Forest Bird Habitat Suitability Models and the Development of General Habitat Models

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This publication may be cited as:

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by

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Abstract. Habitat Suitability Index (HSI) models were developed to assess the sensitivity of wildlife to habitat perturbations. Because most models consider a single species, their generality is limited. We evaluate the feasibility of combining such models for species occupying similar habitats to create more general models of wildlife–habitat relations. We base our evaluation on an analysis of HSI models for 16 forest bird species. Several features make it difficult to consolidate existing models into general, multispecies habitat models. The minimum area requirements of species are based on different criteria in different models, and life requisites (limiting factors) include categories that are not equivalent. Standardization of both measurement and definition of minimum area and life requisites is necessary to permit model aggregation. Most of the habitat types occur in only a few of the models, and the models differ considerably in the number of habitat types considered (1–12). Of the 61 habitat variables used in the 16 models, 46 occur in only 1 model. There is also great variety in how habitat suitability is related to particular habitat variables through Suitability Index (SI) graphs and mathematical functions (HSI equations) that combine SI functions. Because the HSI equations combine SI functions in complex ways, any errors in specifying the SI graphs (or in the assumptions underlying these graphs) in individual models are amplified when these models are combined. Combining SI functions that have different threshold values creates "average" SI curves that have no biological reality. Individual HSI models should also be validated if they are to be the basis for development of more general models. Validation should focus especially on assumptions about factors limiting population density and productivity and about how SI values are combined in equations to produce overall HSI values. We emphasize the importance of manipulative field experiments and model sensitivity analyses in such validation activities. We compare the "bottom-up" approach, in which individual models are aggregated to develop more general models, to the "top-down" approach of beginning with broad statements about a system and adding in detail only as it is needed. The bottom-up approach has the advantage of building on known functions and mechanisms that can be validated independently, whereas the top-down approach may include only the most relevant detail. We consider several complications with the bottom-up approach that emerge from our analysis of forest bird models, and note as well several difficulties in implementing the top-down approach. We suggest that the "envirogram" may offer an alternative approach that is founded on a consistent logical structure. Any attempts to model wildlife–habitat interrelations, whether they apply to single species or suites of species, must also consider the importance of the spatial and temporal scales of resolution used and must treat habitat units as part of a larger landscape mosaic.

Key words: Habitat suitability models, general wildlife–habitat models, model validation, forest birds.

The goal of wildlife habitat modeling is to develop models that can be used to assess wildlife–habitat relations and to predict their sensitivity to perturbations. Such models may be valuable tools in developing land-use plans, managing refuges or natural reserves, or mitigating the effects of human activities on wildlife species. To succeed, models should satisfy three criteria. First, they should be valid. That is, they should be founded on functions that are logically sound and biologically realistic. Valid models are more likely to produce accurate predictions. Second, they should be general, so that a single model can apply to a wide range of situations without major modifications. Third, they should be simple and usable. A valid, general model that is also complex or difficult to use, or that requires detailed field measurements of many parameters, is unlikely to be useful to anyone except the modeler.

Ideally, of course, models should be all of these things. However, the priorities of model validity, generality, and usability often compete with one another. Each has benefits but carries costs, and it is difficult to emphasize, for example, validity without some sacrifice in usability. There is therefore no correct balance among these priorities. The objectives of a particular application of a model or series of models determine which may be most important.

The Habitat Suitability Index (HSI) modeling program initiated as part of Habitat Evaluation Procedures (HEP) by the U.S. Fish and Wildlife Service represents an effort to develop an orderly and easily used series of models to evaluate wildlife habitat. In general, HSI models operate by deriving suitability values for different habitat types, converting these to habitat unit (HU) values by adjusting for the areas of those types present, and then adding the HU values to obtain an overall suitability index for a given area. The modeling approach has emphasized usability. Efforts have also been made during model development to ensure that they are biologically valid and operationally robust. Because the focus of HEP has been on species rather than habitats, the models apply to single species occurring in specified habitat conditions. Their generality is therefore limited. Moreover, because these models have not always been developed with the same purposes in mind, the objectives of the modeling efforts may differ.

A common feeling persists among modelers and managers alike that wildlife–habitat models that are general in their applications but specific in their predictions would be useful. Generality may be achieved in any of three dimensions by: (1) extending the coverage from species to include sets of ecologically similar species (guilds) or entire communities, (2) increasing the area or regions in which a model may be employed, or (3) broadening the range of cover types to which a model may apply. The limits to generality in each of these dimensions are defined by differences in the ecology of target species, area-dependent changes in habitat responses, and variations in ecological responses among cover types, respectively. Developing greater model generality in the second and third of these dimensions involves adjusting or extending current species-specific models by incorporating area- or habitat-dependent changes in model functions. Although relatively little work has been done in this area, such changes largely represent logical and methodological extensions of existing themes. Some efforts have been made in the first direction, either by considering ecologically similar species as a group (Short 1984; Schroeder 1986, 1987, and unpublished report) or by combining single-species models for a set of similar species (Bain and Robinson 1988).

Our objective is to evaluate the latter "model combination" approach to developing general models of wildlife–habitat relations. We do this by examining in detail a series of Service HSI models developed for birds inhabiting woodlands and forests. We restrict our attention to these HSI models because they have been developed within a common modeling framework and have generally similar objectives, and because they focus on species that occupy the same general habitat. We ask whether these models share a common set of attributes and assumptions that would enable one to combine them into a more general "forest bird" model. After commenting briefly on the objectives of the HSI modeling approach and the set of models we examine, we address this question by examining the forest bird models in detail. We then consider how such models might be validated. We conclude by examining some other approaches to developing general, multispecies models of wildlife–habitat relations. It is not our intention here to undertake a general review of wildlife–habitat modeling, nor to offer a comprehensive critique of the HSI modeling approach and philosophy. Instead, we ask whether it may be worthwhile to attempt to build general models from existing, species-specific HSI models.

The Objectives of HSI Models

Individuals differ in their expectations about the ability of HSI models to provide management guidance. These differences in purpose influence the breadth of model applications and the desired accuracy of model predictions, which in turn affect the way a model is structured. On the one hand, one may wish to make what is known about a species explicit and quantitative, whether or not the information is sufficiently complete. In this instance, the models can be useful for pinpointing where further research should be directed, but they must be regarded as preliminary. On the other hand, there is a need to make available to field personnel and managers models that can be used for predictive purposes and planning. In this instance, the models may be valuable in designing site-specific research on, or anticipating the effects of, planned perturbations. Unless this distinction is made clear, preliminary models of the first sort may be used in the predictive or planning role of the second sort of model. In the absence of site-specific experimental validation of predicted effects, however, such uses would be indefensible. Model validation is therefore a critical phase of the development from preliminary to planning models. Most HSI models have been constructed largely as working versions rather than as final, definitive models. Simplicity has been implicitly valued over comprehensiveness, perhaps for the models to be useful to field managers having little training or experience in this area (A. H. Farmer, National Ecology Research Center, Fort Collins, Colorado, personal communication). The model structure is therefore simple, and the functions that go into the models are relatively easy to understand. Model software is accompanied by instructions that allow the user to modify functions easily. The functions that are included in each model are based on both published and unpublished information that indicates variables that can influence the potential density of a species through direct or indirect effects on its life requisites. Because this information is often limited, however, one should probably not rely absolutely on the resulting functions. Nonetheless, the models have been published in a way that makes them appear to be final products rather than working quantitative summaries of the information available to the developers of the models. Most HSI models therefore contain elements of both of the models mentioned previously: although they are in many respects incomplete and preliminary,

they are nonetheless intended to be used as planning tools.

We believe that most HSI models should be seen as quantitative expressions of our best working understanding of the relations between easily measured environmental variables and habitat quality (we assume that habitat suitability or quality is best understood as a function both of density and of survival and reproduction by individuals of a given species [Van Horne 1983, 1986]) for a species. If this is so, then efforts should be made to validate these models before using them as predictive management tools. We consider model validation later in this report; here however, we observe that initial validation should be directed toward evaluating the internal operational structure of models rather than determining whether the current models are sufficiently accurate predictors of field situations, because validating the internal structure of models is easier and because trustworthy model predictions must be founded on logically and operationally sound model structure.

