable models that link bird numbers and habitat conditions at regional scales.

Habitat suitability index (HSI) models provide one method for linking bird numbers and habitat conditions. This approach translates quantitative measures of individual habitat features into relative assessments of habitat suitability (scaled from 0 to 1) for a particular species based on its unique habitat associations. Suitability scores for individual habitat features are then combined into a composite score (also scaled 0–1) that represents the overall quality of a location for that species (U.S. Fish and Wildlife Service 1981). Although initially developed to assess habitat quality for species based on field measurements of habitat attributes at the scale of an individual management unit (e.g., forest stand), the recent availability of large-scale spatial data sets and the technological advancement needed to utilize them now permit application of HSI models at scales never envisioned at their conception (VanHorne and Wiens 1991, Stauffer 2002). As a result, HSI models that include remotely sensed landscape-level variables are being developed and applied to increasingly large areas (Storch 2002, Larson et al. 2003, Rittenhouse et al. 2007).

Although widely used, HSI models have been criticized as unreliable and lacking scientific rigor (Cole and Smith 1983, Roloff and Kernohan 1999). In response, Brooks (1997) presented a 4-stage process for creating and testing HSI

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models: development, calibration, verification, and validation, successful completion of which allows HSI models to be used with high confidence and low risk. The first 2 stages focus on the actual construction of the model (development) and testing to ensure the model produces a range of HSI scores from 0 to 1 (calibration). Verification consists of a preliminary analysis of HSI model performance against an independent data set to determine if HSI scores are positively correlated (typically through rank comparisons) with species use, abundance, or occurrence. Lastly, validation is a formal quantitative assessment of the relationship between HSI scores and independent, unranked abundance data (Brooks 1997).

This 4-stage process has been applied to site-scale (1–100 ha) HSI models (e.g., Prosser and Brooks 1998), but it has not been widely employed to test ecoregional-scale ($\geq$1,000-ha) models. Paucity of data on habitat conditions and bird abundance at ecoregional scales makes the process inherently difficult. However, consistent national monitoring programs for forest structure (Forest Inventory and Analysis [FIA]; Miles et al. 2001), landscape composition (National Land Cover Dataset [NLCD]; Vogelmann et al. 1998), and birds (Breeding Bird Survey [BBS]; Sauer et al. 2008) offer promise for developing and testing HSI models at large scales. Our objective was to use BBS data to verify and validate newly developed ecoregional-scale HSI models that predict habitat suitability for priority landbird species from FIA and NLCD data (Tirpak et al. 2009*a*, *b*).

STUDY AREA

We assessed HSI models developed within the approximately 33-million-ha Central Hardwoods Bird Conservation Region (BCR) and the approximately 22-million-ha West Gulf Coastal Plain/Ouachitas BCR (Fig. 1). The Central Hardwoods BCR was centrally located on the North American continent, stretching across a 10-state area that straddled the Mississippi River. The mixed mesophytic and oak (*Quercus* spp.)–hickory (*Carya* spp.) forests of the Central Hardwoods provided habitat for many high-priority bird species (U.S. North American Bird Conservation Initiative Committee 2000), including cerulean warbler (*Dendroica cerulea*), worm-eating warbler (*Helmitheros vermivorum*), and Louisiana waterthrush (*Seiurus motacilla*).

The West Gulf Coastal Plain/Ouachitas BCR extended across 4 states and was dominated by pine forests, mainly loblolly pine (*Pinus taeda*) but with increasing proportions of shortleaf pine (*P. echinata*) in the north and longleaf pine (*P. palustris*) in the south. These forests provided habitat for red-cockaded woodpeckers (*Picoides borealis*), brown-headed nuthatches (*Sitta pusilla*), and Bachman's sparrows (*Aimophila aestivalis*; U.S. North American Bird Conservation Initiative Committee 2000). This BCR also contained extensive bottomland hardwood forests that provided habitat for Swainson's warblers (*Limnothlypis swainsonii*), prothonotary warblers (*Protonotaria citrea*), and wintering waterfowl (U.S. North American Bird Conservation Initiative Committee 2000).

