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Management and Conservation Article

Evaluation of Habitat Suitability Models for Forest Passerines Using Demographic Data

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ABSTRACT Habitat suitability is often used as a surrogate for demographic responses (i.e., abundance, survival, fecundity, or population viability) in the application of habitat suitability index (HSI) models. Whether habitat suitability actually relates to demographics, however, has rarely been evaluated. We validated HSI models of breeding habitat suitability for wood thrush (*Hylocichla mustelina*) and yellow-breasted chat (*Icteria virens*) in Missouri, USA. First, we evaluated HSI models as a predictor of 3 demographic responses: within-site territory density, site-level territory density, and nest success. We demonstrated a link between HSI values and all 3 types of demographic responses for the yellow-breasted chat and site-level territory density for the wood thrush. Second, we evaluated support for models containing HSI values, models containing measured habitat features (e.g., tree age, tree species, ecological land type), and models containing management treatments (e.g., even-aged and uneven-aged forest regeneration treatments) for each demographic response using model selection. Models containing HSI values received more support, in general, than models containing only habitat features or management treatments for all 3 types of wildlife response. The assumption that changes in habitat suitability represent wildlife demographic response to vegetation change is supported by our models. However, differences in species ecology may contribute to the degree to which HSI values are related to specific demographic responses. We recommend validation of HSI models with the particular demographic data of interest (i.e., density, productivity) to increase confidence in the model used for conservation planning.

KEY WORDS habitat suitability, habitat suitability index model, *Hylocichla mustelina*, *Icteria virens*, logistic-exposure, model validation, nest success, territory density, wood thrush, yellow-breasted chat.

Land-management planning, such as national forest plans, often involves simulation of vegetation change and evaluation of associated wildlife response using habitat-relationship models (Kliskey et al. 1999, Klaus et al. 2005). Planning approaches that use habitat suitability index (HSI) models provide a means of quantifying and ranking differences in habitat suitability among sites or alternative management strategies (Gustafson et al. 2001, Marzluff et al. 2002, Larson et al. 2004, Dijak and Rittenhouse 2009). When choosing among management alternatives, planners and managers often assume that habitat suitability is a surrogate for animal response, either in terms of occupancy (i.e., probability a site is occupied by a species of interest) or demography (i.e., survival, fecundity, or population viability) and that changes in habitat suitability correspond to numerical changes in wildlife populations. In this way, HSI models are important tools for land-management planning if they capture variables that meet biological requirements of the species of interest, if those variables can be manipulated by managers, and if suitability is associated with demographic measures of reproductive success or productivity.

Model validation is necessary to assess whether there is a link among habitat management, habitat suitability, and demographic response (Rykiel 1996). Reliability of the link may vary depending on species ecology (Van Horne 1983), spatial scale (Orians and Wittenberger 1991, Chalfoun and Martin 2007), and the type of wildlife demographic data used for model validation. We might expect a stronger relationship between suitability and demographic response when a specific habitat feature affects suitability for a habitat specialist. For example, yellow-breasted chats (*Icteria virens*) are associated with early successional forest and rarely use mid- to late-successional forest (Annand and Thompson 1997, Eckerle and Thompson 2001). Nest success and territory density for yellow-breasted chat are higher in young forest stands than in mature forest stands (Thompson et al. 1992, Annand and Thompson 1997, Gram et al. 2003). In contrast, wood thrush (*Hylocichla mustelina*), a habitat generalist, uses a range of forest habitats and age classes resulting from forest regeneration techniques during nesting and postfledging periods (Thompson et al. 1992, Annand and Thompson 1997, Anders et al. 1998, Gram et al. 2003), and, as a result, we might expect a weaker

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relationship between suitability and nest success for habitat generalists. An assessment of these issues may reduce uncertainty in planning decisions based on HSI models and thereby improve the reliability of the planning process.

We addressed 2 important questions regarding the use of HSI models for management decisions: 1) are HSI models sufficient for their intended purpose, and 2) how do HSI models compare to alternative models? We asked these questions in the context of determining wood thrush and yellow-breasted chat response to even-aged and uneven-aged forest management techniques. Thus, our first objective was to determine whether a link exists between HSI values and demographic responses of wood thrush and yellow-breasted chat to habitat management. Our second objective was to compare HSI models with models of specific habitat features that increase risk of nest predation and brood parasitism (i.e., distance to edge), as well as models of habitat management treatments. We anticipated 2 possible outcomes when evaluating HSI models with demographic data. Variation in expert opinion, uncertainty in habitat suitability relationships, and model complexity may negatively influence HSI model performance (Johnson and Gillingham 2004), particularly when applied to a specific study site and validated with site-specific data. Alternatively, we might expect HSI models to perform as well as, or better than, statistical models of habitat features or management effects because the HSI models are conceptually strong, were developed to evaluate breeding habitat suitability, and inherently consider demography (Rittenhouse et al. 2007).

STUDY AREA

We obtained all data from the Missouri Ozark Forest Ecosystem Project (MOFEP), a large-scale, long-term experiment conducted by the Missouri Department of Conservation and collaborators to determine the effects of even-aged and uneven-aged management on biotic and abiotic ecosystem attributes of a predominantly oak (*Quercus* spp.) and hickory (*Carya* spp.) forest located in the Ozark hills of south-central Missouri, USA (Brookshire et al. 1997). The experimental design consisted of 9 sites: 3 each of control sites, even-aged management (EAM) sites, and uneven-aged management (UAM) sites. The sites ranged from 312 ha to 514 ha. Before harvest, all sites were $\geq$84% forested and contained overstory trees that were 50–70 years old (Brookshire and Dey 2000). Harvest treatments occurred in May–November 1996. The EAM treatments included clear cutting (EAM clear cut) and intermediate cutting (i.e., thinning; EAM thinning) applied to stands of 1–31 ha on each EAM site (Kabrick et al. 2002). The total area treated by both methods for the 3 EAM sites was 123 ha (34%) of site 3, 103 ha (33%) of site 5, and 69 ha (15%) of site 9. The UAM included small group and single-tree selection cuts applied to stands of 3–80 ha in size. The total area treated by UAM was 354 ha (69%) of site 2, 297 ha (62%) of site 4, and 208 ha (41%) of site 7. The total area of group openings was 5% of each UAM site or 19 ha of site 2, 15 ha of site 4, and 10 ha of site 7. Approximately 10% of the forest area within EAM and UAM treatment sites was designated old growth preserve and remained uncut. No tree harvest occurred on control site 1 (389 ha), site 6 (440 ha), or site 8 (340 ha).

METHODS

Demographic Data

We used nest success, within-site territory density, and site-level territory density information from MOFEP for HSI model validation. Within-site density and site-level territory density were related to habitat-patch and landscape scales, respectively, and represented different spatial resolutions of data (10-m cells vs. 300–500-ha sites), whereas nest success was an attribute of an individual organism and its territory. Trained observers used spot-mapping to determine territory density for each of the 9 MOFEP sites. Observers visited each site 10 times at 2–3 day intervals from mid-May to the first week of July each year from 1991 to 1995 and from 1997 to 2002. During each visit, observers marked all detections of birds on an enlarged topographic map of each site. We used a composite map containing detections from all visits by year to determine the number of territories, with a territory defined as a cluster of $\geq$3 observations across all visits within a year (Clawson et al. 1997). The MOFEP data set contained 1,297 wood thrush territories and 357 yellow-breasted chat territories from 1991 to 2000. We lacked territory information for years 2001 and 2002.

Concurrent with spot-mapping, observers located and monitored nests for target species. Observers monitored nests every 3–5 days until nest fate was determined. Because of insufficient sample sizes for yellow-breasted chats before treatment, we limited the analysis to posttreatment years for nest success (1997–2002) and territory density (1997–2000). We analyzed fates of 244 wood thrush nests and 66 yellow-breasted chat nests from 1991–2002, resulting in effective sample sizes (no. of observation days $\times$ no. of nests; Rotella et al. 2000) of 2,556 for wood thrush and 618 for yellow-breasted chats. Median interval length between nest visits was 3 days for both species, with 99% of all intervals $<$8 days for wood thrush and $<$7 days for yellow-breasted chats.