The Forest Bird Models

To assess the structure of HSI models and the feasibility of aggregating single-species models to create general models, we reviewed all the Service HSI models (Appendix) that were published as of June 1988 that described habitat suitability for birds whose primary habitat is deciduous or evergreen forest. We expected these 16 models to have many features in common. We therefore believed that comparisons among them might be particularly valuable in highlighting consistencies and inconsistencies in model structure and approaches. Such features are a foundation for developing more general HSI models of habitat suitability for guilds or communities of birds with overlapping habitat use. To aid in our comparisons, we separated the 16 species into four guilds or "taxonomic assemblages" (Jaksić 1981) based on phylogenetic and ecological similarity (Table 1).

Analysis and Evaluation of the Forest Bird HSI Models

We assessed the forest bird HSI models according to the logic behind model construction, consistency among models, and the validity of the assumptions made by the models.

Table 1. *Species assignment to guilds, scientific names, period, and minimum areas considered in HSI models for these species.*

Species(code)	Scientific name	Period[a]	Minimum area
Galliformes			
Blue grouse(BG)	*Dendragapus obscurus*	Breeding	unknown
Ruffed grouse (RG)	*Bonasa umbellus*	Year	4 ha (20 ha recommended)
Sharp-tailed grouse (PG)	*Tympanuchus phasianellus*	Year	5.3 km^2
Northern bobwhite (NB)	*Colinus virginianus*	Year	4.9 ha
Wild turkey (WT)	*Meleagris gallopavo*	Year	900 ha
Woodpeckers			
Downy woodpecker (DW)	*Picoides pubescens*	Year	4 ha
Lewis' woodpecker (LW)	*Melanerpes lewis*	Year	none
Pileated woodpecker (PW)	*Dryocopus pileatus*	Year	130 ha
Williamson's sapsucker (WS)	*Sphyrapicus thyroideus*	Breeding	4 ha
Owls			
Barred owl (BO)	*Strix varia*	Breeding	unknown
Spotted owl (SO)	*Strix occidentalis*	Year	1,963.5 ha
Passerines			
Pine warbler (PI)	*Dendroica pinus*	Breeding	10 ha
Yellow warbler (YW)	*Dendroica petechia*	Breeding	0.15 ha
Black-capped chickadee (BC)	*Parus atricapillus*	Breeding	none
Brown thrasher (BT)	*Toxostoma rufum*	Breeding	1 ha
Veery (V)	*Catharus fuscescens*	Breeding	0.4 ha

[a] Model applied to year-round habitat suitability (year) or suitability for the breeding season only (breeding).

Season and Minimum Habitat Area

Models for all the passerines and one member of each of the three other groups apply to habitat relations only during the breeding season (Table 1). The passerines are migratory; inclusion of winter habitat information in the models would not be possible under the present model structure. Of course, models that apply only to the breeding season are intended to generate useful predictions only of the effects of changes in breeding habitat on population density and productivity. Such predictions are valid, however, only insofar as breeding-season habitat alone limits population density; changes in habitat quality in the wintering or migratory stopover areas are assumed to have no effect on demography. This assumption is not likely to be satisfied in "open" populations, in which the dynamics observed at a given breeding location are influenced by events elsewhere in the species' overall range (May 1981; Wiens 1989a). If this occurs, the model will be incomplete and it will not be possible to verify its predictive power.

Seasons are vaguely defined in some models (e.g., winter may include all or part of the fall and spring seasons). Seasons should be clearly defined in each model. For example, a definition based on some phenological cue (e.g., vernal equinox ± bud break) might serve to standardize the onset of spring.

Minimum habitat area is defined for all models as the minimum amount of contiguous habitat that is required before an area will be occupied by a species. This definition is vague (does an occasional visit count as occupation?) and does not explicitly describe the minimum habitat area required to support a self-sustaining population. Thus, a habitat might be assigned a high suitability value without being able to sustain a population. Whether or not it is of any value depends on whether the larger landscape has sustainable populations that use the habitat in a way that enhances the ability of individuals to survive and reproduce. If not, it seems improper to give it a positive suitability value. Further, consideration of habitat area alone fails to recognize the distinction between edge and interior portions of a given habitat

area, which may be important for many forest-dwelling bird species (Lynch 1987; Wiens 1989b).

These problems are not dealt with in the models but must be considered by the managers in model application. In fact, minimal area could be defined with reference to an individual (even a transient), a breeding pair, a self-sustaining population, a population maintaining a given level of genetic diversity, or some other biological groupings. The areas included by each of these definitions may differ dramatically; which is most relevant depends on one's objectives.

For the species we considered, minimum areas were not specified for the blue grouse *(Dendragapus obscurus)* and barred owl *(Strix varia)*, and no minimum area was assumed for the Lewis' woodpecker *(Melanerpes lewis)* and black-capped chickadee *(Parus atricapillus)*. The remaining minimum areas (Table 1) are based on minimum territory sizes (yellow warbler, *Dendroica petechia;* veery, *Catharus fuscescens;* downy woodpecker, *Picoides pubescens)*, home range (Williamson's sapsucker, *Sphyrapicus thyroideus)*, maximum density and expert recommendation by personal communication (two different values; ruffed grouse, *Bonasa umbellus)*, lek distances (sharp-tailed grouse, *Tympanuchus phasianellus)*, citation of minimum area (northern bobwhite, *Colinus virginianus)*, and unknown sources (wild turkey, *Meleagris gallopavo;* pileated woodpecker, *Dryocopus pileatus;* pine warbler, *Dendroica pinus;* and brown thrasher, *Toxostoma rufum)*.

Clearly, minimum area will vary as a function of several factors. The scale at which habitats are identified or how cover types are arrayed in a larger landscape mosaic may influence minimum area. For a given species, the area required by an individual is likely to vary in relation to its seasonal activity (e.g., breeding), its energy demands (e.g., thermoregulatory costs in winter), and the cover types it occupies, and it is not obvious which of these is likely to be the most limiting minimum. Perhaps the best way to strengthen the minimum area values is to collect information on breeding density (and perhaps success) in locations of varying sizes and suitabilities. Minimum area could then be described as a function of suitability (Fig. 1) and used in interpreting model output. A coarser approach is to estimate minimal areas by using allometric home range–body mass relations (Schoener 1968; Calder 1984). We have used the equation

$$A = 98.6M^{1.15},$$

where home range–territory size (*A*, in ha) to body
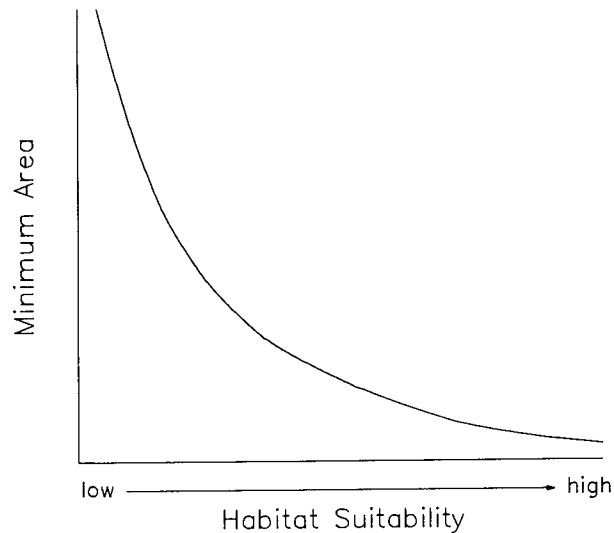
Fig. 1. A hypothetical function relating changes in minimum area required by individuals of a given species to increasing habitat suitability.

mass (*M*, in kg) to predict the home ranges expected for the species we considered in this analysis (Fig. 2). Of course, home range–territory size is only one possible measure of minimum area. Some of the values used in the HSI models agree closely with the allometric predictions, but there are substantial departures (both positive and negative) for the remaining values. Clearly, the present approach has produced wide variation among the models for different species. Regardless of whether an allometric function or some other relation provides the most appropriate estimate of minimum areas, some standardization of both definition and measurement is needed. In the absence of such standardization it would be premature to ignore the suitability of habitats occurring in areas less than the minimum sizes, particularly where these habitats are in a larger mosaic of habitats of varying suitabilities. For instance, two or more "contiguous" habitats that are individually smaller than a specified minimum area may be large enough in combination to exceed minimum area requirements.