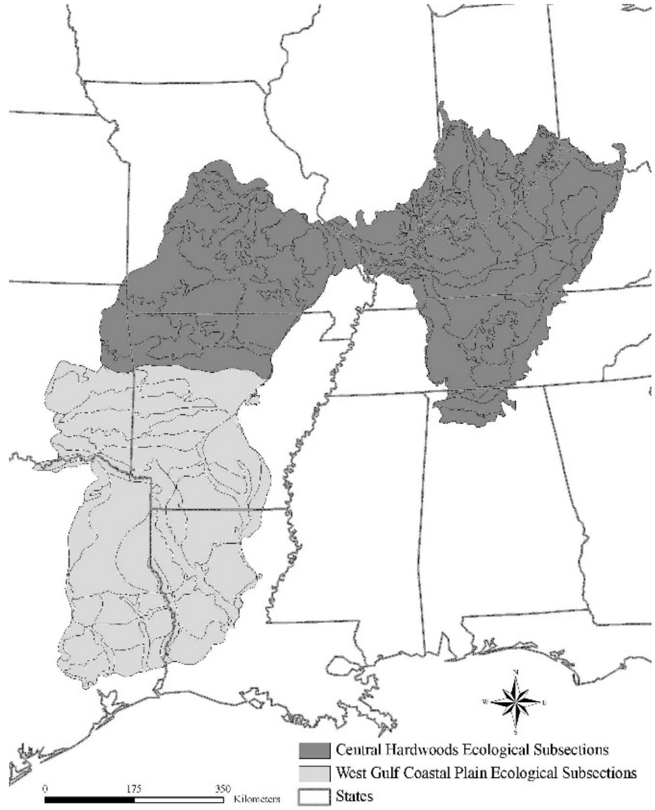

Figure 1. Ecological subsections within the Central Hardwoods and West Gulf Coastal Plain/Ouachitas Bird Conservation Regions in the central and south-central United States, 2005.

METHODS

Models

We developed new HSI models (Tirpak et al. 2009*b*) for 40 priority forest-breeding landbird species that had a Partners in Flight regional combined score $\geq$15, on a scale of 5–25, in either the Central Hardwoods or West Gulf Coastal Plain/Ouachitas BCR (Panjabi et al. 2005). The regional combined score is a relative measure of a species' vulnerability and reflects its conservation importance within a specific BCR based on the extent of its distribution, threats to its habitat, and its population size and trend (Rich et al. 2004, Panjabi et al. 2005). We constructed HSI models as a priori hypotheses on the numerical response of species to site-specific habitat characteristics and landscape variables deemed important based on a literature review. We revised each model based on 2–5 independent reviews by avian ecologists with knowledge of each species' specific habitat requirements. Model parameters for each species were documented in Tirpak et al. (2009*b*). Details of the modeling framework, particularly use of nationally consistent spatial data sets (e.g., NLCD and FIA data), were presented by Tirpak et al. (2009*a*).

We derived spatially explicit estimates of habitat suitability for each species from spatial data layers depicting specific habitat characteristics. We initially calculated HSI scores for each pixel (30-m resolution); however, imputation of FIA data (Tirpak et al. 2009*a*) made estimates of forest structure spatially exact only within ecological subsections (Bailey et al. 1994). Therefore, we used the Zonal Statistics tool in ArcGIS 9.2 to calculate the mean HSI score for each species in each of 59 ecological subsections within the Central Hardwoods and 29 ecological subsections within the West Gulf Coastal Plain/Ouachitas BCR (Fig. 1).

Evaluating Model Performance

We used data from the BBS as an independent data set to evaluate these newly developed HSI models because BBS was the only source of data that provided consistent abundance estimates for the full suite of modeled species, spanned the entire geographic extent of our study area, and was contemporaneous with the habitat data on which we ran HSI models (Roloff and Kernohan 1999). To determine subsection-specific abundance estimates for each species, we used data layers depicting bird species abundance derived from BBS data collected 1994–2003 that we geographically smoothed by applying inverse distance weighting between routes (Sauer et al. 1995). We intersected these data layers with ecological subsection boundaries and calculated area-weighted abundance estimates for each species within each subsection. We used BBS data only for verification and validation and did not use them in model development.

For model verification, we conducted 2 Spearman rank correlation analyses to verify models. The first included data from all subsections to provide insight into overall model performance. In the second analysis, we removed all subsections with a mean abundance estimate of zero to assess whether any positive relationship existed between HSI score and abundance, independent of occurrence. We ranked ecological subsections on mean HSI score and BBS abundance independently within each BCR to compensate for distributional differences in bird densities not captured in the models (e.g., relative scarcity of blue-winged warblers [*Vermivora pinus*] in the West Gulf Coastal Plain/Ouachitas compared with the Central Hardwoods). However, we conducted all correlations on the joint data set (i.e., one containing tied ranks) to maximize the ability to detect patterns. We considered models verified if a significant ($P \leq 0.10$) positive correlation existed between mean HSI score and BBS abundance.

