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TESTING HABITAT-RELATIONSHIP MODELS FOR FOREST BIRDS OF THE SOUTHEASTERN UNITED STATES

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Abstract: The bird-habitat relationships proposed by Hamel (1992) represent the most comprehensive description of habitat suitability for all birds that breed and/or winter in forests of the southern United States. These relationships were developed from compilations of published census and natural history data, field experience, and expert opinion. As such, these relationships can be considered untested models of bird-habitat associations. We tested the ability of these models to predict the distribution of 25 common breeding birds among the forest habitat types of the Southern Blue Ridge physiographic province. We used point-count survey data from national forests in Virginia, Tennessee, and Georgia to test the models. Thirteen of 25 models (52%) performed well (i.e., positive association between ranks from model predictions and ranks from the observed data) on the Tennessee data, while only 33% and 23% of the models performed well on the Georgia and Virginia data, respectively. Models for some species with distributions restricted to mid-aged to mature deciduous habitats (e.g., black-and-white warbler [Mniotilta varia] and black-throated blue warbler [Dendroica caerulescens]) and/or restricted to high elevations (e.g., veery [Catharus fuscescens]) performed well across study sites. However, models for other mature deciduous forest species did not perform as well because these species (e.g., ovenbird [Seiurus aurocapillus], scarlet tanager [Piranga olivacea], and wood thrush [Hylocichla mustelina]) tended to occur more frequently than predicted in early age classes or mixed forest types. For these species, we suggest that early-aged deciduous habitat types be considered marginal habitat (rather than unused, as defined in Hamel's publication) for these relatively widespread forest birds in the Southern Blue Ridge region. Models for habitat generalists (e.g., Carolina chickadee [Poecile carolinensis], Carolina wren [Thryothorus ludovicianus], and red-eyed vireo [Vireo olivaceus]) did not perform well. We suggest that Hamel's models be used cautiously for most birds in mature forest habitats. Further tests of these models are needed to clarify the discrepancies between the predicted and observed patterns of habitat use we observed.

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The bird-habitat relationships presented by Hamel (1992) represent a comprehensive description of forest habitat types in the southern United States and their suitability for all birds likely to breed and/or winter in that region. Hamel's (1992) work not only provided narrative species accounts, which included descriptions of the major vegetation types occupied by each bird species, but also presented a set of matrices indicating qualitative rankings (optimal, suitable, marginal, unused) of the suitability of successional stages in each major forest type for each bird species. As such, these matrices represent predictive models of habitat associations for birds in forested habitats of the southern United States. These matrices were based on the general natural history information available for each

Because of the comprehensive nature of these works, they provide forest managers with some of the best (and sometimes only) guidance on how to plan effective management activities that provide for the diverse needs of the avifauna that they often are entrusted to maintain. However, the relationships were presented by Hamel

species and on published census information. Field experience and professional judgment also were used when insufficient published data were available. Hamel's work represents the most complete compilation of information on bird-habitat associations in forest habitats for the southern United States, comparable to similar efforts for the western Sierra Nevada area (Verner and Boss 1980) and the northeastern United States (DeGraaf and Rudis 1986, DeGraaf et al. 1992). These efforts provide predictions for determining which vegetation types and successional stages are most likely to be used on a species by species basis for the full complement of breeding and wintering birds of the respective regions.

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(1992) as working hypotheses, frequently based on field observations rather than experimental studies, with acknowledged imprecision in much of the data (Hamel 1992:3–4). Therefore, testing these relationships represents an important step in the process of developing accurate models and providing land managers with the best available information for conducting their management activities.