Life Requisites

Life requisites are the general factors that could limit a species in a given habitat or series of habitats. The life requisites specified in HSI models are food, cover, and reproduction. These categories, however, are not equivalent. Food and cover are features of the
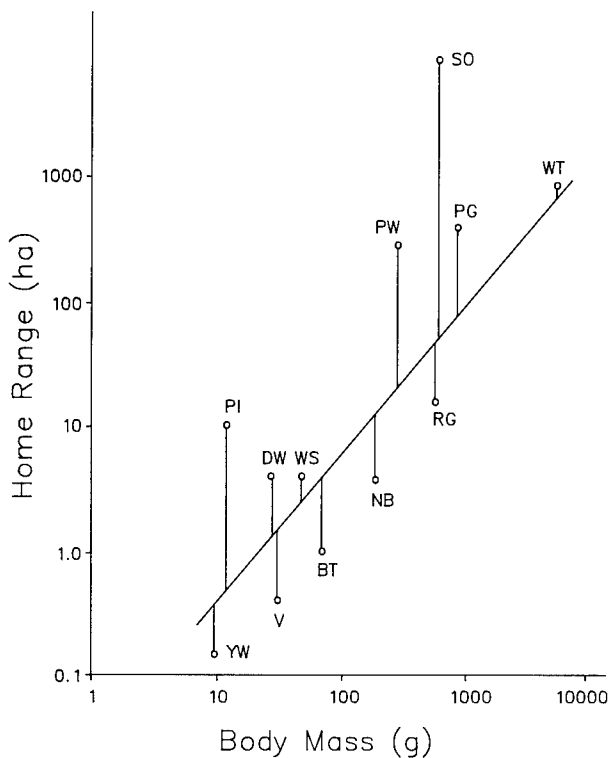
Fig. 2. The relation between minimum areas specified in Habitat Suitability Index (HSI) models for forest bird species (*open circles*) and the size of individual territories or home ranges predicted from a home range–body mass function (indicated position on *line*). Species codes are YW = yellow warbler, PI = pine warbler, DW = downy woodpecker, V = veery, WS = Williamson's sapsucker, BT = brown thrasher, NB = northern bobwhite, PW = pileated woodpecker, RG = ruffed grouse, SO = spotted owl, PG = sharp-tailed grouse, WT = wild turkey.

environment that may be considered independently of the species of interest. In contrast, reproduction is a characteristic of the species that is dependent on food, cover, and perhaps other life requisites. Changes in food or cover might well influence reproduction, but the reverse does not occur except indirectly as changes in reproductive rates lead to changes in density. Likewise, mortality and survival might also depend on food, cover, and other requisites. In addition, different species' models combine life requisites into single categories in different ways (e.g., cover + reproduction, food + cover). This makes it difficult to compare among models, much less synthesize them into more general models.

The models could be made more explicit by separating the life-history traits (reproduction, mortality and survival) from the measured environmental

variables in such a way that any change in the measured variables must influence food, cover, nest sites, or some other factor that, in turn, affects reproduction and survival. Later in this report we examine one way of ordering the interrelations among life requisites more logically.

Of the HSI models we considered, all but those for the blue grouse and ruffed grouse include reproduction as a life requisite that is directly affected by changes in some or all of the variables measured for model input (Table 2). However, the blue grouse model is applied only to breeding-season habitat (Table 1). The barred owl and spotted owl (*Strix occidentalis*) and yellow warbler models consider reproduction the only life requisite affected by changes in the measured variables. If we assume that effects on reproduction are always mediated by some factor such as adult food, nestling food, availability of nest sites, or protection from predators, then the causal relation between reproduction and the measured variables is not explicit in these three models. In the remaining models, which include either food or cover life requisites along with reproduction, the effects of habitat variables on reproduction are clearly mediated by food and cover (and perhaps by other factors as well).

When life requisites (and seasons) are specified in HSI models, the assumptions about what general factors or seasons may be limiting to a species become explicit. One must remember, however, that the factors actually limiting population dynamics are known for few species, and the specifications included in the models therefore usually represent no more than educated guesses. Such specifications are necessary to proceed with a modeling effort, of course, but the eventual success of a model as a predictive tool (rather than as a working model) may be quite sensitive to how valid the assumptions about limiting factors or time periods really are. If one has failed to include in a model the correct limiting factors or times of the year, has interrelated them incorrectly, or has measured variables that do not relate closely to these limiting factors, the model predictions may be false or misleading.

Habitats

Groups of birds that occupy similar habitats are potential candidates for combination into multispecies models. Some similarities exist in the habitat types included in the models for members of each of the four groups of birds (Table 3). The five galliform

Table 2. *Life requisites included in each Habitat Suitability Index (HSI) model. All are listed separately even when they were combined in the models (i.e, cover plus reproduction). Winter food or cover may also apply to fall and spring food or cover.*

Species	Food			Cover		Reproduction
	All year	Summer	Winter	All year	Winter	
Galliformes						
Blue grouse	X			X		
Ruffed grouse			X		X	
Northern bobwhite			X	X		X
Plains sharp-tailed grouse			X	X	X	
Wild turkey	X			X		X
Woodpeckers						
Downy woodpecker	X					X
Lewis' woodpecker		X	X			X
Pileated woodpecker	X			X		X
Williamson's sapsucker				X		X
Owls						
Barred owl						X
Spotted owl						X
Passerines						
Pine warbler				X		X
Yellow warbler						X
Black-capped chickadee	X					X
Brown thrasher	X			X		X
Veery				X		X

models all include deciduous forest, evergreen forest, deciduous tree savanna, evergreen tree savanna, and deciduous shrubland habitats. In addition, three habitat types are common to four of the five models. Two habitat types are found only in one model each. The four woodpecker models all contain deciduous and evergreen forest types; three of the models include deciduous forested wetland. Deciduous wetland is found only in the Lewis' woodpecker model. Evergreen forest is included in both owl models, whereas the barred owl model contains two additional habitat types. The passerines form the most heterogeneous group. Four of the five passerine models include deciduous forest and evergreen forest. The brown thrasher model contains nine habitat types that are not included in the other passerine models; this model is more similar to the galliform models than to those of the other passerines. Because we focused our analysis on forest habitat types, deciduous forest and evergreen forest (14 and 15, respectively of the 16 models) are the most common habitats included in the models

(Table 3). The next most common habitats, deciduous tree savanna, evergreen tree savanna, and deciduous shrubland, are each included in eight models. Five of the habitat types occur in two or fewer models.

To aggregate species-level models to form more general models, most habitat types should appear in most models. Clearly, this is not the case. The reason becomes apparent when one considers the number of habitats included in individual species' models. The broadest range of habitats (12) is found in the models for brown thrashers, northern bobwhites, and wild turkeys (Table 3). The narrowest range (1) occurs in the spotted owl model, followed by the pine warbler and yellow warbler models (2). The owl may have a narrow habitat specialization, but for the warblers, which occur in other, nonforested habitat types as well, no such conclusion is justified. If many of the species are restricted to only a few habitat types, it will be difficult to develop general models by aggregating species models unless (a) the analysis is restricted to a particular habitat type, or (b) the distinctions between habitat types are ignored.

Table 3. *Habitat types included in the forest bird HSI models.*

Species	C	DSW	EFW	DW	DFW	PFO	DF	EF	DTS	ETS	DS	ES	DSS	ESS	G	F	O	P/H	Σ
Galliformes																			
Blue grouse							X	X	X	X	X	X	X	X	X	X		X	11
Ruffed grouse							X	X	X	X	X	X							6
Sharp-tailed grouse							X	X	X	X	X	X	X	X			X		9
Northern bobwhite	X						X	X	X	X	X	X	X	X	X	X		X	12
Wild turkey	X				X		X	X	X	X	X		X	X	X	X		X	12
Σ	2	0	0	0	1	0	5	5	5	5	5	4	4	4	3	3	1	3	
Woodpeckers																			
Downy woodpecker			X		X		X	X											4
Lewis' woodpecker				X	X		X	X	X	X									6
Pileated woodpecker			X		X		X	X											4
Williamson's sapsucker							X	X	X	X									4
Σ	0	0	2	1	3	0	4	4	2	2	0	0	0	0	0	0	0	0	
Owls																			
Barred owl						X	X	X											3
Spotted owl								X											1
Σ	0	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	
Passerines																			
Pine warbler							X	X											2
Yellow warbler		X										X							2
Black-capped chickadee			X		X		X	X											4
Brown thrasher							X	X	X	X	X	X	X	X	X	X	X	X	12
Veery		X	X		X		X	X				X							6
Σ	0	2	2	0	2	0	4	4	1	1	3	1	1	1	1	1	1	1	
Overall Σ	2	2	4	1	6	1	14	15	8	8	8	5	5	5	4	4	2	4	

[a] C = cropland, DSW = deciduous shrub wetland, EFW = evergreen forested wetland, DW = deciduous wetland, DFW = deciduous forested wetland, PFO = palustrine forested wetland, DF = deciduous forest, EF = evergreen forest, DTS = deciduous tree savannah, EFF = evergreen shrub savannah, G = grassland, F = old field, O = orchard, P/H = pasture and hay fields.