Habitat Suitability Index Models

We determined breeding habitat suitability for wood thrush and yellow-breasted chat using Landscape HSImodels software (version 2.1, <www.nrs.fs.fed.us/hsi>, accessed 29 Nov 2007; Dijak et al. 2007). Details for wood thrush and yellow-breasted chat HSI model development, including citations supporting the suitability relationships for each species, are provided in Rittenhouse et al. (2007). Both models assigned suitability for breeding based on tree age class, landform type, and patch size. The wood thrush HSI model contained 5 suitability indexes:

$$HSI = SI_1 \times \left(\sqrt[3]{SI_2 \times SI_3 \times SI_5}\right) \qquad (1)$$

where SI_1 is a function of tree species groups (forest types) suitable for nesting, SI_2 is a function of tree age and landform, SI_3 is a function of forest area requirements, and

SI_5 is a function of the proportion of postfledging habitat within 1 km of natal sites. We used SI_4 to identify early successional forest as part of the calculation for SI_5, and it was not included in the HSI equation. The yellow-breasted chat HSI model contained 3 suitability indexes:

$$HSI = \left(\sqrt[2]{SI_1 \times SI_2}\right) \times SI_3 \qquad (2)$$

where SI_1 is a function of early successional forest based on tree age and landform, SI_2 is a function of patch area requirements, and SI_3 represents suitability as a function of distance from early successional habitat to mid- to late-successional forest.

We developed a landform map using a 30-m digital elevation model resampled to 10-m resolution and the Topographic Position Index (TPI) extension (Jenness Enterprises, Flagstaff, AZ) for ArcView 3.x. We defined 5 landform classes based on different combinations of slope, aspect, and TPI: 1) ridges, 2) south and west slopes, 3) upland drainages, 4) north and east slopes, and 5) bottomlands.

We used the woody vegetation inventory from 1994 to 1995 to establish the initial vegetation conditions (tree age and species) for the MOFEP sites and to create the Geographic Information System (GIS) layers required for the HSI models, all at 10 × 10-m cell resolution (0.01 ha). Shifley et al. (2000) and Brookshire and Dey (2000) presented details of the woody vegetation sampling procedure and information obtained from 648 permanent vegetation plots located throughout the MOFEP. Each vegetation plot contained 4 subplots of 0.2 ha each, within which, diameter at breast height and species of all trees ≥11 cm was recorded. The inventory contained approximately 55,000 trees and 48 tree species. To facilitate establishment of initial vegetation conditions and to keep the data compatible with habitat suitability models (Rittenhouse et al. 2007), we collapsed tree species into the following tree species groups: white oaks (*Quercus alba*, *Quercus stellata*, *Quercus muehlenbergii*), black oaks (*Quercus velutina*, *Quercus rubra*, *Quercus coccinea*), conifers (*Pinus echinata*, *Juniperus virginiana*), and other hardwoods (*Acer rubrum*, *Acer saccharum*, *Carya* spp.). Additionally, we considered only dominant, overstory trees within each plot. We defined dominant, overstory trees as the top 9 trees ranked by diameter at breast height for each plot. We determined the proportion of each tree species group within the top 9 trees and assigned tree species to each cell based on those proportions. Because age data were not collected for all trees, we assigned an approximate age based on diameter at breast height using species (group)-specific equations (S. R. Shifley, United States Department of Agriculture, Forest Service, Northern Research Station, unpublished data). The initial vegetation composition for the landscape approximated the spatial patterns of the vegetation conditions of the MOFEP.

We applied EAM by resetting tree age to 4 years on harvested cells. For UAM group selection, we reset tree age to 4 years. Because UAM single-tree harvest removed only the dominant tree from a cell, we assigned a new tree species and tree age by sampling from the top 10–18 trees ranked by diameter at breast height. These trees averaged 10–25 years younger than the harvested tree.

We applied HSI models to the MOFEP landscape and used the resulting habitat suitability maps to summarize habitat suitability at the territory and site scales. For the territory scale, we used a moving-window analysis to calculate mean HSI value (mnHSI_terr) from each 10 × 10-m cell within an area equivalent to the average territory size for each species. We used a 120-m radius moving window for wood thrush, which resulted in a moving-window size of 4.52 ha and approximated a mean natal territory size of 4.5 ha (Anders et al. 1998). For yellow-breasted chat, we used a 60-m-radius moving window, which resulted in a moving-window size of 1.13 ha and approximated a mean territory size of 1.2 ha (Thompson and Nolan 1973). For the site scale, we calculated mean HSI value of each of the 9 sites (mnHSI_site). For nest success, we plotted nest locations on the territory-scale map to obtain corresponding mnHSI_terr values. We used mnHSI_terr and mnHSI_site as independent variables in subsequent analyses.

Validation of HSI Models

Our first objective was to evaluate the HSI models as a predictor of 3 demographic responses, within-site territory density, site-level territory density, and nest success, by fitting generalized linear mixed models with the appropriate HSI term as the predictor variable. We conducted likelihood ratio tests (LRT) to determine whether the model containing the HSI variable had a greater likelihood than an intercept-only model. We defined the LRT statistic as $2[\ln(L_{model}) - \ln(L_{null})]$, where $\ln(L_{model})$ was the maximum log likelihood of the model containing the HSI term and $\ln(L_{null})$ was the log likelihood of the null model. We also examined significance of the estimated coefficient for the HSI effect using a Type III test of fixed effects. Finally, we plotted predicted density or nest success as a function of the HSI variable for all statistically significant models.

Within-site and site-level territory density.—We defined territory density in 2 ways: as a surface or map containing a density value for each 10 × 10-m cell (within-site territory density), and as a single value for each site (site-level territory density). These 2 response variables represent different resolutions of data that may be suitable depending on data availability or management objectives. Within-site territory density provided density values for every 10-m^2 cell on every site, whereas site-level territory density provided one density value for an entire site. We defined site-level territory density as the count of all territories within a site by year, divided by the site's area.

We created the within-site territory density response variable by applying a weighted distance function to the composite map of territories for each year. We calculated distance (d_i) from a focal cell to each territory centroid within a 3-km radius of the focal cell. The 3-km radius approximated the longest dimension of a MOFEP site. The weighted density estimate W for each cell was

$$W = \sum_{i=1}^{n} \left(\frac{1}{d_i} \right) \tag{3}$$

where d_i was distance (m) from the cell to territory i. In other words, if 10 territories occurred within the focal cell and no other territories occurred within a 3-km radius, density was 10 territories per 28.3 km^2. The weighted density estimate rapidly declined toward zero as distance between territories increased. To address spatial correlation in the response variable, we used a semivariogram to estimate the range (distance) at which correlation was insignificant for each species (200 m for wood thrush, 350 m for yellow-breasted chat). We then sampled GIS layers at either the 200-m or 350-m interval to obtain within-site territory density and HSI values and used those values for analysis. We also examined semivariogram plots of the residuals of the fitted models and found no evidence of spatial correlation (Cressie 1993).

We used a mixed-effects model for repeated measures, with year as the repeated effect and within-site territory density or site-level territory density as the dependent variable. In repeated-measures analyses, failure to account for potential correlation among multiple observations of the same subject (i.e., cell) over time (i.e., yr) can increase the Type I error rate and produce biased estimates of standard errors for coefficients. We examined the form of temporal correlation in a systematic manner by fitting 4 models, each model containing a different covariance structure: simple (independent within-subject errors for all pairs of yr), compound symmetry (uniform, nonzero correlations for within-subject errors for all pairs of yr), autoregressive (stronger correlations for within-subject errors for pairs of yr adjacent in time compared with pairs farther apart in time), and unstructured (unique correlations for within-subject errors for each pair of yr). We used Akaike's Information Criterion (AIC) to determine which covariance structure was appropriate for the model that included the most fixed effects (i.e., global model; Wolfinger 1993, 1996; Diggle et al. 1994). The unstructured covariance model received the most support for both species, and we used it for all within-site territory density models. For the site-level territory density analysis, the compound symmetry covariance structure received the most support for the wood thrush, and the autoregressive covariance structure received the most support for the yellow-breasted chat. We conducted analyses using the MIXED procedure of SAS software (version 9.1; SAS Institute, Cary, NC).