We test the ability of Hamel's (1992) bird-habitat relationships to predict the relative occurrence of 25 common breeding birds among habitat types within forests of the Blue Ridge physiographic province in the southern Appalachian Mountains. We compared the predictions of breeding habitat suitability with observed occurrences of the birds within forest stands of various habitat types at 3 different sites across the Blue Ridge physiographic province (Georgia, Tennessee, Virginia). We based our tests on the assumption that the proportion of surveyed stands occupied by a species should be highest for the habitat(s) predicted to be optimal by Hamel, with correspondingly lower proportions of occupied stands for the remaining ordinal habitat rankings of suitable, marginal, and unused.

STUDY AREA

Our study area was the Southern Blue Ridge physiographic province of the southern Appalachian Mountains. Within this large area, we used bird survey data collected from 3 national forests (NF) in 3 states, representing a north-south transect: Virginia (George Washington and Jefferson NF), Tennessee (Cherokee NF), and Georgia (Chattahoochee NF). These forests comprised predominantly even-aged stands (established primarily through clearcutting) of several major forest types, including southern yellow pines (Pinus spp.) at lower elevations, oak-hickory (Quercus spp.-Carya spp.) and cove hardwood types at middle elevations, and northern hardwoods at the highest elevations. The cove hardwood type was characterized by tulip poplar (Liriodendron tulipifera), northern red oak (Q. borealis), white oak (Q. alba), and a mixture of other hardwood species, while the northern hardwood type was dominated by beech (Fagus grandifolia), birch (Betula spp.), and maple (Acer spp.). The age distribution of all forest types was typically skewed toward mature forest stands, but all successional stages were well represented.

METHODS

Bird Surveys and Habitat Types

To document bird use, unlimited-radius 10-min point counts were conducted using standard protocols (Ralph et al. 1995). Detections were recorded as either ≤50 m or >50 m from the point, and we used only the ≤50 m data for this study. Within each major forest type, 3 successional age classes were surveyed: seedling-shrub, sapling-poletimber, and sawtimber. In Tennessee, we surveyed 6 major forest types: yellow pine, mixed pine-hardwood, oak-hickory, cove hardwoods, eastern hemlock-white pine (Tsuga canadensis-P. strobus), and northern hardwoods. These same forest types were surveyed in Georgia, with the exception of northern hardwood, and in Virginia, with the exceptions of northern hardwood and yellow pine. The number of stands surveyed per habitat type varied roughly in proportion to the availability of the habitat types in the landscape, with the exception of Tennessee, where the surveys were distributed roughly equally between stands of the different forest types.

We defined different habitat types by the different combinations of age class and forest type (e.g., seedling-sapling-cove hardwood, sawtimber-northern hardwood). We surveyed 18, 15, and 9 habitat types (i.e., forest type-age class combinations) in Tennessee, Georgia, and Virginia, respectively. In Tennessee, we surveyed 215 stands (38 yellow pine, 39 mixed pine-hardwood, 29 oak-hickory, 35 hemlock-white pine, 40 cove hardwood, 34 northern hardwood) with a range of 6-16 stands per habitat type. In Georgia, 650 stands were surveyed (208 yellow pine, 155 mixed pine-hardwood, 134 oak-hickory, 62 hemlockwhite pine, and 91 cove hardwood), with a range of 10-84 stands per habitat type. A total of 702 stands were surveyed in Virginia (175 mixed pine-hardwood, 433 oak-hickory, 22 hemlockwhite pine, and 72 cove hardwood), with a range of 8-203 stands per habitat type.

One survey point was randomly located in each stand, with the point located at least 100 m inside the stand boundary. Each stand was surveyed once per year, for 5 consecutive years, with all surveys completed between mid-May and early July. The Tennessee and Georgia data were collected from 1992 to 1996, and the Virginia data were collected from 1993 to 1997. We considered a species to be present within a stand if we detected the species at the survey point in that stand at least once during the 5 years of surveys. For each

habitat type, the proportion of occupied stands was calculated as the number of stands in which a species was present divided by the total number of stands surveyed in that habitat type.