Measured Variables

We have grouped similar variables across models (Table 4) to determine whether models of species in the same group have similar or identical variables, identify variables that are sufficiently similar that they could be combined into a single measurement, and search for variables that might have unexpected dynamics in models. In these models, variables are measured in a series of habitat types that may be a subset of the range of habitat types included in the model, and a given variable may be used to index the food, cover, or reproductive value of a habitat area. The life requisites may likewise be a subset of all life requisites included in the model for that species.

Overall, some 61 variables are included in the 16 models we reviewed. Of these, 1 variable appears in 5 models and 2 variables are elements of 4 models; 46 variables appear in only a single model (Table 4). To a large degree, the models are species-specific or idiosyncratic in the variables they employ. At a more general level, variables related to tree height, tree density, size (trunk diameter at breast height, dbh), and canopy cover are measured for a wide variety of species models. All of the variables used in the owl models fall into these categories. With the exception of one variable in the black-capped chickadee model, the snag and log-related variables are found only in the woodpecker models. Herb height, herb cover and type, and crop-related variables are used mostly

Table 4. *Variables measured or used in forest bird HSI models.*[a]

Variable	BG	RG	PG	NB	WT	DW	LW	PW	WS	BO	SO	PI	YW	BC	BT	V	Σ model in which the variable appears
Tree height																	
Average height overstory trees												X		X			2
Average lowest branch height of conifers		X															1
Tree diameter at breast height																	
Mean dbh overstory				X						X	X						3
Avg dbh pine or oak			X														1
Avg dbh overstory aspen									X								1
Tree number and type																	
Density trees ≥ 51 cm dbh								X		X							2
Density deciduous trees		X															1
Density coniferous trees		X															1
Density pine or oak			X														1
Tree canopy																	
% canopy cover overstory trees ≥ 80% tallest tree										X							1
% canopy cover trees ≥ 5 m							X								X		2
% canopy closure trees ≥ 5 m				X		X	X			X				X			5
% canopy cover evergreen	X			X													2
% overstory tree canopy closure pines												X					1
% pine canopy closure with deciduous understory												X					1
% area aspen dominated									X								1
tree canopy volume/area														X			1
tree story canopy diversity											X						1
Ave radius circle with 20 mature aspen		X															1
Snag density																	
> 15 cm						X											1
≥ 30.5 cm							X										1
> 38 cm								X									1
> 51 cm								X									1
soft									X								1
10–25 cm > 1.8 m tall														X			1
Snag diameter at breast height																	
Average dbh snags > 38 cm								X									1
Average dbh snags > 51 cm								X									1
Stumps and logs																	
# stumps of specified sizes								X									1
Trees and shrubs																	
Average height woody stems		X															1
Density woody stems > 1 m tall															X		1
Basal area woody vegetation						X											1
Shrub height																	
Average height deciduous shrubs	X												X	X			3
Shrub density																	
density deciduous shrub		X															1

Column group headers: Galliformes (BG, RG, PG, NB, WT); Woodpeckers (DW, LW, PW, WS); Owls (BO, SO); Passerines (PI, YW, BC, BT, V).

Table 4. *Continued.*

Variable	Galliformes					Woodpeckers				Owls		Passerines					Σ model in which the variable appears
	BG	RG	PG	NB	WT	DW	LW	PW	WS	BO	SO	PI	YW	BC	BT	V	
Shrub cover type																	
% shrub > 5 m crown cover	X			X		X											3
% canopy over woody vegetation > 2 m				X													1
% deciduous crown cover													X		X		2
% area of shrubby cover			X														1
Mast																	
Average dbh of mast-producing trees				X													1
Density of mast tree				X													1
% tree cover that is mast tree							X										1
% crown cover mast shrubs							X										1
% crown cover soft mast shrubs						X											1
Herbs-height																	
Average height herbaceous canopy	X			X	X										X		4
Herbs-cover and type																	
% herbaceous canopy cover	X			X	X										X		4
% canopy cover of NB food				X													1
% herb canopy grass				X													1
% types providing cover			X														1
Diversity herb vegetation	X																1
Mean visual obstruction			X														1
Crops																	
Crop type				X	X												2
% grain crops within specific distance			X														1
Standing corn							X										1
Crop harvesting				X	X												2
Water																	
% covertype spring flooded															X		1
Soil moisture				X											X		2
% deciduous shrub canopy hydrophytic												X					1
Bare ground																	
% cover litter > 1 cm															X		1
% cover light litter				X													1
Distance																	
mast storage site							X										1
forest or tree savanna	X				X												2
between cover types		X															1
Total variables per species	7	6	5	11	12	3	7	7	4	3	3	3	3	4	3	6	

[a] BG = blue grouse, RG = ruffed grouse, PG = plains sharp-tailed grouse, NB = northern bobwhite, WT = wild turkey, DW = downy woodpecker, LW = Lewis' woodpecker, PW = pileated woodpecker, WS = Williamson's sapsucker, BO = barred owl, SO = spotted owl, PI = pine warbler, YW = yellow warbler, BC = black-capped chickadee, BT = brown thrasher, V = veery.

for the galliform species, although the models for these species also include variables from most of the other categories. Thus, although the specific variables used differ markedly among models, there are some similarities within groups of species in the general categories of variables that appear. The galliform and woodpecker models contain more variables than do most of the owl or passerine models (Table 4).

It is difficult to assess which variables from different models might be closely enough related to one another to allow use of measurements of a single variable in two or more models. In some cases, however, variables are identical. For galliformes, three variables are found in common in three of the five models: shrub cover (measured in slightly different ways; Fig. 3A), height of herbaceous canopy (Fig. 3B), and percent herbaceous canopy cover (Fig. 3C). The functions describing the relations between percent shrub-crown cover and habitat suitability, however, have very different forms for the blue grouse, plains sharp-tailed grouse, and wild turkey (Fig. 3A). Average height of herbaceous canopy is related to habitat suitability in similar ways for three of the galliform species (Fig. 3B). Similarly, percent herbaceous canopy cover is optimal for these three species over similar ranges (Fig. 3C). The herbaceous variables influence different life requisites for each of the three species: food, cover, and reproduction for the wild turkey, food and cover for the blue grouse, and reproduction for the northern bobwhite. The blue grouse and wild turkey models share a variable describing the distance to forest or tree savanna cover types, although the ranges over which this variable is optimal differ (Fig. 3D). In the wild turkey model this variable is used to modify both herbaceous and shrub cover types, whereas in the blue grouse model it is used to modify herbaceous cover types only. The variables describing suitability of different types of crops are similar but not identical in the northern bobwhite and wild turkey models.

In sum, height and cover of herbaceous canopy types have a similar relation to habitat suitability for three of the five galliform species, and type of crop may have a similar influence on the northern bobwhite and wild turkey. The effect of distance to forest or tree savanna cover types shows some similarity for the blue grouse and the wild turkey. The differences among these variables are perhaps subtle enough to justify using the same measures in more than one model. There are 18 additional variables measured in the 5 models that have little overlap, however, either

because they consist of different types of measurements or because the functions describing their effects on habitat suitability take different forms for the different species.

The HSI models for the woodpeckers contain one variable, percent canopy cover of trees, that is found in three of the four models (Fig. 3E), and the variable, basal area of woody vegetation, in the downy woodpecker model incorporates some of the same information. The relation of canopy cover to the habitat suitability index value differs greatly for the three models, however (Fig. 3E). Percent canopy cover is believed to affect the food life requisite for the Lewis' woodpecker, the cover and reproduction life requisites for the Williamson's sapsucker, and all three life requisites for the pileated woodpecker. Three of the four woodpecker models contain a variable representing density of snags, but the minimum diameter for a snag to be included is only 15 cm dbh for the downy woodpecker, whereas it is 30.5 cm for the Lewis' woodpecker and 38 cm and 51 cm (two functions) for the pileated woodpecker. Because these differences are roughly related to the body masses of these species, it might be possible to combine the variables using a mass-related scaling function. Snag density affects only the reproduction life requisite for the downy and Lewis' woodpeckers but affects all three life requisites in the pileated woodpecker model. The remaining 13 variables used in the 4 woodpecker models exhibit little synonymy among models.