To validate HSI models, we developed generalized linear models (PROC GLM, SAS/STAT®; SAS Institute, Cary, NC) to predict mean BBS abundance as a function of mean HSI score within subsections. Again, to compensate for known distributional differences of species across BCRs, we included BCR as a categorical dummy variable in the linear model. We considered a model validated if 1) it passed the verification test that included all subsections, 2) the model predicting BBS abundance from HSI and BCR was an improvement over an intercept-only null model ($P < 0.10$), and 3) the relationship between the HSI predictor variable and BBS abundance was significantly >0 ($P < 0.10$).

RESULTS

Most of the 40 bird species we modeled were widespread, though not necessarily common, in both BCRs. Twenty-seven species occurred in ≥ 80 subsections (approx. 90% of subsections) and 21 species occurred in all subsections (Table 1). Correlation analyses that included data for all subsections produced significant correlations for 37 species (Table 1). Only models for brown thrasher (*Toxostoma rufum*), great crested flycatcher (*Myiarchus crinitus*), and red-headed woodpecker (*Melanerpes erythrocephalus*) were unverified. When we removed from analysis subsections where BBS data indicated a species did not occur (i.e., abundance $= 0$), correlations for an additional 5 species (Bachman's sparrow, Mississippi kite [*Ictinia mississippiensis*], red-cockaded woodpecker, Swainson's warbler, and swallow-tailed kite [*Elanoides forficatus*]) were not significant (Table 1). Of 19 species that were absent from ≥ 1 subsection, 11 exhibited a poorer correlation between HSI score and abundance when we included only subsections with occurrence in the analysis (Table 1). Declines in the correlation coefficient were not only more common, but also of greater magnitude ($n = 11$; $\bar{x} = -0.16$; range $= -0.40$ to 0.00) than improvements observed for other species ($n = 8$; $\bar{x} = 0.10$; range $= 0.02$–0.33). None of the 3 species that failed the validation test that encompassed all subsections subsequently passed the validation test that included only subsections of occurrence.

Models including HSI and BCR variables were better predictors of abundance ($P \leq 0.10$) than intercept-only null models for 38 of 40 species. Neither BCR nor HSI was a significant predictor of abundance in 3 species' models: Bewick's wren (*Thryomanes bewickii*), great crested flycatcher, and orchard oriole (*Icterus spurius*). The overall model for orchard oriole was significant, though neither HSI nor BCR was a significant predictor on its own. Bird Conservation Region was a significant predictor of abundance in 29 models, whereas HSI was a significant predictor in 25 models (Table 2). For 11 models, BCR alone was a significant predictor; HSI was the lone significant predictor in 8 models. Both BCR and HSI were significant predictors of abundance for 17 models (Table 2). Model fit (R^2) averaged 0.310, ranging from 0.015 to 0.738 (Table 2).

Of the 8 species whose models failed ≥ 1 verification test, 5 (i.e., brown thrasher, great crested flycatcher, Mississippi kite, red-headed woodpecker, and Swainson's warbler) also failed ≥ 1 validation test (Table 3). Models for an additional 10 species failed to demonstrate any relationship between HSI and BBS abundance and were not validated (Table 3). Even so, more than half (25) the species for which we developed new HSI models met all validation criteria. We deemed these models valid and useful for conservation planning (Table 3).

DISCUSSION

Models used to guide management should be tested for reliability by comparing their predictions against independent data (Morrison et al. 1998). We demonstrated how the framework proposed by Brooks (1997) can be adapted to assess ecoregional-scale HSI models with independent bird abundance estimates from the BBS. Our use of the BBS as a completely independent comparison dataset for ecoregional-scale models is a novel approach. More commonly, BBS

Table 1. Spearman rank correlation verification statistics between Habitat Suitability Index model scores and abundance estimates from Breeding Bird Survey data (1994–2003) for 40 priority landbird species within 88 ecological subsections of the Central Hardwoods ($n = 59$) and West Gulf Coastal Plain/Ouachitas ($n = 29$) Bird Conservation Regions, USA.