We determined the association between mnHSI_terr on within-site territory density and mnHSI_site on site-level territory density for specific HSI values. Because HSI values for each species ranged from zero to 1.0, we predicted within-site territory density and site-level territory density for the entire range of HSI values.

Nest success.—Methods for estimating nest success typically assume survival is constant within a nest stage (e.g., Mayfield's estimator; Mayfield 1961, 1975). Violation of this assumption can lead to biased estimates of nest success (Shaffer 2004). A method for incorporating nonconstant survival within nest stage is to fit a model that includes nest age information in addition to nest stage (Shaffer 2004, Grant et al. 2005). Because we were also interested in nontemporal factors that influenced nest success, yet needed to control for known temporal factors, we conducted the nest success analysis in 2 stages (Grant et al. 2006). In the first stage, we developed a set of models that contained only temporal effects (i.e., nest stage; linear, quadratic, and cubic effects of Julian date; and yr) as univariate models and combinations of the 5 temporal variables. We fit all models using the logistic-exposure method to estimate nest success (Shaffer 2004, Shaffer and Thompson 2007) and ranked them using the difference in AIC models adjusted for small sample size (ΔAIC_c) to determine the most-supported temporal model (Burnham and Anderson 2002). The most-supported temporal model for each species contained nest stage with an Akaike weight (w_i) of 0.55 for wood thrush and 0.39 for yellow-breasted chat. In the second stage, we used the most-supported temporal model as the base model and added the HSI variable mnHSI_terr to the base model. In this way, temporal factors were included as nuisance parameters in the analysis (Link and Sauer 2002, Thogmartin et al. 2004, Thogmartin and Knutson 2007). We fit logistic-exposure models using the GENMOD procedure of SAS software (version 9.1).

We determined the effect of the continuous HSI covariate mnHSI_terr on nest survival by estimating average daily survival rate (DSR) for specific HSI values while holding effects of other covariates in the model (e.g., nest stage) constant at their mean value. Because the estimated HSI values for each species ranged from 0 to 1.0, we predicted DSR for the entire range of HSI values.

Comparison of Competing Models

Our second objective was to evaluate support for HSI models versus other models, using model selection (Burnham and Anderson 2002). Whereas HSI models incorporate habitat features in the calculation of habitat suitability via suitability relationships, models of specific habitat features contain only the measured attribute(s) of habitat feature(s). If HSI models fare no better than models of specific habitat features or habitat treatments, then habitat features or habitat treatments could be used to model demography directly.

We conducted a separate model-selection analysis for each demographic response. The candidate model set for both species included the relevant HSI variable (mnHSI_terr for within-site territory density and nest success, mnHSI_site for site-level territory density), the specific habitat features that contribute to increased risk of nest predation or brood parasitism (distance to edge, distance to forest, and tree age) singly or in combination with other habitat features, and the management effects of period (pretreatment or posttreatment), treatment type (EAM clearcut, EAM thinning,

Table 1. Summary statistics for wood thrush and yellow-breasted chat habitat suitability and landscape attributes by treatment type on the Missouri Ozark Forest Ecosystem Project, south-central Missouri, USA, 1991–2002. Even-aged (EAM) and uneven-aged (UAM) harvest treatments were each applied to 3 sites in 1996, with 3 sites serving as nonharvest controls. Variables WOTH_HSI and YBCH_HSI refer to wood thrush and yellow-breasted chat habitat suitability index (HSI) values, respectively.

		Pretreatment (1991–1995)				Posttreatment (1997–2002)			
Treatment	Variable	$\bar{x}$	SD	Min.	Max.	$\bar{x}$	SD	Min.	Max.
Control	WOTH_HSI	0.35	0.04	0.21	0.43	0.37	0.06	0.22	0.62
	YBCH_HSI					0.00	0.02	0.00	0.27
	Tree age (yr)	87.8	4.7	76.0	101.9	87.7	5.2	48.3	101.9
	Distance to edge (m)	507.9	279.5	20.0	1,152.1	198.6	112.4	10.0	544.9
	Distance to forest (m)					0.0	0.0	0.0	0.0
EAM	WOTH_HSI	0.36	0.03	0.24	0.43	0.49	0.14	0.05	0.80
	YBCH_HSI					0.07	0.19	0.00	0.94
	Tree age (yr)	87.7	6.7	31.1	101.1	75.4	24.8	1.5	101.1
	Distance to edge (m)	430.5	240.4	0.0	100.4	90.5	87.8	0.0	393.2
	Distance to forest (m)					4.8	14.9	0.0	80.6
UAM	WOTH_HSI	0.35	0.04	0.16	0.42	0.38	0.07	0.17	0.65
	YBCH_HSI					0.00	0.00	0.00	0.00
	Tree age (yr)	88.1	6.5	6.0	106.2	83.5	8.7	6.0	99.8
	Distance to edge (m)	483.3	403.8	0.0	1,716.9	79.5	62.5	0.0	332.4
	Distance to forest (m)					0.2	1.8	0.0	22.4

UAM, or control), and a period × treatment interaction. Because no yellow-breasted chats occurred in sufficient sample sizes before treatment, we omitted period and period × treatment interaction from all yellow-breasted chat analyses.

We fit the mixed-effects models, with the appropriate covariance structure as described above, using full maximum likelihood instead of restricted maximum likelihood to enable comparison of models with different fixed effects (Wolfinger 1993, 1996; Diggle et al. 1994). We fit logistic-exposure models in the same manner as described above. We used likelihood ratio tests to determine whether each global model was a significant improvement over the corresponding null model and then proceeded with fitting the candidate models. We ranked models using ΔAIC_c, calculated relative likelihood of a model given the data and set of models for each species using w_i, and reported evidence ratios (Burnham and Anderson 2002).

RESULTS

The MOFEP landscape was largely homogenous with respect to tree age and distance to edge before management treatments (Table 1). Following tree harvest, the mean tree age declined 12.3 years on EAM sites as a result of harvest treatments on 295 ha and 4.6 years on UAM sites as a result of harvest treatments on 859 ha. Correspondingly, the distance to edge decreased 5-fold on EAM sites and 6-fold on UAM sites after treatment. The mean habitat suitability value for the wood thrush was greater on EAM sites than on UAM sites (Table 1). The mean habitat suitability value for yellow-breasted chat was 0.00 on all UAM sites, compared with 0.07 on EAM sites. The maximum HSI (1.00) was achieved for yellow-breasted chat on all 3 EAM sites after treatment. No yellow-breasted chat habitat occurred before treatment.

Validation of HSI Models

Within-site territory density.—The wood thrush model containing mnHSI_terr was not a good predictor of within-site territory density because the fitted model did not have greater likelihood than the intercept-only model (χ^2 = 0.12, df = 1, P = 0.752) and no significant effect of mnHSI_terr on density existed ($F_{1,1187}$ = 0.13, P = 0.714). Therefore, we did not develop a plot of the effect of mnHSI_terr on within-site territory density. A post hoc addition of distance to edge to the mnHSI_terr model produced a model with greater likelihood than the intercept-only model (χ^2 = 138.2, df = 2, $P < 0.001$).

The yellow-breasted chat model containing mnHSI_terr was a good predictor of within-site territory density because the fitted model had a greater likelihood than the intercept-only model (χ^2 = 124.39, df = 1, $P < 0.001$) and the effect of mnHSI_terr on within-site territory density was positive and significant ($F_{1,223}$ = 189.6, $P < 0.001$; Table 2). Within-site territory density increased 8.5 times from HSI = 0.0 to HSI = 1.0 (Fig. 1).