The barred and spotted owl models share a variable that describes the mean dbh of overstory trees, although the ranges over which values represent optimal or unsuitable habitat differ (Fig. 3F). In both models this variable is associated with the reproduction life requisite. The remaining four variables are heterogeneous.

In the passerine group there are four variables that are each common to two of the five models. Average height of overstory trees is shared in the black-capped chickadee and pine warbler models (Fig. 3G), although it affects the food life requisite in the former and the cover and reproduction life requisites in the latter. Suitability values for this variable are generally similar in the two models. The brown thrasher and black-capped chickadee models each have a variable that describes percent canopy cover of trees (Fig. 3H). In both cases this applies to the food life requisite, although in the brown thrasher it also influences cover and reproduction. The relation between this variable and suitability differs for the two species (Fig. 3H). A variable describing average height of decidu-
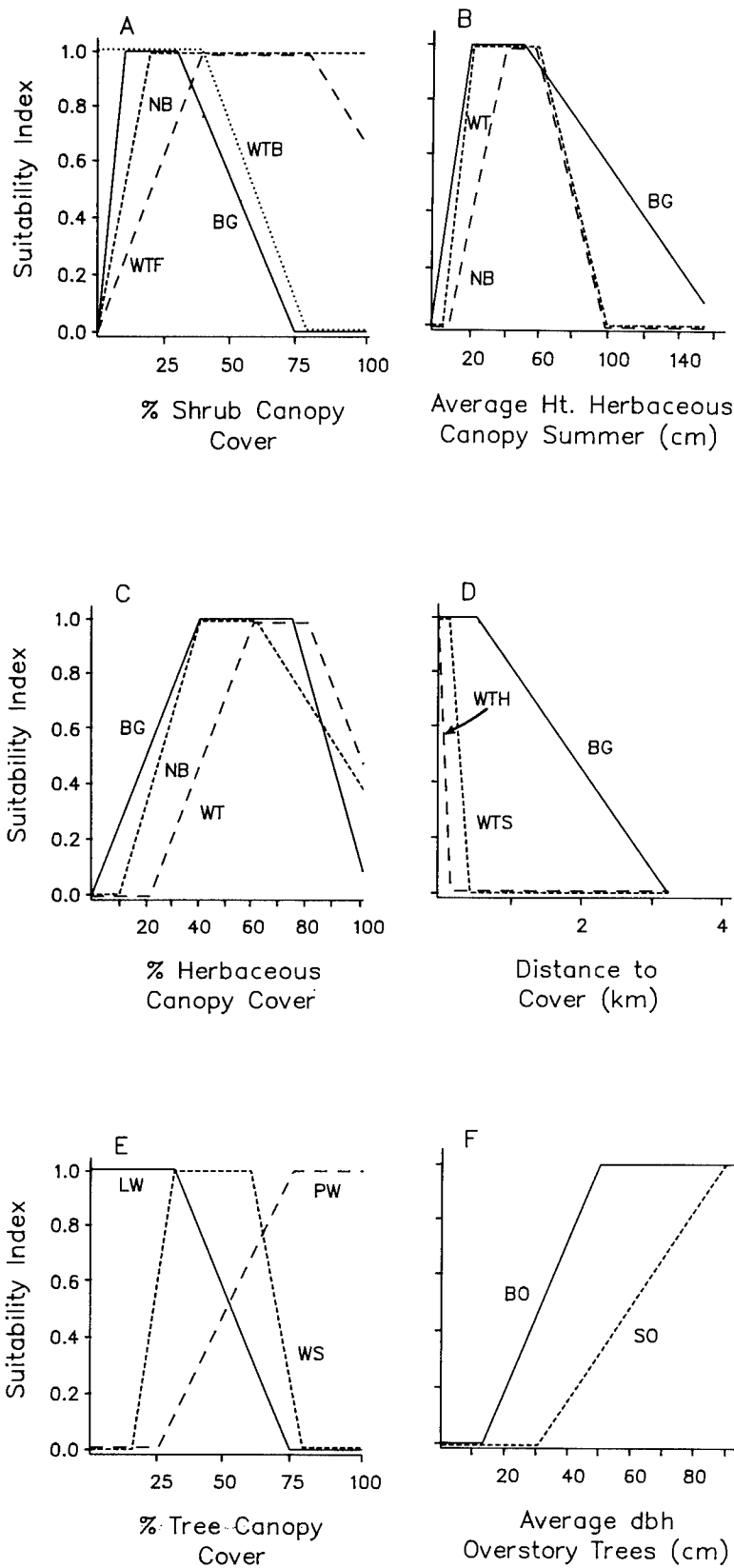
Fig. 3. Overlays of Suitability Index (SI) graphs for variables common to several species models within guilds or taxonomic groups. Species codes for the graphs are NB = northern bobwhite, WT = wild turkey, WTF = wild turkey (food life requisite), WTB = wild turkey (behavior or cover life requisite), WTH = wild turkey herbaceous cover, WTS = wild turkey shrub cover, BG = blue grouse, LW = Lewis' woodpecker, RW = pileated woodpecker, WS = Williamson's sapsucker, BO = barred owl, SO = spotted owl, BC = black-capped chickadee, PI = pine warbler, BT = brown thrasher, YW = yellow warbler, V = veery.
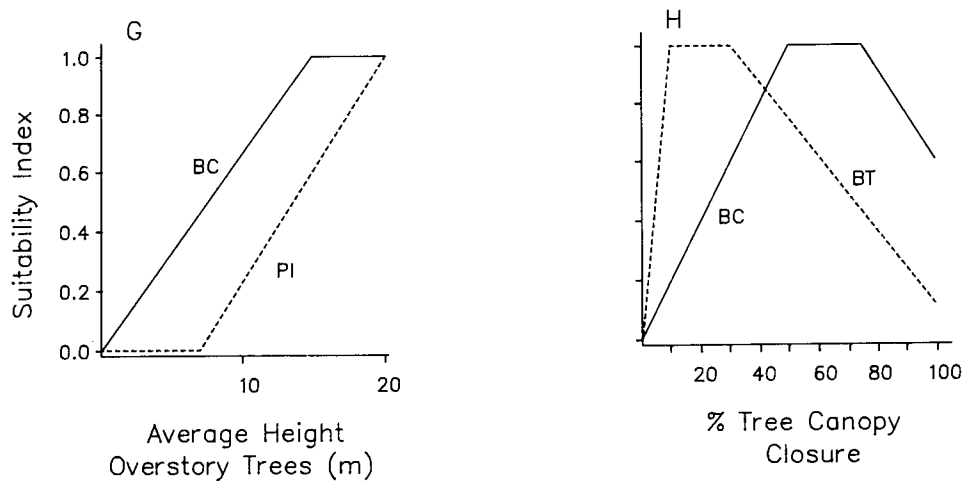
Fig. 3. *Continued.*
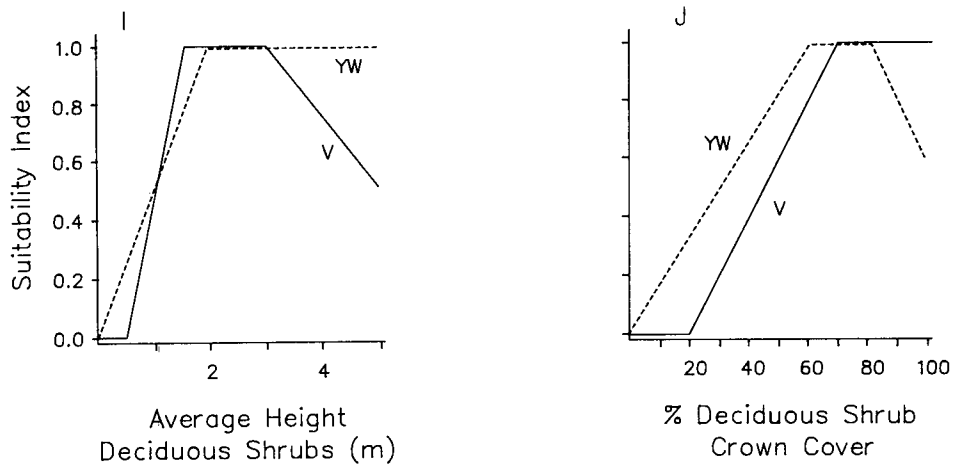
ous shrubs plays a role in both the veery and the yellow warbler models (Fig. 3I). It affects reproduction in both, and cover as well in the veery model. Suitability functions for this variable and for a variable describing percent deciduous crown cover (Fig. 3J) for these species are quite similar. The remaining 11 variables are heterogeneous.