		All subsections		Subsections with abundance >0		
Species	**Scientific name**	r_s	P	n	r_s	P
Acadian flycatcher	*Empidonax virescens*	0.47	≤0.001	88	0.47	≤0.001
American woodcock	*Scolopax minor*	0.36	≤0.001	50	0.68	≤0.001
Bachman's sparrow	*Aimophila aestivalis*	0.62	≤0.001	29	0.24	0.208
Bell's vireo	*Vireo bellii*	0.44	≤0.001	54	0.46	≤0.001
Bewick's wren	*Thryomanes bewickii*	0.40	≤0.001	74	0.35	0.002
Black-and-white warbler	*Mniotilta varia*	0.54	≤0.001	85	0.53	≤0.001
Blue-gray gnatcatcher	*Polioptila caerulea*	0.58	≤0.001	88	0.58	≤0.001
Blue-winged warbler	*Vermivora pinus*	0.26	0.014	64	0.28	0.026
Brown thrasher	*Toxostoma rufum*	−0.07	0.517	88	−0.07	0.517
Brown-headed nuthatch	*Sitta pusilla*	0.58	≤0.001	37	0.80	≤0.001
Carolina chickadee	*Poecile carolinensis*	0.55	≤0.001	88	0.55	≤0.001
Cerulean warbler	*Dendroica cerulea*	0.44	≤0.001	60	0.42	≤0.001
Chimney swift	*Chaetura pelagica*	0.50	≤0.001	88	0.50	≤0.001
Chuck-will's-widow	*Caprimulgus carolinensis*	0.34	≤0.001	86	0.32	0.003
Eastern wood-pewee	*Contopus virens*	0.46	≤0.001	88	0.46	≤0.001
Field sparrow	*Spizella pusilla*	0.54	≤0.001	87	0.55	≤0.001
Great crested flycatcher	*Myiarchus crinitus*	0.11	0.308	88	0.11	0.308
Hooded warbler	*Wilsonia citrina*	0.49	≤0.001	84	0.42	≤0.001
Kentucky warbler	*Oporornis formosus*	0.71	≤0.001	88	0.71	≤0.001
Louisiana waterthrush	*Seiurus motacilla*	0.56	≤0.001	88	0.56	≤0.001
Mississippi kite	*Ictinia mississippiensis*	0.31	0.003	49	0.14	0.337
Northern bobwhite	*Colinus virginianus*	0.29	0.006	88	0.29	0.006
Northern parula	*Parula americana*	0.51	≤0.001	88	0.51	≤0.001
Orchard oriole	*Icterus spurius*	0.34	≤0.001	88	0.34	≤0.001
Painted bunting	*Passerina ciris*	0.56	≤0.001	38	0.58	≤0.001
Pileated woodpecker	*Dryocopus pileatus*	0.33	0.002	88	0.33	0.002
Prairie warbler	*Dendroica discolor*	0.41	≤0.001	88	0.41	≤0.001
Prothonotary warbler	*Protonotaria citrea*	0.39	≤0.001	83	0.41	≤0.001
Red-cockaded woodpecker	*Picoides borealis*	0.49	≤0.001	10	0.17	0.645
Red-headed woodpecker	*Melanerpes erythrocephalus*	0.11	0.308	88	0.11	0.308
Swainson's warbler	*Limnothlypis swainsonii*	0.31	0.003	31	-0.03	0.893
Swallow-tailed kite	*Elanoides forficatus*	0.73	≤0.001	8	0.33	0.432
Whip-poor-will	*Caprimulgus vociferus*	0.30	0.005	76	0.47	≤0.001
White-eyed vireo	*Vireo griseus*	0.33	0.002	88	0.33	0.002
Wood thrush	*Hylocichla mustelina*	0.52	≤0.001	88	0.52	≤0.001
Worm-eating warbler	*Helmitheros vermivorum*	0.66	≤0.001	88	0.66	≤0.001
Yellow-billed cuckoo	*Coccyzus americanus*	0.24	0.024	88	0.24	0.024
Yellow-breasted chat	*Icteria virens*	0.40	≤0.001	88	0.40	≤0.001
Yellow-throated vireo	*Vireo flavifrons*	0.51	≤0.001	88	0.51	≤0.001
Yellow-throated warbler	*Dendroica dominica*	0.51	≤0.001	87	0.48	≤0.001

data are used to both develop and test models via data resampling or withholding strategies (Thogmartin et al. 2004, Niemuth et al. 2005, Fearer et al. 2007). However, these methods may overlook spurious model parameters or poor model fit (Peterjohn 2001). By relying on BBS solely as a comparison data set, we avoided these potential pitfalls and strengthened the inference of validated HSI models.