Site-level territory density.—The wood thrush model containing mnHSI_site was not a good predictor of site-level territory density because the fitted model did not have a greater likelihood than the intercept-only model when using both the pretreatment and posttreatment data (χ^2 = 0.2, df = 1, P = 0.655) and no significant effect of mnHSI_site on site-level territory density existed ($F_{1,71}$ = 0.17, P = 0.686). When considering only posttreatment data, the wood thrush model containing mnHSI_site was a good predictor of site-level territory density because the fitted model had a greater likelihood than the intercept-only model (χ^2 = 6.6, df = 1, P = 0.010) and the effect of mnHSI_site on site-level territory density posttreatment was positive and significant ($F_{1,7}$ = 9.74, P = 0.017; Table 2). Site-level territory density for wood thrush after treatment ranged from 0.01 territories/ha at HSI = 0.30 to 0.15 territories/ha at HSI = 1.0 (Fig. 2). The 95% confidence interval was narrowest in the range of HSI values that encompassed the MOFEP sites (95% CI = 0.34–0.50; Table 1; Fig. 2). A change in mean HSI value of 0.35 on control sites to 0.49 on EAM sites was equivalent to

Table 2. Parameter estimates (β), standard error, and lower and upper 95% confidence levels (LCL, UCL, respectively) from mixed-effects models for wood thrush (WOTH) and yellow-breasted chat (YBCH) predicting within-site territory density and site-level territory density from territory scale (mnHSI_terr) and site scale (mnHSI_site) habitat suitability values, respectively, for 9 sites in the Missouri Ozark Forest Ecosystem Project, south-central Missouri, USA, 1991–2002.

Scale	Species	Parameter	β	SE	LCL	UCL
Within-site	WOTH	Intercept	0.033	0.003	0.028	0.039
		mnHSI_terr	0.003	0.007	−0.011	0.016
	YBCH	Intercept	0.011	0.001	0.009	0.012
		mnHSI_terr	0.080	0.006	0.069	0.092
Site	WOTH	Intercept	−0.069	0.032	−0.132	−0.005
		mnHSI_site	0.238	0.076	0.085	0.390
	YBCH	Intercept	0.013	0.007	−0.002	0.027
		mnHSI_site	0.449	0.172	0.105	0.792

a 223% increase in wood thrush territories (from 17 to 55; Table 1; Fig. 2).

The yellow-breasted chat model containing mnHSI_site was a good predictor of site-level territory density because the fitted model had a greater likelihood than the intercept-only model ($\chi^2 = 4.75$, df = 1, $P = 0.029$) and the effect of mnHSI_site on site-level territory density was positive and significant ($F_{1,7} = 6.81$, $P = 0.035$; Table 2). Site-level territory density for yellow-breasted chat ranged from 0.01 territories/ha at HSI = 0.00 to 0.46 territories/ha at HSI = 1.0 (Fig. 2). Similar to wood thrush, the 95% confidence interval was narrowest in the range of mnHSI_site values that encompassed the MOFEP sites (95% CI = 0.00–0.09; Table 1; Fig. 2). A change in the mean HSI value of 0.00 on control and UAM sites to 0.07 on EAM sites was equivalent to a 257% increase in the number of yellow-breasted chat territories (from 14 to 50; Table 1; Fig. 2).

Nest success.—The wood thrush nest-survival model containing mnHSI_terr and nest stage was not a good predictor of nest success because the fitted model did not have a greater likelihood than the nest stage-only model ($\chi^2 = 1.34$, df = 1, $P = 0.247$) and no significant effect of mnHSI_terr on nest success existed ($\chi^2 = 2.46$, df = 1, $P = 0.117$; Table 3). Therefore, we did not develop a plot of the effect of mnHSI_site on site-level territory density for the wood thrush.

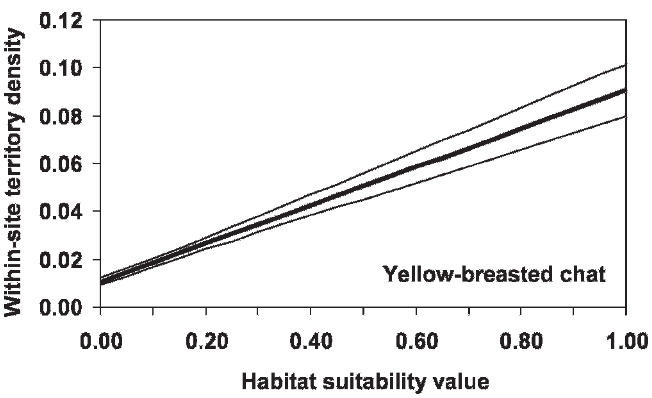
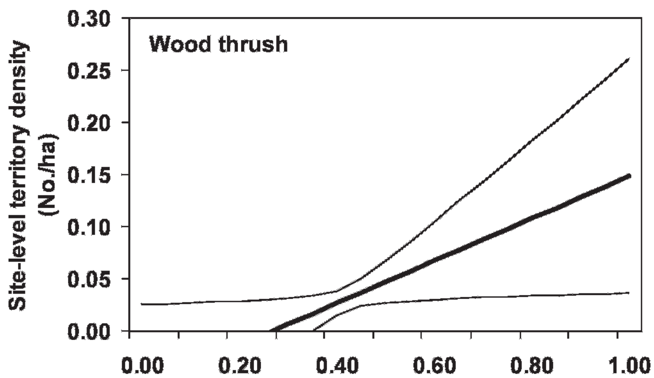


Figure 1. Predicted within-site territory density and 95% confidence level of yellow-breasted chats after treatment based on a habitat suitability value at the territory scale for 9 sites in the Missouri Ozark Forest Ecosystem Project, south-central Missouri, USA, 1997 to 2000. Territory density was a distance-weighted estimate of the number of territories within a 3-km radius of a focal cell.

The yellow-breasted chat nest-survival model containing mnHSI_terr and nest stage was a good predictor of nest success because it had a greater likelihood than the nest stage-only model ($\chi^2 = 3.14$, df = 1, $P = 0.076$) and the effect of mnHSI_terr on yellow-breasted chat nest success was positive and significant ($\chi^2 = 4.43$, df = 2, $P = 0.035$; Table 3). The DSR of yellow-breasted chats increased from 0.93 at HSI = 0.0 to 0.99 at HSI = 1.0 (Fig. 3). The probability of a nest surviving the 23-day incubation and nestling period (i.e., period survival) increased from 0.23 (95% CL = 0.09–0.33) at HSI = 0.0 to 0.80 (95% CL = 0.27–0.96) at HSI = 1.0.



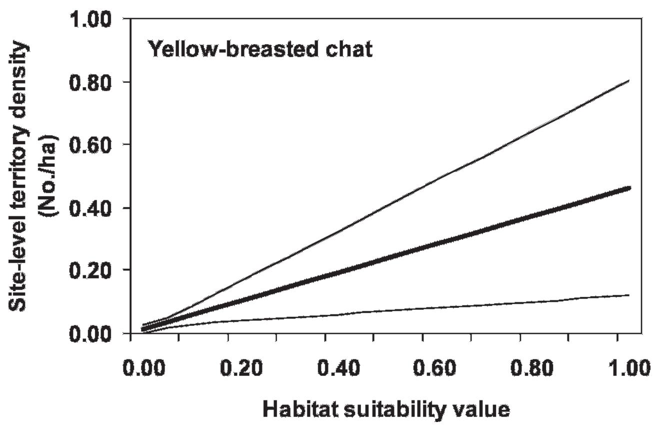


Figure 2. Predicted site-level density and 95% confidence level of wood thrush and yellow-breasted chat territories after treatment in relation to the mean habitat suitability value for 9 sites in the Missouri Ozark Forest Ecosystem Project, south-central Missouri, USA, 1997 to 2000.

Table 3. Logistic-exposure model estimates of regression coefficients relating daily survival rate of wood thrush (WOTH) and yellow-breasted chat (YBCH) nests to nest stage and mean habitat suitability index value within a moving-window size equivalent to the average territory size (mnHSI_terr). Parameter estimates (β), standard error, lower and upper 95% confidence levels (LCL and UCL, respectively), and test statistics and *P*-values for Type III test of significance for fixed effects are reported for 9 sites in the Missouri Ozark Forest Ecosystem Project, south-central Missouri, USA, 1991–2002.