Thus, there are indeed some variables that are common to more than one species within groups of similar species, but in most cases the functions describing the relation between the values of variables and habitat suitability differ among these species. Also, the life requisites influenced by these variables often differ among species. Some models could be made similar with minor adjustments (i.e., density of snags greater than 30.5 cm in diameter for Lewis' woodpecker and density of snags greater than 38 cm in

diameter for the pileated woodpecker; Table 4). Most of the models are built on unique sets of variables, however. It is doubtful that an attempt to develop a single model as an indicator of habitat suitability for any one of these four groups of species (as was developed for riverine fishes by Bain and Robinson (1988)) would be sufficiently successful to be worthwhile.

In reviewing the variables used in these models, we also considered whether variables might be expected to behave in an unstable fashion. Because the calculation of Habitat Units (HU) in HEP involves weighing the HSI values for particular cover types or habitats by their area, all the variables are sensitive to the definition of patch or cover types used for calculating the separate suitability indices, as this definition will affect the area values used in the calculations.

There are no firm guidelines for identifying patch boundaries, yet the values of variables such as "percent of overstory that is aspen" will be greatly affected by the patch boundaries that are used. A second source of instability can be found in the commonly used definition of the overstory as "trees at least 80% of the height of the tallest tree." At the extreme, one might imagine two areas that have been clearcut–logged, each of which has a regenerating canopy at about 2 m but one of which has a seed tree that has been left standing to encourage natural reseeding of the area. By the preceding definition, the clearcut with the seed tree would have almost no overstory canopy, whereas the one without such a tree would be extremely dense. A third source of instability comes from vagueness in variable definition and the associated subjectivity that must be used by the investigators gathering the data. An example of this from the plains sharp-tailed grouse model is the variable "percent of cover types providing potential nest–brood cover."

Variables for Which Variance is Important

For most variables in these HSI models, the mean value for the variable in a given habitat type is used to calculate the suitability index. In some cases, however, the variance of values may be more informative than the mean. For example, the variance in such variables as "tree canopy volume per unit area" in the black-capped chickadee model, "average height of woody stems" in the ruffed grouse model, or "mean visual obstruction reading of residual vegetation" in the plains sharp-tailed grouse model may bear a closer relationship to habitat suitability than the mean values for these variables. Similarly, spatial dispersion may play an important role that is obscured by the use of summary totals or means in models. For instance, variables measuring densities of snags are found in several woodpecker models. Equivalent snag densities in two areas might produce different reproductive values, however, if the trees were clumped at less than minimum nest spacing in one area but not in the other. Variables that measure mean densities or canopy closure may all be affected by the pattern of spatial dispersion. The variance of measures or the dispersion patterns recorded are sensitive to the intensity and distribution of sampling. Comparing such features among areas for a species, or between models that are based on different sampling intensities, will therefore yield inconclusive or incorrect results. In situations in which spatial distribution of vegetation is

likely to be important, a measure of dispersion could be included directly in the models. Because variance depends on sample sizes, efforts should also be made to standardize or, at the very least, specify the intensity at which one should sample the variables used in HSI models. This would facilitate the use of variance measures as variables in the models.

Suitability Index Graphs and Families of Curves

The suitability index (SI) graphs in the models we reviewed are based primarily on general descriptions of values of a given variable that represent unsuitable habitats, values associated with optimal suitability (SI = 1), and straight lines connecting these (the SI for percent conifers in the ruffed grouse model is an exception). A few of the variables, such as those describing the suitability values for different types of crops (wild turkey, northern bobwhite), crop management practices (wild turkey, northern bobwhite, Lewis' woodpecker), broad categories of soil moisture (northern bobwhite, veery), or tree canopy diversity (spotted owl) are categorical, with one suitability value assigned for a given type of crop, crop management practice, soil moisture category, or number of stories in the tree canopy.

Although the responses of species to changes in habitat conditions are often nonlinear, the use of curved rather than straight lines to describe habitat-suitability functions in these models is probably not warranted by the level of accuracy of estimation of the functions or measurement of the variables. In a few situations, however, the functions could be constructed more carefully. For instance, in the black-capped chickadee model, suitability declines from 1.0 to 0.0 as the height of the overstory declines from >15 m to 0 m (Fig. 3G). It is unlikely that an overstory height of less than 1 m truly has a positive suitability value, however. One could similarly criticize the function describing the relation between average height of deciduous shrub canopy and suitability for the yellow warbler (Fig. 3I) and the blue grouse, average height of herbaceous canopy versus suitability for the veery, and perhaps other functions for which the behavior of the function might be expected to be inconsistent near a suitability value of zero. The general approach of the SI graphs is probably valid, in that the suitability of habitat to a species is likely to exhibit strong thresholds below which the habitat is usually unsuitable and above which further changes in habitat features make little difference. Considerable care must be taken in specifying these thresholds, however, as model predic-

tions are likely to be extremely sensitive to small differences in threshold levels. Where possible, the location and existence of habitat-response thresholds should be documented empirically.

The Equations Used to Calculate HSI

The variety of mathematical functions used to combine SI values in the models can be sorted into a few general types (Fig. 4). The choice of function can greatly influence the expected mean of HSI values produced by a given model, as well as the degree to which variables can be compensatory; that is, the degree to which an increase in one variable can substitute for a decrease in another in maintaining the same HSI level.

The Product of Individual Suitability Index Values

This operation allows individual variables to have a large potential influence on depressing overall HSI values. In the special case when all SI's except one are optimal, it produces a life requisite value that is equal to the lowest SI value. More often, the resulting life requisite value is lower than the lowest SI value. The surface defined by this operation involving only two variables (Fig. 4A) decreases steeply with reductions in the value of either variable. Typically, one of the multipliers would be an SI representing distance, percent cover, or crop type and management.

Addition Without Truncation

One may add together SI values or functions thereof after first multiplying each by the same appropriate fraction so that their sum cannot exceed 1.0. In this operation (Fig. 4B), it is assumed that the SI's do not modify each other and can fully compensate for each other at low suitability values but that neither variable can be compensatory when it has passed its optimal threshold. There is no compensation when the resulting sum is optimal (a value of 1).

Mixed Addition and Truncation

Alternatively, one may use additive functions in which one SI value is multiplied by a fraction so that it can never completely compensate for the other, while the other value can still reach a maximum of one and thus completely compensate for the first (Fig. 4C). This procedure assumes that there is some compensation on the part of one variable and full compensation on the part of the other. The veery and sharp-tailed grouse models provide examples. In the veery model,

herb cover can partly compensate for suboptimal shrub cover, whereas in the grouse model, grain crops can partly compensate for suboptimal shrubby areas. The asymmetry of the functions produces a surface of SI values that is unevenly truncated at values of 1.0.

Addition With Truncation

This function (Fig. 4D) assumes that, at values of individual SI's that add to <1.0, the SI's do not modify each other, as in the preceding addition without truncation function. When the SI's sum to >1.0, however, habitat suitability is not changed by variation in one or both variables. The variables are completely compensatory; a low value of one can be completely compensated for by a high value of another.

### Root of a Product Equals the Number of Values Multiplied (Geometric mean)

Examples of this function (Fig. 4E) would be the square root of a product of two SI's or the cube root of a product of three SI's. This operation assumes that SI's are partly compensatory, but the overall value is weighted by the smallest value. A zero value for any individual SI will lead to an overall zero value. If three SI's are equal, the overall SI will be the same as the individual values.

Root of a Product Does Not Equal the Number of Values Multiplied

Generally this function takes the form of a product of three SI's taken to the square root. Some idea of the nature of this function can be gathered from Fig. 4F, although graphing constraints dictate that variables 2 and 3 are identical in value and can therefore be expressed as Y^2. In cases such as this, where the root is smaller than the number of SI's, the SI's are assumed to be partly compensatory and weighted by the smallest value. This weighing, however, is less than that in simple multiplication. Three equal values less than one and greater than zero will give a result that is lower than these values.