Within the model assessment framework applied to the HSI models in our study, verification provided a cursory appraisal of the potential utility of these models, and validation provided a more rigorous test of model performance. All models that failed the first verification test based on the all-subsections data set also failed ≥1 validation test. Thus, verification may be useful as a preliminary assessment of models. Conducting verification analyses prior to more formal, thorough, and time-consuming validation tests would provide early evidence of flawed models.

The 5 species that failed only the second verification test (i.e., based on subsections with abundance >0) were generally the rarest of the species we modeled. Sample size is widely recognized as an important determinant of accuracy of bird–habitat models (Brotons et al. 2007, Murray et al. 2008), and Stockwell and Peterson (2002) observed maximal accuracy of species distribution models developed with ≥50 data points. None of the 5 species that failed the second verification test occurred in ≥50 subsections and only 2 species (brown-headed nuthatch and painted bunting [*Passerina ciris*]) that occurred in <50 subsections passed the second verification test. Although we did not develop HSI models from empirical spatial data, assessment of these HSI models is subject to the reduced power and lower variability that small sample sizes and lower likelihoods of occurrence produce (Boone and Krohn 1999, Karl et al. 2002). Because the second verification test may reflect a species' occurrence as much as its model's performance and provides little new information from the first verification test (all species that failed the first test also failed the second), we recommend relying solely on

Table 2. Fit statistics, coefficients, and performance criteria for models relating mean Habitat Suitability Index scores to area-weighted mean abundance estimates derived from Breeding Bird Survey data (1994–2003) for 40 priority landbird species within 88 ecological subsections of the Central Hardwoods and West Gulf Coastal Plain/Ouachitas Bird Conservation Regions, USA.