Species	Model rank	Parameter	β	SE	LCL	UCL	χ^2	*P*
WOTH	1	Intercept	2.61	0.41	1.80	3.42	39.56	<0.001
		Stage-egg	−0.39	0.19	−0.76	−0.02	4.38	0.037
		mnHSI_terr	1.54	0.98	−0.38	3.46	2.46	0.117
	2	Intercept	3.24	0.13	2.99	3.49	655.35	<0.001
		Stage-egg	−0.40	0.19	−0.77	−0.04	4.67	0.031
	3	Intercept	4.04	0.92	2.24	5.83	19.35	<0.001
		Stage-egg	−0.42	0.19	−0.78	−0.05	4.90	0.027
		Tree age	−0.01	0.01	−0.03	0.01	0.77	0.380
YBCH	3	Intercept	3.17	0.32	2.54	3.80	98.32	<0.001
		Stage-egg	−0.82	0.38	−1.57	−0.07	4.56	0.033
		mnHSI_terr	1.97	0.94	0.14	3.80	4.43	0.035
	1	Intercept	2.96	0.35	2.28	3.64	72.91	<0.001
		Stage-egg	−0.75	0.39	−1.50	0.01	3.76	0.053
		Distance to forest	0.03	0.02	0.00	0.07	4.89	0.027
	2	Intercept	2.35	1.08	0.24	4.45	4.76	0.029
		Stage-egg	−0.75	0.39	−1.50	0.01	3.77	0.052
		Tree age	0.01	0.01	−0.02	0.04	0.36	0.549
		Distance to forest	0.05	0.03	−0.01	0.10	2.96	0.085

Comparison of Competing Models

Within-site territory density.—The global model for wood thrush was a significant improvement over the null model ($\chi^2 = 356.5$, df = 17, $P < 0.001$), so we proceeded with the comparison of competing models. The global model was the most supported model, followed by the management effects model, and then the distance to edge model (Table 4). The model containing only mnHSI_terr had $\Delta AIC_c = 324.08$ and $w_i = 0.00$, indicating no support for the mnHSI_terr model (Table 4). All models containing distance to edge received more support than models containing only mnHSI_terr (Table 4), suggesting that including a suitability relationship for distance to edge may improve the wood thrush HSI model.

For yellow-breasted chat, the global model was a significant improvement over the null model ($\chi^2 = 136.97$, df = 6, $P < 0.001$), so we proceeded with the comparison of competing models. The most supported model was the global model, indicating that yellow-breasted chat respond to simultaneous changes in habitat features and habitat treatments, followed by the model that contained mnHSI_terr (Table 4). The data did not support models containing only habitat features or habitat management effects (Table 4).

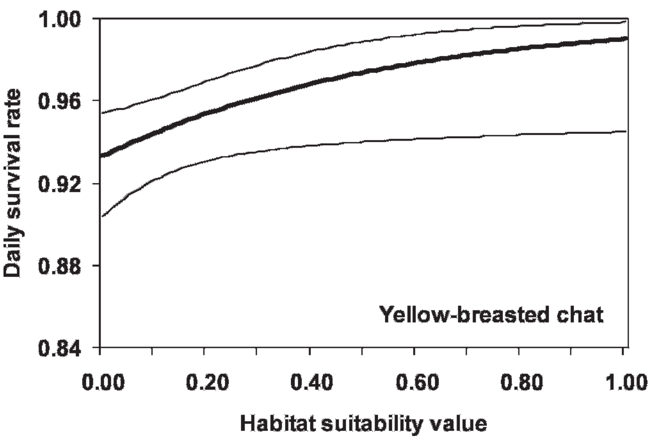


Figure 3. Predicted daily survival rates and 95% confidence level of yellow-breasted chats in relation to habitat suitability values in the Missouri Ozark Forest Ecosystem Project, south-central Missouri, USA, 1997 to 2002.

Site-level territory density.—The global model for wood thrush was an improvement over the null model ($\chi^2 = 37.98$, df = 14, $P < 0.001$), so we proceeded with the comparison of competing models. The most supported model for the complete data set (1991–2000) was the model containing management effects ($w_i = 0.67$), followed by the model containing tree age and distance to edge ($\Delta AIC_c = 2.35$; Table 5). The model containing mnHSI_site had $\Delta AIC_c = 10.17$ and $w_i = 0.00$, indicating no support for the habitat-suitability variable (Table 5). When we fit models for just the posttreatment period, the model containing mnHSI_site was the most supported model ($w_i = 0.66$) with no competing models (Table 5).

For yellow-breasted chat, the global model for site-level territory density was a marginally significant improvement over the null model ($\chi^2 = 8.95$, df = 4, $P = 0.062$), so we proceeded with the comparison of competing models. The most supported model for the posttreatment period contained management effects, competing with tree age ($\Delta AIC_c = 1.13$), distance to forest ($\Delta AIC_c = 2.45$), and the model containing mnHSI_site ($\Delta AIC_c = 2.72$; Table 5).

Nest success.—The global model for wood thrush nest success was not an improvement over the nest-stage model ($\chi^2 = 2.35$, df = 3, $P = 0.503$); however, the most supported model contained effects of nest stage and mnHSI_terr (Table 6). The nest-stage model had $\Delta AIC_c = 0.67$, and the nest stage and tree age model had $\Delta AIC_c = 1.82$, indicating competition among the top temporal, habitat features, and HSI models (Table 6). Incubation

Table 4. Model selection criteria for analysis of within-site territory density of wood thrush (WOTH) and yellow-breasted chats (YBCH) for 9 sites in the Missouri Ozark Forest Ecosystem Project (MOFEP), south-central Missouri, USA, 1991–2002. The MOFEP data set contained 1,297 wood thrush territories and 357 yellow-breasted chat territories.

Species	Model[a]	K[b]	$-2 \times \ln(L_{model})$[c]	AIC_c[d]	ΔAIC_c[e]	w_i[f]
WOTH	Global	63	−30,899.4	−30,756.2	0.00	1.00
	P + T + P × T	60	−30,832.6	−30,711.7	60.71	0.00
	DE	47	−30,673.4	−30,578.9	193.58	0.00
	TA + DE	48	−30,674.2	−30,577.6	194.80	0.00
	TA	47	−30,546.8	−30,452.3	320.18	0.00
	Intercept only	46	−30,542.8	−30,450.3	322.16	0.00
	mnHSI_terr	47	−30,542.9	−30,448.4	324.08	0.00
YBCH	Global	18	−3,474.49	−3,437.71	0.00	0.52
	mnHSI_terr	12	−3,461.91	−3,437.56	0.15	0.48
	DF	12	−3,452.79	−3,428.44	9.12	0.00
	TA + DF	13	−3,453.75	−3,427.34	10.37	0.00
	Treatment	15	−3,441.27	−3,410.72	26.99	0.00
	TA	12	−3,407.20	−3,382.85	54.86	0.00
	Intercept	11	−3,337.52	−3,315.22	122.49	0.00

[a] DE: distance to edge (m); DF: distance to forest (m); mnHSI_terr: mean habitat suitability index (HSI) value of territory; P: period; T: treatment; P × T: period-by-treatment interaction; TA: tree age (yr).
[b] No. of parameters. Wood thrush models contain 45 parameters and yellow-breasted chat models contain 10 parameters for estimating the unstructured covariance structure.
[c] Twice the negative value of the maximized log-likelihood function.
[d] Akaike's Information Criterion adjusted for small-sample bias.
[e] Difference in AIC_c relative to the min. AIC_c.
[f] Akaike wt.

stage had a negative effect on DSR for the top 3 models, but there was no significant effect of tree age or mnHSI_terr (Table 3).

For yellow-breasted chat, the global model for nest success was not an improvement over the null model (χ^2 = 4.40, df = 3, P = 0.221). The most supported model contained effects of nest stage and distance to forest (Table 6). The model containing nest stage and mnHSI_terr competed with the top model (ΔAIC_c =1.74). Incubation stage had a negative effect on DSR for the model containing nest stage

Table 5. Model selection criteria for analysis of site-level territory density of wood thrush (WOTH) and yellow-breasted chats (YBCH) for 9 sites in the Missouri Ozark Forest Ecosystem Project (MOFEP), south-central Missouri, 1991–2002. The MOFEP data set contained 1,297 wood thrush territories and 357 yellow-breasted chat territories.