Testing Hamel's Models

To test qualitative predictions of the models developed by Hamel (1992) in an empirical manner, we assigned ranks to habitat types based on the predicted habitat suitabilities and also ranked the habitat types based on our observed data. We then used Kendall's tau (t) to test for independence (Hollander and Wolfe 1973:185-195) between the 2 sets of rankings and to describe the strength of the association between predictions of the models and our observations. This procedure tested the assumption that the ordinal rankings (optimal, suitable, marginal, unused) used by Hamel (1992) to describe levels of suitability across habitat types also could be used to predict the observed relative occupancy rates at which a given bird species occurred across habitat types. The proportion of occupied stands was our measure of relative occupancy rate.

To assign ranks to habitat types based on Hamel's predictions, we ranked the habitat types in descending order based on the predicted suitabilities from Hamel (1992), with optimal habitats receiving the smallest numerical ranks (e.g., 1, 2, 3), suitable habitats the next largest ranks (e.g., 4, 5, 6), and so on. In the case of ties where multiple habitat types had the same predicted suitability, we assigned each of the tied habitat types the median value of the ranks occupied by that number of habitat types. To assign ranks based on the observed data, we ranked the habitat types in descending order based on the proportion of occupied stands; the habitat type with the highest proportion of occupied stands received the rank of 1.

We tested for the alternative $\tau > 0$ (i.e., a positive association between ranks from Hamel's predications and ranks from the observed data) versus the null hypothesis that the 2 sets of ranks were independent ($\tau = 0$). We set the significance level for these tests at a = 0.10 to reduce the chances of making a Type II error and to increase the power of the test.

To calculate standardized differences in ranks, we subtracted the rank based on our observed data from the rank based on Hamel's predictions for each habitat type at each study site, and then divided the difference by the largest possible difference in ranks for each study site. Thus, a posi-

tive difference indicated that a species occurred more frequently in a habitat type than suggested by our interpretation of Hamel's (1992) predictions, while a negative value indicated that the species occurred less frequently than predicted.

RESULTS

Thirteen of the 25 models (52%) performed well (i.e., a significant positive association between ranks from Hamel's predictions and ranks from the observed data) on the Tennessee data, while only 33% and 23% of the models performed well on the Georgia and Virginia data, respectively (Table 1). Considerable variation was evident in the degree to which Hamel's (1992) predictions of habitat suitability correlated with the observed proportion of occupied stands within the different habitat types. Species for which the predicted habitat suitabilities did not match our observations very well were species that tended to be either widely distributed among forest types and successional stages (e.g., Carolina chickadee, Carolina wren, eastern towhee [Pipilo erythrophthalmus], tufted titmouse [Baeolophus bicolor], red-eyed vireo, rose-breasted grosbeak [Pheucticus ludovicianus], and yellow-billed cuckoo [Coccyzus americanus]) or that tended to have large territories (blue jay [Cyanocitta cristata] and pileated woodpecker [Dryocopus pileatus]). Species more restricted in the number of habitat types occupied had a much better association between the predicted habitat suitabilities and the observed proportion of occupied stands in the different habitat types (e.g., black-and-white warbler, black-throated blue warbler, black-throated green warbler [Dendroica virens], blue-headed vireo [Vireo solitarius], and veery).

We chose 2 representative species from both of these groups to illustrate why, according to our analyses, Hamel's (1992) models worked well for some of the habitat specialists (species occurring in a limited number of habitat types) but poorly for the widely distributed generalists. Models that performed poorly (e.g., Carolina chickadee and red-eyed vireo) tended to overpredict (large negative values) the occurrence of widely distributed species in sawtimber habitats and underpredict (large positive values) their occurrence in seedling-sapling age classes (Figs. 1A,B). The pole age class also tended to be incorrectly predicted, although no clear trends were apparent across species, with the rate of occupancy of pole stands overpredicted for some species but underpredicted for others. Although we illustrate

Table 1. Relationships between rankings of habitat suitability as predicted by Hamel (1992) and rankings based on the observed occurrence of 25 common forest bird species within different habitat types at 3 locations in the Blue Ridge physiographic province in the Southern Appalachian Mountain region, 1992–1997.