Species	Model		Intercept		BCR[b]			HSI[d]		
	P[a]	R^2	β_0	SE	B_1	SE	P[c]	β_2	SE	P[c]
Acadian flycatcher	0.095	0.054	1.264	0.459	0.453	0.333	0.177	4.250	2.072	0.043
American woodcock	≤0.001	0.218	0.001	0.002	0.011	0.003	≤0.001	0.090	0.023	≤0.001
Bachman's sparrow	≤0.001	0.567	0.147	0.019	−0.149	0.020	≤0.001	0.908	0.511	0.079
Bell's vireo	0.042	0.072	0.411	0.105	−0.275	0.108	0.013	−19.906	32.651	0.544
Bewick's wren	0.517	0.015	0.226	0.123	0.145	0.128	0.260	−3.193	17.703	0.857
Black-and-white warbler	≤0.001	0.380	0.762	0.317	−1.530	0.249	≤0.001	3.194	0.692	≤0.001
Blue-gray gnatcatcher	≤0.001	0.210	2.472	1.129	−1.691	0.785	0.034	19.265	4.052	≤0.001
Blue-winged warbler	≤0.001	0.232	0.064	0.106	0.498	0.102	≤0.001	1.717	1.766	0.334
Brown thrasher	≤0.001	0.719	2.173	0.424	2.704	0.277	≤0.001	−7.087	2.943	0.018
Brown-headed nuthatch	≤0.001	0.738	0.097	0.082	−0.146	0.081	0.075	4.712	0.549	≤0.001
Carolina chickadee	≤0.001	0.473	9.053	1.179	−4.628	0.708	≤0.001	5.142	2.436	0.038
Cerulean warbler	≤0.001	0.205	−0.009	0.041	0.105	0.064	0.102	0.627	0.270	0.023
Chimney swift	≤0.001	0.208	4.220	2.503	4.741	2.434	0.055	5.043	7.880	0.524
Chuck-will's-widow	≤0.001	0.312	1.333	0.232	−1.024	0.165	≤0.001	0.569	0.695	0.415
Eastern wood-pewee	≤0.001	0.472	2.260	0.757	4.572	0.527	≤0.001	5.183	1.545	≤0.001
Field sparrow	≤0.001	0.690	−2.045	1.145	13.765	1.076	≤0.001	37.060	7.637	≤0.001
Great crested flycatcher	0.152	0.043	4.655	0.440	−0.427	0.285	0.137	−2.740	1.888	0.151
Hooded warbler	≤0.001	0.551	1.955	0.807	−3.885	0.507	≤0.001	8.190	1.819	≤0.001
Kentucky warbler	≤0.001	0.346	0.540	0.407	0.194	0.276	0.484	6.351	0.958	≤0.001
Louisiana waterthrush	≤0.001	0.263	0.028	0.050	0.146	0.038	≤0.001	3.664	0.978	≤0.001
Mississippi kite	≤0.001	0.287	0.235	0.034	−0.210	0.036	≤0.001	−0.176	0.686	≤0.001
Northern bobwhite	≤0.001	0.440	10.268	1.785	9.134	1.229	≤0.001	−37.119	15.075	0.016
Northern parula	≤0.001	0.276	−0.303	0.370	1.171	0.246	≤0.001	5.250	1.278	≤0.001
Orchard oriole	0.088	0.056	2.544	0.421	0.567	0.378	0.137	2.442	1.981	0.221
Painted bunting	≤0.001	0.480	3.342	0.613	−4.902	0.566	≤0.001	70.737	21.116	≤0.001
Pileated woodpecker	≤0.001	0.313	1.625	0.348	−0.696	0.251	0.007	8.852	1.722	≤0.001
Prairie warbler	0.005	0.117	0.703	0.354	0.518	0.330	0.121	15.317	4.615	≤0.001
Prothonotary warbler	≤0.001	0.249	0.378	0.078	−0.178	0.073	0.017	2.271	0.713	0.002
Red-cockaded woodpecker	≤0.001	0.203	0.006	0.006	−0.068	0.006	0.285	0.094	0.045	0.042
Red-headed woodpecker	≤0.001	0.225	0.702	0.123	0.745	0.155	≤0.001	−3.359	15.349	0.827
Swainson's warbler	≤0.001	0.260	0.479	0.093	−0.438	0.082	≤0.001	−0.298	0.570	0.602
Swallow-tailed kite	≤0.001	0.522	0.003	0.003	−0.005	0.004	0.193	0.725	0.086	≤0.001
Whip-poor-will	0.002	0.139	−0.161	0.316	0.663	0.257	0.012	1.270	1.048	0.229
White-eyed vireo	≤0.001	0.529	15.335	1.539	−10.098	1.070	≤0.001	−9.070	11.114	0.417
Wood thrush	≤0.001	0.311	0.425	0.650	1.985	0.433	≤0.001	9.992	2.410	≤0.001
Worm-eating warbler	≤0.001	0.408	−0.022	0.078	0.087	0.083	0.298	1.798	0.254	≤0.001
Yellow-billed cuckoo	≤0.001	0.190	9.396	0.615	−3.088	0.701	≤0.001	5.265	5.068	0.302
Yellow-breasted chat	≤0.001	0.379	10.562	1.582	−3.278	1.555	0.038	93.367	26.759	≤0.001
Yellow-throated vireo	0.002	0.133	0.744	0.185	0.053	0.136	0.697	2.811	0.778	≤0.001
Yellow-throated warbler	0.003	0.125	0.042	0.242	0.590	0.173	≤0.001	2.870	1.208	0.020

[a] Model df = 2; residual df = 85.
[b] Dummy variable for Bird Conservation Region (BRC): Central Hardwoods = 1; West Gulf Coastal Plain/Ouachitas = 0.
[c] df = 85.
[d] Habitat Suitability Index (HSI) score.

verification tests involving all subsections for initial assessment of models, particularly when sample sizes are small ($n < 50$).

Although BBS data were useful for validating a majority of (25) the HSI models, we did identify limitations to the use of BBS data as well. Specifically, BBS protocols poorly sample some species and thus yield inaccurate estimates of their abundance (Robbins et al. 1989). These biases are the result of either the location of routes relative to a species' preferred habitat (e.g., Swainson's warbler; Bednarz et al. 2005) or the timing of sampling relative to a species' peak daily activity period (e.g., chuck-will's-widow [*Caprimulgus carolinensis*] and whip-poor-will [*Caprimulgus vociferus*]; Wilson 2008). Validation tests based on biased estimates of abundance are likewise biased and cannot be used to definitively validate or invalidate models. Where available, we recommend use of alternative data sets collected with methodologies specific to sampling species underrepresented in BBS (e.g., The Nightjar Survey Network; Wilson 2008) for a more thorough assessment of models for species with known BBS abundance biases.