Species (yr)	Model[a]	K[b]	$-2 \times \ln(L_{model})$[c]	AIC_c[d]	ΔAIC_c[e]	w_i[f]
WOTH (1991–2000)	P + T + P × T	14	−417.87	−383.51	0.00	0.67
	TA + DE	5	−391.96	−381.16	2.35	0.21
	DE	4	−387.95	−379.42	4.08	0.09
	Global	17	−419.78	−376.07	7.44	0.02
	Intercept	3	−381.80	−375.49	8.02	0.01
	mnHSI_site	4	−381.86	−373.33	10.17	0.00
	TA	4	−381.85	−373.32	10.18	0.00
WOTH (1997–2000)	mnHSI_site	4	−180.74	−171.45	0.00	0.66
	TA	4	−177.12	−167.83	3.62	0.11
	Intercept only	3	−174.14	−167.39	4.06	0.09
	TA + DE	5	−197.19	−167.19	4.26	0.08
	Treatment	6	−180.38	−165.48	5.97	0.03
	DE	4	−174.36	−165.07	6.38	0.03
	Global	9	−182.12	−157.20	14.25	0.00
YBCH (1997–2000)	Treatment	4	−180.64	−171.35	0.00	0.42
	TA	4	−179.51	−170.22	1.13	0.24
	DF	4	−178.19	−168.90	2.45	0.12
	mnHSI_site	4	−177.92	−168.63	2.72	0.11
	TA + DF	5	−179.57	−167.57	3.78	0.06
	Intercept	3	−173.17	−166.42	4.93	0.04
	Global	7	−182.12	−164.12	7.23	0.01

[a] DE: distance to edge (m); DF: distance to forest (m); mnHSI_site: mean habitat suitability index (HSI) value of site; P: period; T: treatment; P × T: period-by-treatment interaction; TA: tree age (yr).
[b] No. of parameters. All models contain 2 parameters for estimating the compound symmetry and autoregressive covariance structures for wood thrush and yellow-breasted chat, respectively.
[c] Twice the negative value of the maximized log-likelihood function.
[d] Akaike's Information Criterion adjusted for small-sample bias.
[e] Difference in AIC_c relative to the min. AIC_c.
[f] Akaike wt.

Table 6. Model selection criteria for analysis of daily survival rates of wood thrush (WOTH) and yellow-breasted chats (YBCH) for 9 sites in the Missouri Ozark Forest Ecosystem Project, south-central Missouri, USA, 1991–2002. Effective sample size was 2,556 for wood thrush and 618 for yellow-breasted chats.

Species	Model[a]	K[b]	$-2 \times \ln(L_{model})$[c]	AIC_c[d]	ΔAIC_c[e]	w_i[f]
WOTH	S + mnHSI_terr	3	−332.23	670.49	0.00	0.34
	S	2	−333.57	671.15	0.67	0.25
	S + TA	3	−333.14	672.31	1.82	0.14
	Global	5	−331.22	672.51	2.02	0.12
	S + DE	3	−333.53	673.09	2.60	0.09
	-S + TA + DE	4	−333.02	674.09	3.60	0.06
YBCH	S + DF	3	−78.77	163.66	0.00	0.45
	S + TA + DF	4	−78.59	165.38	1.72	0.19
	S + mnHSI_terr	3	−79.64	165.40	1.74	0.19
	Global	5	−78.38	167.06	3.40	0.08
	S + TA	3	−80.56	167.24	3.58	0.07
	S	2	−82.78	169.62	5.96	0.02

[a] S: nest stage, included as a nuisance variable in all models; DE: distance to edge (m); DF: distance to forest (m); mnHSI_terr: mean habitat suitability index (HSI) value of territory; TA: tree age (yr).
[b] No. of parameters. All models contain 2 parameters for estimating the compound symmetry and autoregressive covariance structures for wood thrush and yellow-breasted chat, respectively.
[c] Twice the negative value of the maximized log-likelihood function.
[d] Akaike's Information Criterion adjusted for small-sample bias.
[e] Difference in AIC_c relative to the min. AIC_c.
[f] Akaike wt.

and mnHSI_terr, but the effect was not significant for the top 2 competing models (Table 3).

DISCUSSION

The ultimate goal of HSI model validation is to identify the level of risk associated with using a model to influence management decisions (Brooks 1997). Confidence intervals (Bender et al. 1996) and reliability bounds (Burgman et al. 2001) quantify uncertainty associated with estimating HSI values but do not address uncertainty regarding the relationship of HSI values to demographic rates. Habitat suitability index models are conceptual models representing a synthesis of existing knowledge on an animal's response to habitat. As such, HSI models have been criticized as haphazard constructions of different variables that may not represent a unified biological relationship between the variables and an aspect of an organism's ecology. Because HSI models are not statistical models, rigorous statistical methods for model validation, including significance testing, data partitioning methods (e.g., *k*-fold cross-validation), and threshold-independent measures of classification error (e.g., plots of receiver operating characteristics) are not applicable or may be difficult to implement with animal density or nest success information (Fielding and Bell 1997, Pearce and Ferrier 2000, Boyce et al. 2002, Shifley et al. 2009). Our approach to HSI model validation is unique because we cast the HSI value as a variable in a general linear model framework. In doing so, we made the quantitative strengths of general linear models available, namely parameter estimates and log-likelihoods for significance testing as well as model selection, to test the link between habitat management, habitat suitability, and demographic response. We established this link for within-site territory density, site-level territory density, and nest success for yellow-breasted chat, and for posttreatment site-level density for wood thrush. Based on our validation results, our HSI models represented wildlife demographic responses to vegetation change.

We developed the HSI models to assess habitat suitability for breeding. Defining habitat suitability for breeding presented a challenge because HSI model development involved expert opinion and empirical data from multiple data sources (Rittenhouse et al. 2007). Models should be developed with a specific objective in mind, and in our case, we developed HSI models to reflect factors affecting breeding abundance and reproductive success. Therefore, we were not surprised that we validated their relationship to multiple forms of demographic responses to habitat conditions. The yellow-breasted chat HSI model was a significant predictor of within-site territory density, site-level territory density, and nest success. Our estimate of territory density in high-quality habitat (0.46 territories/ha at HSI = 1.00) was comparable to estimates of territory density in glade habitat (0.533 ± 0.281 SE territories/ha) but below that of regenerating forest (0.968 ± 0.072 SE territories/ha) for the MOFEP sites (Fink et al. 2006). Similarly, our estimated, daily nest-survival rate was 0.990 at HSI=1.00, which is higher than the daily survival rate at MOFEP sites (Fink et al. 2006) but comparable to the range of daily survival rates (0.96 ± 0.009 to 0.97 ± 0.011) observed by Ricketts and Ritchison (2000) in Kentucky, USA. These results suggest that our estimates of yellow-breasted chat territory density and nest success from HSI values are reasonable.

In contrast, the wood thrush HSI model was not a significant predictor of within-site territory density, site-level territory density, or nest success. However, we obtained statistically significant models when we included distance to edge with mnHSI_terr as a predictor of within-site territory density and when we repeated the site-level territory density analysis using only the posttreatment data. Taken together, these results suggest that the wood thrush HSI model may fail to capture important suitability relationships in homogenous (with respect to forest cover and tree age) forest landscapes. Wood thrushes are considered area sensitive (Robbins et al. 1989, Hoover et al. 1995, Mueller et al. 2000), but area sensitivity depends on landscape context (Driscoll and Donovan 2004). In general, fragmented landscapes have lower fledging success than contiguous forests (Donovan et al. 1995). We recommend adding a suitability relationship for edge sensitivity to improve the predictive ability of the wood thrush HSI model when applying it to homogenous forest landscapes.

Alternatively, the wood thrush HSI model may not be a significant predictor of within-site territory density, site-level territory density, or nest success if factors experienced during the nonbreeding season decouple the link between breeding habitat suitability and wood thrush demographics. For example, the North American Breeding Bird Survey estimated a survey-wide population trend of -1.6% for wood thrush for 1966–2006 (Sauer et al. 2007), yet during that same period, the amount of forest cover in the eastern United States increased (Trani et al. 2001). If nonbreeding season-habitat conditions limit wood thrush, then we might expect some suitable breeding habitat to remain unoccupied. In that situation, the wood thrush HSI model still predicts suitable breeding habitat.