	Tennessee (na = 18)		Georgia (n = 15)		Virginia (n = 9)	
Species	Kendall's τ	Р	Kendall's τ	Р	Kendall's τ	P
Acadian flycatcher ^b	0.222	0.107	0.333	0.046	0.194	0.238
Black-and-white warbler	0.229	0.100	0.257	0.099	0.389	0.090
Blue jay	-0.052	0.604	0.324	0.051	-0.194	0.791
Blue-headed vireo	0.288	0.052	0.371	0.030	0.417	0.075
Black-throated blue warbler	0.301	0.044	0.467	0.009	0.639	0.009
Black-throated green warbler	0.235	0.094	0.248	0.086	0.194	0.272
Carolina chickadee	0.046	0.441	0.181	0.187	-0.111	0.694
Canada warbler ^b	0.281	0.056	c		-0.194	0.791
Carolina wren	0.163	0.162	0.048	0.422		
Chestnut-sided warbler	0.320	0.034	0.314	0.057	0.028	0.500
Dark-eyed juncob	0.373	0.013				
Eastern towhee	-0.039	0.574	-0.054	0.635	0.333	0.130
Tufted titmouse	-0.033	0.559	0.105	0.310	-0.056	0.619
Hooded warbler	-0.007	0.500	-0.181	0.839	0.111	0.381
Indigo bunting ^b	-0.203	0.870	0.181	0.187	0.500	0.038
Ovenbird	0.255	0.076	0.238	0.117	0.222	0.233
Pileated woodpecker	0.275	0.061	0.114	0.293	-0.111	0.694
Rose-breasted grosbeak	0.209	0.123			0.278	0.179
Red-eyed vireo	-0.366	0.982	-0.010	0.539	-0.111	0.694
Scarlet tanager	0.307	0.041	0.190	0.174	-0.056	0.619
Veery	0.320	0.034			0.389	0.090
Worm-eating warbler	0.072	0.354	-0.114	0.740	0.139	0.334
Wood thrush	0.484	0.005	-0.076	0.672	0.194	0.272
Yellow-billed cuckoo	-0.052	0.603	0.019	0.480	0.111	0.381
Yellow-throated warbler ^b	0.346	0.024	0.029	0.461		

^a n indicates the number of distinct habitat types (i.e., forest type–successional stage combinations) for which sufficient bird survey data were available at each study site.

results for only 2 of the generalist species, the pattern of overpredicting sawtimber and underpredicting seedling–sapling age classes was evident for many of the species for which the models did not perform well: blue jay, Carolina chickadee, Carolina wren, tufted titmouse, hooded warbler (Wilsonia citrina), rose-breasted grosbeak, pileated woodpecker, and yellow-billed cuckoo. For some of these species, such as Carolina chickadee (Fig. 1A), blue jay, Carolina wren, tufted titmouse, pileated woodpecker, and rose-breasted grosbeak, these discrepancies among the different stand age classes were the primary sources of error between model predictions and the observed occurrences.

For some generalist species, the models also incorrectly predicted the forest types in which a species was most likely to occur. For example, red-eyed vireos (Fig. 1B) occurred considerably less often than predicted (large negative values) in cove hardwood, mixed pine-hardwood, and oak-hickory forest types, but occurred much more often than predicted (large positive values) in hemlock-white pine and yellow pine forest types. Similar errors in predicting the most frequently used forest types occurred for eastern towhee, hooded warbler, and yellow-billed cuck-oo. These errors in predictions of forest types were in addition to errors in predictions of stand age classes. For most species, these patterns were fairly consistent across the 3 study sites.