For species well represented on BBS routes, failure to validate their HSI models suggests the models poorly depict the species' habitat relationships, either due to presence of poorly parameterized functions in the model or absence of key limiting factors from the model. The red-headed woodpecker model offers an example of the former. Although the overall model was highly significant ($P <$ 0.001), this was primarily due to the inclusion of BCR as a model predictor. The coefficient on HSI was negative and

Table 3. Verification and validation status of Habitat Suitability Index (HSI) models for 40 priority landbird species in the Central Hardwoods and West Gulf Coastal Plain/Ouachitas Bird Conservation Regions, USA, 1994–2003.

Species	Verification		Validation		Status[a]
	All subsections	Subsection abundance >0	Model	HSI	
Acadian flycatcher	Pass[b]	Pass	Pass[c]	Pass[d]	Validated
American woodcock	Pass	Pass	Pass	Pass	Validated
Bachman's sparrow	Pass	Fail	Pass	Pass	Validated
Bell's vireo	Pass	Pass	Pass	Fail	Not validated
Bewick's wren	Pass	Pass	Fail	Fail	Not validated
Black-and-white warbler	Pass	Pass	Pass	Pass	Validated
Blue-gray gnatcatcher	Pass	Pass	Pass	Pass	Validated
Blue-winged warbler	Pass	Pass	Pass	Fail	Not validated
Brown thrasher	Fail	Fail	Pass	Fail	Not validated
Brown-headed nuthatch	Pass	Pass	Pass	Pass	Validated
Carolina chickadee	Pass	Pass	Pass	Pass	Validated
Cerulean warbler	Pass	Pass	Pass	Pass	Validated
Chimney swift	Pass	Pass	Pass	Fail	Not validated
Chuck-will's-widow	Pass	Pass	Pass	Fail	Not validated
Eastern wood-pewee	Pass	Pass	Pass	Pass	Validated
Field sparrow	Pass	Pass	Pass	Pass	Validated
Great crested flycatcher	Fail	Fail	Fail	Fail	Not validated
Hooded warbler	Pass	Pass	Pass	Pass	Validated
Kentucky warbler	Pass	Pass	Pass	Pass	Validated
Louisiana waterthrush	Pass	Pass	Pass	Pass	Validated
Mississippi kite	Pass	Fail	Pass	Fail	Not validated
Northern bobwhite	Pass	Pass	Pass	Fail	Not validated
Northern parula	Pass	Pass	Pass	Pass	Validated
Orchard oriole	Pass	Pass	Pass	Fail	Not validated
Painted bunting	Pass	Pass	Pass	Pass	Validated
Pileated woodpecker	Pass	Pass	Pass	Pass	Validated
Prairie warbler	Pass	Pass	Pass	Pass	Validated
Prothonotary warbler	Pass	Pass	Pass	Pass	Validated
Red-cockaded woodpecker	Pass	Fail	Pass	Pass	Validated
Red-headed woodpecker	Fail	Fail	Pass	Fail	Not validated
Swainson's warbler	Pass	Fail	Pass	Fail	Not validated
Swallow-tailed kite	Pass	Fail	Pass	Pass	Validated
Whip-poor-will	Pass	Pass	Pass	Fail	Not validated
White-eyed vireo	Pass	Pass	Pass	Fail	Not validated
Wood thrush	Pass	Pass	Pass	Pass	Validated
Worm-eating warbler	Pass	Pass	Pass	Pass	Validated
Yellow-billed cuckoo	Pass	Pass	Pass	Fail	Not validated
Yellow-breasted chat	Pass	Pass	Pass	Pass	Validated
Yellow-throated vireo	Pass	Pass	Pass	Pass	Validated
Yellow-throated warbler	Pass	Pass	Pass	Pass	Validated

[a] Validated models passed the all-subsections verification test and both validation tests.
[b] Passing models were significantly different from zero at $P \leq 0.100$.
[c] Passing models were significantly different from an intercept-only null model at $P \leq 0.100$.
[d] Passing models had HSI predictors significantly >0 at $P \leq 0.100$.

nonsignificant ($\beta = -3.359$, $P = 0.827$), indicating that HSI does not improve prediction of red-headed woodpecker abundance. Conversely, the Bewick's wren model represents a potential example of a model lacking a critical limiting factor. The Bewick's wren has experienced a drastic contraction from its eastern range over the past century due, in part, to competition with house wrens (*Troglodytes aedon*; Kennedy and White 1996). By not explicitly considering house wren abundance in our model, we may be ignoring a primary limiting factor for this species. As a result, sites that are suitable based on vegetative structure may remain unoccupied due to interspecific competition (Sánchez-Cordero et al. 2008). Because HSI models are built on a priori knowledge, they estimate potential habitat and typically overestimate available habitat especially for unsaturated populations (Fielding and Bell 1997, Hepinstall et al. 2002). Similar circumstances may exist for other species whose models we did not validate (e.g., the loss of suitable open chimneys as nesting substrates for chimney swifts [*Chaetura pelagica*]).