The Product of a Squared SI Value and Another SI, All to the Cube Root

This method is a special case of the geometric mean, in that the SI that is squared is given more weight than the other in determining the HSI (Fig 4G). It contrasts with the simple case in which the root of a product equals the number of values multiplied. The Williamson's sapsucker model contains an example in which factors related to nesting are consid-
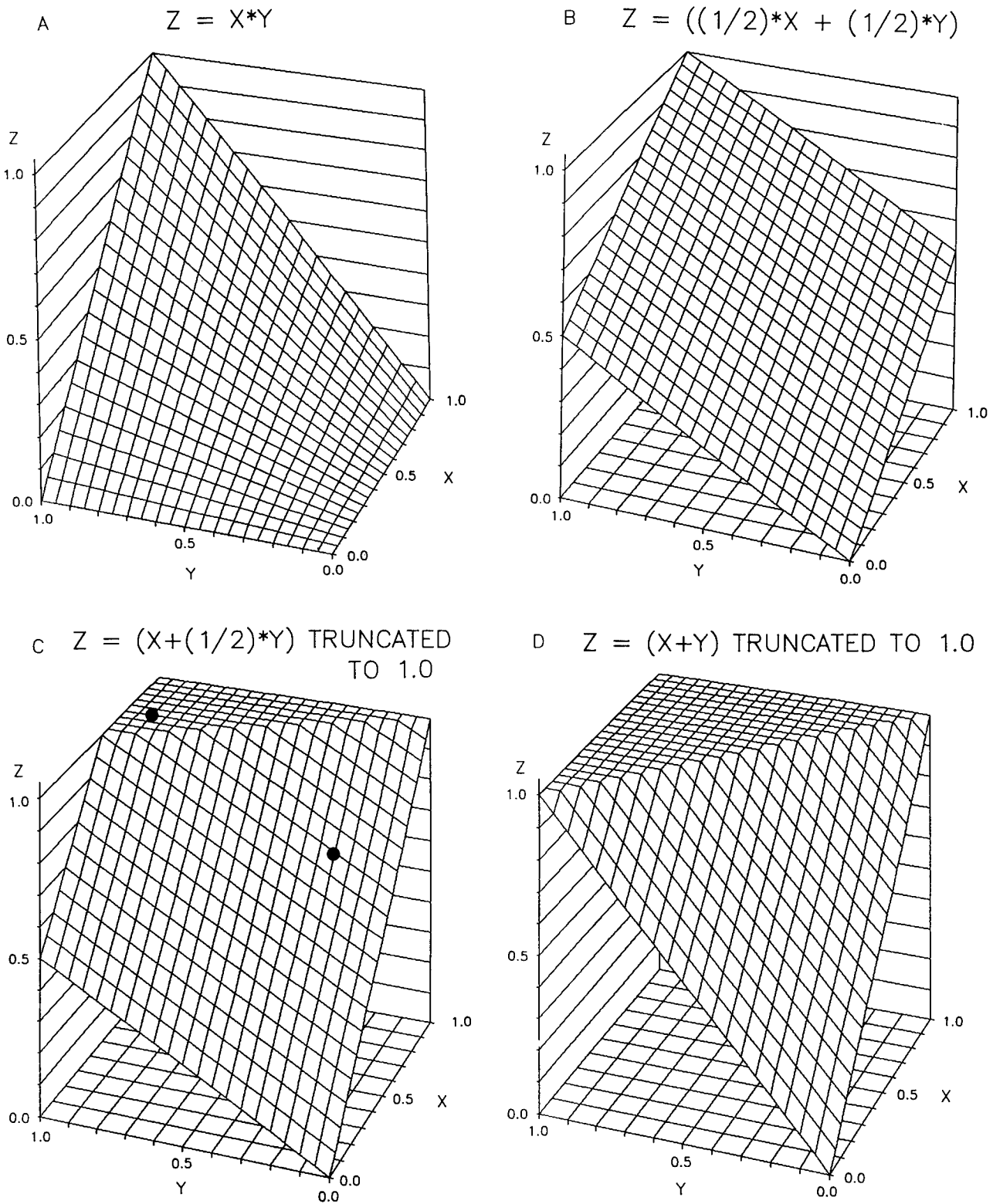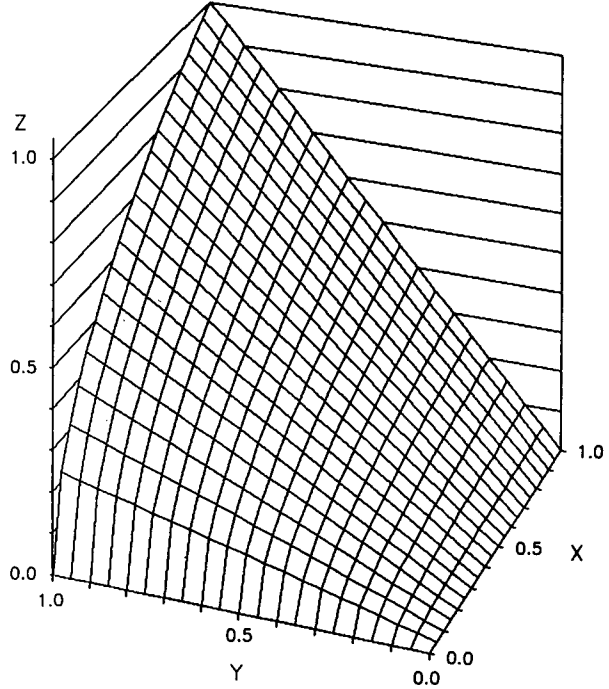
Fig. 4. Examples of the performance of different mathematical functions relating variables X and Y to the output value of value. In A, Z equals the product of two variables; B, addition without truncation; C, mixed addition and truncation; G, root of a squared SI value and another SI value, all to the cube root.
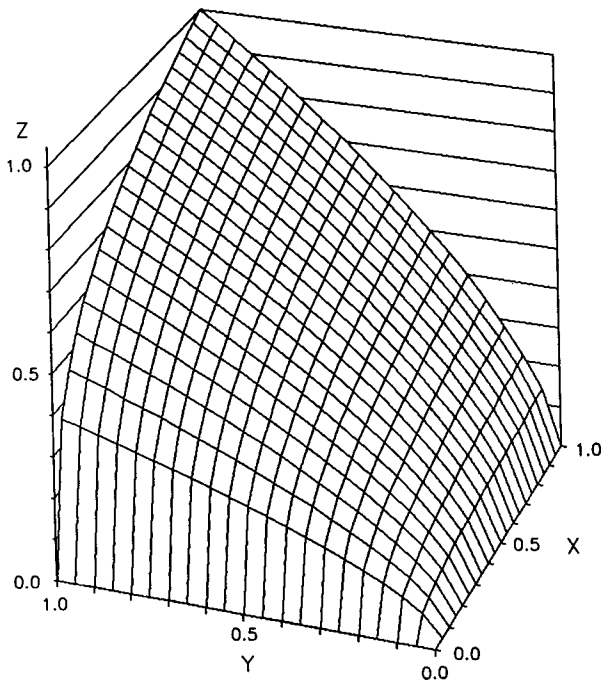
E $Z = (X*Y)**(1/2)$
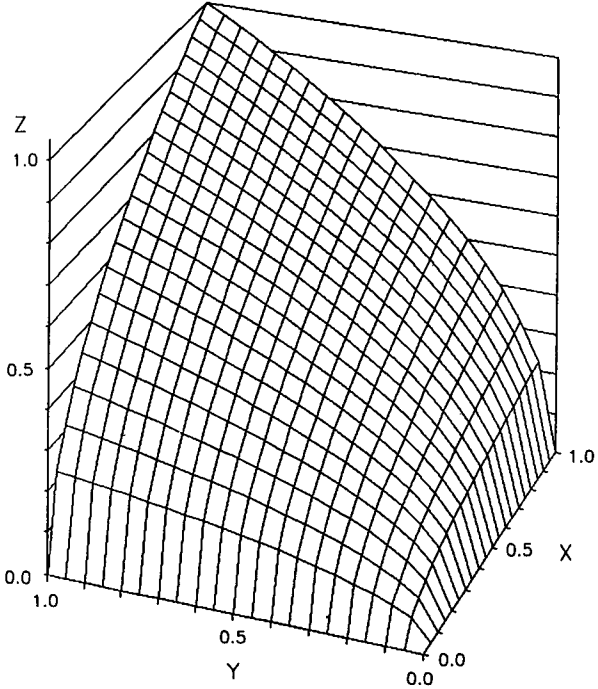
F $Z = (X*Y**2)**(1/2)$

G $Z = (X*Y**2)**(1/3)$

Z. In Habitat Suitability Index (HSI) models, X and Y might be two Suitability Index (SI) values, Z the resulting HSI
D, addition with truncation; E, geometric mean; F, root of a product does not equal the number of values multiplied;

ered more important than canopy cover. This method is similar to the simple case in that, when the values of both SI's are the same, the final HSI will have that value.