Models for the specialist species performed well because of small discrepancies in ranks for most of the habitat types. For example, only 2 of

b Scientific names for species not already listed in text: Acadian flycatcher (*Empidonax virescens*), Canada warbler (*Wilsonia canadensis*), chestnut-sided warbler (*Dendroica pensylvanica*), dark-eyed junco (*Junco hyemalis*), indigo bunting (*Passerina cyanea*), yellow-throated warbler (*Dendroica dominica*).

^c Missing entries in the table indicate an insufficient number of detections at that location for conducting Kendall's test of independence.

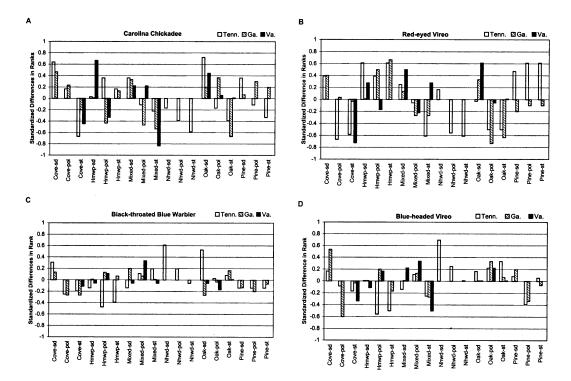


Fig. 1. Standardized differences in ranks of habitat types based on Hamel's (1992) matrices and observed bird occurrences from surveys in 3 states within the Blue Ridge physiographic province in the Southern Appalachian Mountain region, 1992–1997. Carolina chickadee and red-eyed vireo are considered generalist species for the comparisons illustrated in this figure, while black-throated blue warbler and blue-headed vireo are considered specialist species. Codes for habitat types listed along the X-axis are: cove = cove hardwood (forest type dominated by tulip poplar, northern red oak, and white oak); hmlkwp = eastern hem-lock—white pine; mixed = mixed pine hardwood; nhwd = northern hardwood (forest type dominated by beech, birch, and maple); oak = oak-hickory; pine = southern yellow pine; sd = seedling–shrub; pol = sapling–pole; saw = sawtimber. Positive scores indicate a species occurred more frequently in that habitat type than predicted by Hamel (1992); negative scores indicate a species occurred less frequently than predicted. The legends indicate the 3 states in which surveys were conducted: TN = Tennessee, GA = Georgia, and VA = Virginia.

the habitat types tested across all study sites for black-throated blue warbler resulted in a standardized difference in ranks with an absolute value ≥ 0.5 (Fig. 1C). This magnitude of difference in ranks was reached only 4 times for blueheaded vireo (Fig. 1D). These specialist species were observed in a relatively high proportion of stands in the habitat types predicted to be suitable and optimal by Hamel (1992) and were detected in a relatively low proportion of the stands in the habitat types predicted to be marginal and unused, resulting in the small differences in ranks between observed and predicted habitat use. In comparison, the 0.5 value for absolute difference in ranks was reached 8 times for Carolina chickadee (Fig. 1A) and 16 times for red-eyed vireo (Fig. 1B).

Several other species also were predicted to utilize the same set of mature deciduous habitat types as the specialist species, but our results indicated that these other species (e.g., ovenbird, scarlet tanager, wood thrush, worm-eating warbler [Helmitheros vermivorus]) used a wider range of habitat types than predicted. These widespread deciduous forest birds typically were detected in relatively high proportions of the early-aged stands and/or conifer stands and in relatively low proportions of the mature deciduous stands, resulting in poor agreement between rankings based on observed and predicted habitat use.