Issues of scale when calculating mean HSI values also may have influenced our validation analyses. Many of the species whose models we did not validate reach their highest densities in woodlands (e.g., orchards, parks, and woodlots) or shrublands (e.g., glades, hedgerows, and thickets) within otherwise unsuitable agricultural or developed matrices (Scharf and Kren 1996, Lanyon 1997, Budnik et al. 2000). Because we assumed all non-forested habitats had an HSI score of zero, species that reach their highest densities in subsections dominated by non-forested habitats had lower mean HSI scores for those subsections due simply to the abundance of HSI scores of zero within the subsection (Murray et al. 2008). This bias occurs even though specific functions in the models (e.g., interspersion and edge indices) identify the few forested sites within these landscapes as highly suitable (Tirpak et al. 2009*b*). Thus, it may be more appropriate to validate models for species that are abundant in forested habitats within predominantly non-forested landscapes by using different assessment methods or calculating a mean HSI score only for sites with an HSI score >0.

Despite the challenges and limitations of using BBS data, we successfully validated HSI models for 25 species. Species with valid models were typically habitat specialists that occurred in predominantly forested landscapes (e.g., red-cockaded woodpecker and cerulean warbler). Models for habitat specialists tend to perform better than those for habitat generalists due to the ability of the model to more severely restrict specialists to a smaller range of habitat conditions (Kilgo et al. 2002, Seoane et al. 2005). As habitats in which a species occurs become more broadly defined (i.e., more generalist), models have greater difficulty differentiating suitable from unsuitable habitat, likely because the range of conditions is so broad the models encompass all habitat types and predict the species will occur everywhere (Dettmers et al. 2002, Hepinstall et al. 2002). Species associated with predominantly forested landscapes were also not subject to the aforementioned bias introduced by non-forested habitat when calculating mean HSI at the subsection scale (Crozier and Niemi 2003). This trait may explain why early successional species that are more common in regenerating forests (e.g., prairie warbler [*Dendroica discolor*] and yellow-breasted chat [*Icteria virens*]) had valid HSI models, whereas models of species occurring more frequently in glades (e.g., blue-winged warbler) failed validation (Fink et al. 2006).

MANAGEMENT IMPLICATIONS

The use of bird–habitat models in conservation planning will likely increase as landscape factors are more explicitly considered in management decisions and local management becomes integrated across larger scales (National Ecological Assessment Team 2006). However, the high cost of collecting independent data sets to validate these models may preclude formal accuracy assessments from occurring (Morrison et al. 1998). The use of BBS data as an independent comparison data set for assessing ecoregional-scale models, as we demonstrated, is a cost-effective and practical solution to this problem. Based on our analyses, we are confident that validated models offer not only ecological insight into the response of priority landbirds to habitat conditions but can also serve as useful tools for conservation planning. Habitat Suitability Index models may be used to prioritize subsections for management activities, provide insight into the potential limiting factors determining habitat suitability within a subsection, and serve as a basis for monitoring changes in habitat suitability for priority landbirds. Nevertheless, we continue to recognize that HSI models are a priori hypotheses on the relationship between habitat suitability and environmental variables. The ultimate utility of our models (and the success of management decisions based on them) will depend on a more complete understanding of the validity, limitations, and scale at which models are most applicable. Although we ultimately classified models as achieving or failing validation, this dichotomy was an artificial construct used to differentiate models that actually fell along a continuous gradient of reliability. Prior to their application in conservation planning, users of these models should consider not only the validation status of each model but also measures of their reliability as predictors of a species' abundance (e.g., R^2). Furthermore, although we have shown support for some models at the subsection scale, rigorous testing with spatially explicit, spatially exact, and site-specific data sets of bird abundance and habitat characteristics are needed to further ascertain the validity of these models at finer scales.

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