The comparison of models containing HSI values to models containing habitat features or management effects revealed differences in model support for all 3 response variables and by species. As with statistical significance, the differences in HSI model support may be related to each species' ecology. Factors influencing nest success include predation and brood parasitism (Martin 1988, Paton 1994, Robinson et al. 1995), in addition to microhabitat and macrohabitat features. Although some studies found that the strength of the relationship between nest success and fragmentation changed with increasing spatial scale (Chalfoun et al. 2002, Stephens et al. 2003, Lloyd et al. 2005), some bird species adjusted breeding habitat selection or nest site selection based on local nest predator abundance or space use (Marzluff et al. 2007).

For yellow-breasted chats, nest predation risk can be strongly related to a specific habitat feature; nests close to forest edges have higher predation rates than nests farther from forest edges (Woodward et al. 2001). When we defined habitat suitability for breeding in terms of nest success only, the yellow-breasted chat HSI model performed adequately (i.e., competed with the distance to forest model) but was not the most supported model. Similarly, when we defined suitability for breeding in terms of within-site territory density, the HSI model competed with the most supported model. From a planning perspective, it may be impractical to develop a new model for every metric of avian fitness (i.e., clutch size, clutch mass, nestling mass, nest success, seasonal reproductive success, seasonal productivity) and spatial scale. Thus, it may be desirable to use the yellow-breasted chat HSI model for planning because it captured a general demographic response as well as specific ones, whereas the model based on one habitat feature (e.g., distance to edge) captured nest success but not territory density.

Given differences among species in life history traits and ecologies, a blanket assumption that suitability represents demographic response, without specifying which demographic response, is inappropriate. It is not likely that one demographic response will capture the full range of wildlife response to habitat conditions. Some demographic responses may be decoupled from habitat conditions when species exist below carrying capacity or there is spatial or temporal variation in predation or brood parasitism (Wiens and Rotenberry 1981, Van Horne 1983, Orians and Wittenberger 1991, Chalfoun and Martin 2007, Marzluff et al. 2007). Besides these ecological issues, model validation may also be affected by the data used for validation (Shifley et al. 2009). The volume of data and its availability, how representative the data is of site-specific habitat conditions, and the temporal context of the data may have a profound effect on evaluations of HSI model performance (Bender et al. 1996, Roloff and Kernohan 1999). Thus, an expectation that the HSI model will explain all variation in demographic response might be unreasonable.

Our approach to HSI model validation provides a framework for evaluating whether HSI models can be used for their intended purpose and how well HSI models perform relative to other types of models. We believe knowledge of the absolute and relative ability of HSI models to quantify species-specific demographic responses to habitat change provides greater confidence in their use for making management decisions. Although we did not explicitly address it, verification of the HSI equation (e.g., its mathematical form and computer code used for calculation) and calibration of the HSI model (e.g., adjustment of model parameters to improve agreement between model output and observed data) should be conducted before model validation (Rykiel 1996, Shifley et al. 2009). We suggest that HSI model validation and application explicitly considers the model's purpose and the specific demographic responses it should address. Similarly, model validation should address the relationship between predicted HSI values and the appropriate demographic responses, such as density and reproductive success, for models of breeding habitat suitability. We recommend using our approach to model validation to identify how much of, and how often, the variability in demographic response may be accounted for by the HSI model.

MANAGEMENT IMPLICATIONS

Our results support the claim that HSI models of breeding habitat suitability for wood thrush and yellow-breasted chat quantify demographic response to vegetation change, but results were not consistent across all demographic responses and species. Based on our validation results, we suggest the wood thrush HSI model is most appropriate for evaluating changes in site-level density following harvest treatments, whereas the yellow-breasted chat HSI model is appropriate for evaluating changes in within-site territory density, site-level territory density, and nest success. In study systems similar to ours (i.e., oak–hickory forests), managers may expect an increase of 2.3 wood thrush territories/km^2 and 4.5 yellow-breasted chat territories/km^2 for every 0.10 increase in habitat suitability values, with greater increases in habitat suitability achieved under even-aged management than uneven-aged management. The link between a species' demographic response and habitat management may be weakened where habitat conditions are homogenous and where there is suitable but unoccupied habitat. In these situations, the HSI model may overestimate demographic response to habitat change. We recommend validation of HSI models with the particular demographic data of interest (i.e., density, productivity) to increase confidence in the use of these models for conservation planning.

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LITERATURE CITED

Anders, A. D., J. Faaborg, and F. R. Thompson, III. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile wood thrushes. Auk 115:349–358.

Annand, E. M., and F. R. Thompson, III. 1997. Forest bird response to regeneration practices in central hardwood forests. Journal of Wildlife Management 61:159–171.

Bender, L. C., G. J. Roloff, and J. B. Haufler. 1996. Evaluating confidence intervals for habitat suitability models. Wildlife Society Bulletin 24:347–352.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Brooks, R. P. 1997. Improving habitat suitability index models. Wildlife Society Bulletin 25:163–167.

Brookshire, B. L., and D. C. Dey. 2000. Establishment and data collection of vegetation-related studies on the Missouri Ozark Forest Ecosystem Project study sites. Pages 1–8 *in* S. R. Shifley and B. L. Brookshire, editors. Missouri Ozark Forest Ecosystem Project symposium: site history, soils, landforms, woody and herbaceous vegetation, down wood, and inventory methods for the landscape experiment. U.S. Department of Agriculture, Forest Service, North Central Forest Experimentation Station General Technical Report NC-208, St. Paul, Minnesota, USA.

Brookshire, B. L., R. Jensen, and D. C. Dey. 1997. The Missouri Ozark Forest Ecosystem Project: past, present, and future. Pages 1–25 *in* B. L. Brookshire and S. R. Shifley, editors. Proceedings of the Missouri Ozark Forest Ecosystem Project Symposium: an experimental approach to landscape research. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station General Technical Report NC-193, St. Paul, Minnesota, USA.

Burgman, M. A., D. R. Breininger, B. W. Duncan, and S. Ferson. 2001. Setting reliability bounds on habitat suitability indices. Ecological Applications 11:70–78.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Chalfoun, A. D., and T. E. Martin. 2007. Assessment of habitat preferences and quality depend on spatial scale and metrics of fitness. Journal of Applied Ecology 44:983–992.

Chalfoun, A. D., F. R. Thompson, III, and M. J. Ratnaswamy. 2002. Nest predators and fragmentation: a review and meta-analysis. Conservation Biology 16:306–318.

Clawson, R. L., J. Faaborg, and E. Seon. 1997. Effects of selected timber management practices on forest birds in Missouri oak–hickory forests: pre-treatment results. Pages 274–288 *in* B. L. Brookshire and S. R. Shifley, editors. Proceedings of the Missouri Ozark Forest Ecosystem Project Symposium: an experimental approach to landscape research. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station General Technical Report NC-193, St. Paul, Minnesota, USA.

Cressie, N. A. C. 1993. Statistics for spatial data. Revised edition. Wiley, New York, New York, USA.

Diggle, P. J., K. Y. Liang, and S. L. Zeger. 1994. Analysis of longitudinal data. Clarendon Press, Oxford, United Kingdom.

Dijak, W. D., and C. D. Rittenhouse. 2009. Development and application of habitat suitability models to large landscapes. Pages 367–389 *in* J. J. Millspaugh and F. R. Thompson, III, editors. Models for planning wildlife conservation in large landscapes. Elsevier Science, San Diego, California, USA.

Dijak, W. D., C. D. Rittenhouse, M. A. Larson, F. R. Thompson, III, and J. J. Millspaugh. 2007. Landscape habitat suitability index software. Journal of Wildlife Management 71:668–670.

Donovan, T. M., F. R. Thompson, III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9:1380–1395.

Driscoll, M. J. L., and T. M. Donovan. 2004. Landscape context moderates edge effects: nesting success of wood thrushes in central New York. Conservation Biology 18:1330–1338.

Eckerle, K. P., and C. F. Thompson. 2001. Yellow-breasted chat (*Icteria virens*). Account 575 *in* A. Poole and F. Gill, editors. The birds of North America. Volume 15. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

Fink, A. D., F. R. Thompson, III, and A. A. Tudor. 2006. Songbird use of regenerating forest, glade, and edge habitat types. Journal of Wildlife Management 70:180–188.