For the models that performed well, no large discrepancies regarding over- or underpredicting the use of a particular forest type or successional stage were consistently seen across all 3 study sites (Figs. 1C,D). This similarity was reflected in consistently significant results ($P \le 0.10$) across study sites from the tests of independence for specialist species: black-and-white warbler, blue-headed

vireo, black-throated blue warbler, and veery (Table 1). Nonsignificant results (P > 0.10) consistently were found across study sites for 9 species. Thus, of the 24 species occurring in sufficient numbers on at least 2 study sites, results of the independence tests were consistent across sites for 13 species. For the remaining 11 species, the level of statistical significance of the independence tests was not consistent across study sites. Hence, overall results from our study were mixed, with most tests indicating rather poor performance (16 species had nonsignificant test results for at least 2 study sites), but with test results for models of most species (64%) achieving significance for at least 1 of the study sites.

DISCUSSION

Model Performance

Hamel (1992) intended his matrices to be a starting point from which to begin assembling an accurate, comprehensive database on bird-habitat relationships for forest habitats of the South. He stressed the importance of testing these relationships with empirical data, and then using the results to improve the models. Our study and 1 recently completed in South Carolina (J. C. Kilgo, U.S. Forest Service, unpublished data) are 2 of the first extensive field tests of Hamel's (1992) models. The results from these 2 studies illustrate both the successes and shortcomings of some of the methods developed by Hamel.

Our results were similar to those found in the South Carolina study (J. C. Kilgo, U.S. Forest Service, unpublished data), with deciduous hardwood and sawtimber habitat types typically having high rates of commission (indicating species were found relatively less often in these types than predicted), and early-successional age classes with high rates of omission (indicating species were underpredicted in those types). Within our study sites, some of the species predicted to be associated with mid-age to mature deciduous forest appeared to utilize a wider set of age classes—especially early-successional habitats—than predicted by Hamel (1992). Our results suggest that adding the seedling-shrub age class in deciduous forest types to the list of marginal habitat types (rather than characterizing them as unused) would be appropriate for those deciduous forest birds that typically are thought to be mature forest species but which we found to utilize early-aged classes with some regularity.

Another set of species for which the models did not perform well were those that Hamel (1992) generally described in his species accounts as widespread or commonly occurring across many forest types and ages, such as blue jay, Carolina chickadee, Carolina wren, and tufted titmouse. Although these species were described as generalists in the species accounts, mature forest types generally were listed as the optimal habitats for these species in the habitat matrices. This apparent discrepancy between the description of suitable habitat in the species accounts and the entries in the habitat matrix appeared to contribute to poor performance on our tests because our survey data found that these species occurred relatively often in early-aged habitats. If the habitat types had been more equally ranked in the Hamel's matrices for these species, the results from our tests might have been more favorable. Models for habitat generalists (including some of the same species: Carolina chickadee, Carolina wren, tufted titmouse) also tended to perform more poorly on the tests in the South Carolina study (J. C. Kilgo, U.S. Forest Service, unpublished data) than did models for habitat specialists.

Preliminary attempts to predict bird densities based on habitat suitabilities using methods similar to those in Hamel (1992) provided encouraging results (Hamel et al. 1986). Our results suggested most of the models we tested did not accurately predict species' occurrences among habitat types across a large geographic area. Overall results were mixed from our study, as were results from the study in South Carolina (J. C. Kilgo, U.S. Forest Service, unpublished data), which found Hamel's models to have at least moderate ability to predict habitat quality for 55% of the species they tested. These mixed results suggest that Hamel's models may have misrepresented the use of several habitat types by numerous species across the southeastern United States. However, our study and the South Carolina study are the first attempts to formally test the bird-habitat relationships developed by Hamel (1992), and further tests will help to better understand the usefulness of models such as Hamel's. We recommend placing more biological meaning on patterns of results from these studies that are apparent across suites of species or all species tested than on results for any particular species.

Numerous other modeling methods exist for developing bird-habitat relationships (see Verner et al. [1986] and Scott et al. [2001] for reviews). Empirically based statistical models, such as those developed using logistic regression

or discriminant analysis, can produce good predictive models of wildlife-habitat relationships (Fielding and Haworth 1995, St. Georges et al. 1995). However, rarely have such methods been applied and tested over large geographic areas as was done in this study. Classification and regression tree analysis have shown promising results for modeling over large areas (O'Connor et al. 1996), but few comparisons of whether different models produce successful predictions for large areas have been undertaken. Therefore, it is difficult to know which methods might consistently produce good results.