Gram, W. K., P. A. Porneluzi, R. L. Clawson, J. Faaborg, and S. C. Richter. 2003. Effects of experimental forest management on density and nesting success of bird species in Missouri Ozark forests. Conservation Biology 17:1324–1337.

Grant, T. A., E. M. Madden, T. L. Shaffer, P. J. Pietz, G. B. Berkey, and N. J. Kadrmas. 2006. Nest survival of clay-colored and vesper sparrows in relation to woodland edge in mixed-grass prairies. Journal of Wildlife Management 70:691–701.

Grant, T. A., T. L. Shaffer, E. M. Madden, and P. J. Pietz. 2005. Time-specific variation in passerine nest survival: new insights into old questions. Auk 122:661–672.

Gustafson, E. J., D. W. Murphy, and T. R. Crow. 2001. Using a GIS model to assess terrestrial salamander response to alternative forest management plans. Journal of Environmental Management 63:281–292.

Hoover, J. P., M. C. Brittingham, and L. J. Goodrich. 1995. Effects of forest patch size on nesting success of wood thrushes. Auk 112:146–155.

Johnson, C. J., and M. P. Gillingham. 2004. Mapping uncertainty: sensitivity of wildlife habitat ratings to expert opinion. Journal of Applied Ecology 41:1032–1041.

Kabrick, J. M., R. G. Jensen, S. R. Shifley, and D. R. Larsen. 2002. Woody vegetation following even-aged, uneven-aged, and no-harvest treatments on the Missouri Ozark Forest Ecosystem Project Sites. Pages 84–101 *in* S. R. Shifley and J. M. Kabrick, editors. Proceedings of the Second Missouri Ozark Forest Ecosystem Symposium: post-treatment results of the landscape experiment. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station General Technical Report NC-227, St. Paul, Minnesota, USA.

Klaus, N. A., D. A. Buehler, and A. M. Saxton. 2005. Forest management alternatives and songbird breeding habitat on the Cherokee National Forest, Tennessee. Journal of Wildlife Management 69:222–234.

Kliskey, A. D., E. C. Lofroth, W. A. Thompson, S. Brown, and H. Schreier. 1999. Simulating and evaluating alternative resource-use strategies using GIS-based habitat suitability indices. Landscape and Urban Planning 45:163–175.

Larson, M. A., F. R. Thompson, III, J. J. Millspaugh, W. D. Dijak, and S. R. Shifley. 2004. Linking population viability, habitat suitability, and

landscape simulation models for conservation planning. Ecological Modelling 180:103–118.
Link, W. A., and J. R. Sauer. 2002. A hierarchical analysis of population change with application to cerulean warblers. Ecology 83:2832–2840.
Lloyd, P., T. E. Martin, R. L. Redmond, U. Langner, and M. M. Hart. 2005. Linking demographic effects of habitat fragmentation across landscapes to continental source–sink dynamics. Ecological Applications 15:1504–1514.
Martin, T. E. 1988. Habitat and area effects on forest bird assemblages: is nest predation an influence? Ecology 69:74–84.
Marzluff, J. M., J. J. Millspaugh, K. R. Ceder, C. D. Oliver, J. Withey, J. B. McCarter, C. L. Mason, and J. Comnick. 2002. Modeling changes in wildlife habitat and timber revenues in response to forest management. Forest Science 48:191–202.
Marzluff, J. M., J. C. Withey, K. A. Whittaker, M. D. Oleyar, T. M. Unfried, S. Rullman, and J. DeLap. 2007. Consequences of habitat utilization by nest predators and breeding songbirds across multiple scales in an urbanizing landscape. Condor 109:516–534.
Mayfield, H. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255–261.
Mayfield, H. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.
Mueller, A. J., D. J. Twedt, and C. R. Loesch. 2000. Development of management objectives for breeding birds in the Mississippi Alluvial Valley. Pages 12–17 *in* R. Bonney, D. N. Pashley, R. J. Cooper, and L. Niles, editors. Strategies for bird conservation: the Partners In Flight planning process. Proceedings of the third Partners in Flight international workshop. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station RMRS-P-16, Ogden, Utah, USA.
Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137:S29–S49.
Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology 8:17–26.
Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling 133:225–245.
Ricketts, M. S., and G. Ritchison. 2000. Nesting success of yellow-breasted chats: effects of nest site and territory vegetation structure. The Wilson Bulletin 112:510–516.
Rittenhouse, C. D., W. D. Dijak, F. R. Thompson, III, and J. J. Millspaugh. 2007. Development of landscape-level habitat suitability models for ten wildlife species in the Central Hardwoods Region. U.S. Department of Agriculture, Forest Service, Northern Research Station General Technical Report NRS-4, Newtown Square, Pennsylvania, USA.
Robbins, C. S., D. K. Dawson, and B. A. Dowell. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. Wildlife Monographs 103.
Robinson, S. K., F. R. Thompson, III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987–1990.
Roloff, G. J., and B. J. Kernohan. 1999. Evaluating the reliability of habitat suitability index models. Wildlife Society Bulletin 27:973–985.
Rotella, J. J., D. W. Hoerter, T. P. Sankowski, and J. H. Devries. 1993. Nesting effort by wild mallards with 3 types of radio transmitters. Journal of Wildlife Management 57:690–695.
Rykiel, E. J., Jr. 1996. Testing ecological models: the meaning of validation. Ecological Modelling 90:229–244.
Sauer, J. R., J. E. Hines, and J. Fallon. 2007. The North American Breeding Bird Survey: results and analysis 1966–2006. Version 10.13.2007. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland, USA.
Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526–540.
Shaffer, T. L., and F. R. Thompson, III. 2007. Making meaningful estimates of nest survival with model-based methods. Studies in Avian Biology 34:84–95.
Shifley, S. R., C. D. Rittenhouse, and J. J. Millspaugh. 2009. Validation of landscape-scale decision support models that predict vegetation and wildlife dynamics. Pages 415–448 *in* J. J. Millspaugh and F. R. Thompson, III, editors. Models for planning wildlife conservation in large landscapes. Elsevier Science, San Diego, California, USA.
Shifley, S. R., F. R. Thompson, III, D. R. Larsen, and W. D. Dijak. 2000. Modeling forest landscape change in the Missouri Ozarks under alternative management practices. Computers and Electronics in Agriculture 27:7–27.
Stephens, S. E., D. N. Koons, J. J. Rotella, and D. W. Willey. 2003. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. Biological Conservation 115:101–110.
Thogmartin, W. E., and M. G. Knutson. 2007. Scaling local species-habitat relations to the larger landscape with a hierarchical spatial count model. Landscape Ecology 22:61–75.
Thogmartin, W. E., J. R. Sauer, and M. G. Knutson. 2004. A hierarchical spatial model of avian abundance with application to cerulean warblers. Ecological Applications 14:1766–1779.
Thompson, C. F., and V. Nolan, Jr. 1973. Population biology of the yellow-breasted chat (*Icteria virens* L.) in southern Indiana. Ecological Monographs 43:145–171.
Thompson, F. R., III, W. D. Dijak, T. G. Kulowiec, and D. A. Hamilton. 1992. Breeding bird populations in Missouri Ozark forests with and without clearcutting. Journal of Wildlife Management 56:23–30.
Trani, M. K., R. T. Brooks, T. L. Schmidt, V. A. Rudis, and C. M. Gabbard. 2001. Patterns and trends of early successional forests in the eastern United States. Wildlife Society Bulletin 29:413–424.
Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.
Wiens, J. A., and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecological Monographs 51:21–41.
Wolfinger, R. D. 1993. Covariance structure and selection in general mixed models. Communications in Statistics, Simulation, and Computation 22:1079–1106.
Wolfinger, R. D. 1996. Heterogeneous variance-covariance structures for repeated measures. Journal of Agricultural, Biological, and Environmental Statistics 1:205–230.
Woodward, A. A., A. D. Fink, and F. R. Thompson, III. 2001. Edge effects and ecological traps: effects on shrubland birds in Missouri. Journal of Wildlife Management 65:668–675.

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