A greater percentage of the models performed well on the Tennessee data than on the Georgia or Virginia data. These results may have reflected either biological or experimental effects. The Georgia site was at the southernmost extent of the geographic range of some of the species. Habitat use at range boundaries may differ from that observed closer to the center of the range (Best and Stauffer 1986). The design of the Tennessee surveys may have been more appropriate for model evaluation because the point counts were evenly distributed across all 3 stand age classes within 6 major forest types, resulting in 18 habitat types with fairly balanced sample sizes. Point counts in Georgia and Virginia were distributed based on habitat availability, and thus were not as evenly distributed across habitat types as point counts in Tennessee. These differences in the survey design may have resulted in reduced ability to accurately document avian use of the less common habitat types in Georgia and Virginia. Additionally, our overall assumption that the relative frequency of detections among the different habitat types reflects habitat suitability is rather simplistic and might not be the most appropriate for all species. Additional demographic variables, such as density, reproductive success, and survival, are other factors that could be important in determining habitat suitability for a given species.

Ecological Implications

Models developed by Hamel (1992) were based on the assumption that vegetation structure and composition are sufficient for accurately predicting the composition of bird communities in forested habitats. A second inherent assumption was that the habitat types defined for the bird-habitat matrices were sufficiently refined to adequately describe meaningful variation in vegetative structure and composition. The first assumption represents a long-standing hypothesis that has substantial support in the avian litera-

ture (MacArthur and MacArthur 1961, Recher 1969, Willson 1974, Rotenberry and Wiens 1980, Cody 1985). However, the habitat types defined for Hamel's bird-habitat matrices are likely to encompass much variation in vegetation structure and composition. This variability within and among forest stands almost certainly contributed to the poor performance of some of the models (Best and Stauffer 1986). The amount of understory vegetation can vary considerably between stands of the same forest type and age, and understory vegetation can be a very important component of suitable habitat for some species (e.g., hooded warbler and wood thrush). This variability in vegetation structure and composition within habitat types can lead to variability in the proportion of occupied stands, which makes discerning clear patterns more difficult. Therefore, species for which vegetation structure and composition are more important in defining suitable habitat than forest type or age are likely to be more difficult to model accurately when using Hamel's methods for developing habitat relationships.

MANAGEMENT IMPLICATIONS

The bird-habitat models that we tested were designed to aid forest land managers in prescribing treatments to improve avian habitat and for assessing the potential impacts of management activities on bird communities (Hamel 1992:3). Our results suggest that within the Southern Blue Ridge region, Hamel's models should be used with caution until further field tests are conducted and models can be updated based on more empirical data. While our results were mixed, the predictions of many of the models failed to accurately describe the relative levels of stand occupancy for a given species among habitat types over a large geographic area. We suggest that land managers can use the models for species restricted in their distribution to mid-aged to mature deciduous habitat types (e.g., black-andwhite warbler, black-throated blue warbler, blackthroated green warbler, and blue-headed vireo) and/or limited in distribution by elevation (e.g., black-throated blue warbler and veery) with few concerns regarding inaccuracies in the predicted habitat suitabilities. We also suggest that within the Southern Blue Ridge region, Hamel's models for the more widespread species of mature deciduous forest (e.g., hooded warbler, red-eyed vireo, scarlet tanager, worm-eating warbler, and wood thrush) might most appropriately be used if early-aged deciduous habitats are considered to be at least marginal for these birds that can occur in a variety of age classes and at a variety of elevations. While we do not believe that these species are likely to occur in the very earliest stages of stand regeneration, we interpret our results as indicating that once the sapling stage is reached, these habitat types will begin to receive some use by these species.

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