Various functions have been used to combine variables into HSI values in the models we considered. For each, some justification has been or could be provided (see the reports we reviewed, Appendix). The array of functions used, however, makes it extremely difficult to consolidate existing models or functions into more general, multispecies models. Perhaps more importantly, some of the functions behave in ways that are not intuitively obvious—the response surface of HSI values generated by various combinations of the individual SI values for different situations is not flat or symmetrical. This means that application of the model in situations at different positions on the plane may yield qualitatively different results (e.g., compare the points on the plane of Fig. 4 C). It is not always certain that this is what the framers of the models intended. The output of some functions is skewed toward low or high values when compared with others. For instance, the distributions of the multiplicative functions (Fig. 4A) are skewed toward lower values than those of the additive functions (Fig. 4D), even though both functions have the same range of output (0 to 1).

Model Assumptions

All models contain assumptions; this is a necessary feature of the simplification that accompanies any modeling effort. An evaluation of models must consider both the operational aspects of models (e.g., how SI values are combined in various functions, how life requisites interrelate) and the underlying assumptions of the models. Evaluating the robustness or sensitivity of a model involves assessing the likelihood that these assumptions are correct, or determining the effects on model predictions should they be invalid. In order to do this, the model assumptions must be clearly stated.

In the reports we reviewed, the authors specified many of the assumptions involved in the model, especially with regard to specific variables or SI graphs. If a particular variable is weighted more heavily than another in the calculation of an HSI value, this is usually clearly stated and justified. However, as the equations used to combine SI values into HSI's become more complex (e.g. additive, additive with truncation, multiplicative, roots of multiplicative, combi-

nations of these), the assumptions underlying the operations become less obvious and the functions themselves become even more distantly related to actual data. The assumptions regarding possible compensatory relations among variables are especially important. Because the HSI equations combine individual SI functions in complex ways, any errors in specifying the individual SI graphs (or in the assumptions underlying these graphs) will be amplified. This problem may be especially severe when compensatory relations are included. Moreover, when qualitatively different attributes of the environment are converted to dimensionless SI values that are then combined to derive an HSI value, the qualitative differences between the features are no longer apparent. They are nonetheless still contained within the derived index. One must assume that these differences, and the differences in measurement scales used to determine variable states in a particular situation are, in fact, standardized in an equivalent (and usually linear) way in the SI functions.

Some assumptions are basic not just to individual models but to the entire HEP modeling approach. A basic assumption is that the life requisites addressed in a model do indeed include those factors limiting the species, but the approach fails to recognize that the different life requisites are related to one another in different ways. Is food directly limiting (e.g., in winter) or limiting through its effects on another life requisite, reproduction (e.g., breeding season)? The models also assume that the measured variables do indeed contribute directly to the limiting effects of particular life requisites, or that they are highly correlated with other, unmeasured variables that do have such direct effects. Furthermore, there are boundaries to the characteristics of habitats in which these assumptions will hold. These boundaries must be made explicit, and where they might be exceeded within the model's applicable geographic areas and habitat types, they should be identified. Obviously, the assumptions made about limiting factors and their relations may only apply within the geographical and environmental ranges specified for a particular model.

The form of most SI graphs carries the additional assumption that the relation of HSI to limitation or carrying capacity is linear or can be directly transformed to a linear function. Because HSI values are calculated (at least in principle) as the ratio of an observed or predicted habitat suitability condition to some standard of comparison (the "optimum"), index values are constrained to vary between 0 and 1.0. This

approach has the advantage of standardizing measures for quite different variables with different ranges of absolute values. The difficulty (Farmer, personal communication) is that "optimum" may be defined in different ways. Does this value represent the best habitat condition in a theoretically ideal situation (which may never actually occur), or the best condition actually observed? Is this optimum defined with reference to the entire geographical range of a species or in relation to the region encompassed by a particular model? Assumptions about the specification of "optimum" obviously have a major influence on the SI values derived for a given situation. Differences in this assumption among models may make model comparisons or amalgamation impossible.

The approach used in HEP of deriving SI values for habitat types, converting these to HU values by adjusting for the areas of the habitat types, and then adding the HU values to obtain an overall suitability index for an area also contains several important assumptions: (1) Above the minimal area requirement of a species, area has no direct effects on the suitability per unit area. (2) The same relations hold between carrying capacity or limitation and particular habitat variables at small, local scales and at broad, regional scales. Thus, there is no scale-dependence of these relations (see Wiens 1989c). (3) The area-based conversion from HSI values to HU values is symmetrical (e.g., 50 ha of 0.5 HSI habitat is equivalent to 100 ha of 0.25 HSI habitat). (4) Within the study area, the landscape context of most patches does not influence their suitability functions. The function portrayed in an SI graph for a particular cover type or series of habitats therefore does not change as a result of what other cover types are adjacent to the habitat patches of interest. (5) The landscape effects do not change as a function of area. (6) The landscape context outside the study area has no influence on suitability.

Validation of Models

How well a model provides accurate predictions of the effects of habitat change on species abundance or productivity depends on how closely its assumptions are met, and how effectively and consistently the model performs in combining variables in the desired fashion. There are two general steps. First, the consistency of internal model operations must be established. This may be done by matching the model output to a given set of data by using those data to specify the model parameters to begin with. This step is usually referred to as model *verification* (Horn et al. 1989). In contrast, model *validation* usually involves matching the model output to a new set of data that was not used to frame the model or specify its parameters.

Model Assumptions and Functions

The potential source of the largest magnitude errors in HSI models is in violating assumptions regarding the factors that limit population density and productivity. There are limits to the range of habitats in which such assumptions will hold. These limits should be explicit, and situations where they might be exceeded within the model's applicable geographic area and habitat types should be identified. This approach defines the limits to extrapolation of the model predictions. For instance, reproduction is assumed to be limiting in the barred owl and yellow warbler models. Under certain circumstances, however, other factors, such as food availability or overwinter survival, could be more important. What are these conditions? In the downy woodpecker, black-capped chickadee, Lewis' woodpecker , and several galliform models, HSI is equal to the lowest of several SI values for different life requisites. Do these models adequately describe conditions under which one life requisite becomes more limiting than another, such that we can now ignore variables related to the nonlimiting life requisite? Such questions are rarely considered in HSI models.

The way that final HSI values are calculated from the individual SI's is a more common source of error than violating limiting-factor assumptions. Because this calculation involves the mathematical aggregation of several SI values, errors contained in poorly defined individual SI functions are compounded. Therefore, validation efforts should also be focused on the basis for combining SI values into the final HSI, and the associated assumptions that relate to the weighing and compensatory characteristics of SI's.

How should these aspects of the models be validated? Validating the limiting factor assumptions would be more profitably tested through manipulative field experiments than through descriptive monitoring. Similar but more complex manipulative experiments could be used to test the accuracy of functions used to combine SI's. Such field experiments are perhaps most in keeping with the eventual goal of using the models to make predictions about field situations, but

they are also time-consuming and expensive. We emphasize experimental approaches largely because more straightforward descriptive tests of the accuracy of model predictions are less likely to be productive. If predictions fail to be met in observational field studies, it may be difficult to determine which aspects of the model are at fault. The difficulty of identifying the sources of model failure increases dramatically as models incorporate more variables in more complex functions or as the scale of application is enlarged. The most informative field validation tests are likely to be those in which population survival and reproduction are monitored on paired experimental and control sites in a range of habitats that spans the habitat variation to which the model applies. By manipulating single habitat features (such as canopy density or number of snags) or combinations of features in a balanced design, one may determine the relations of such variables to survival or reproductive rates. Of course, there are difficulties in designing and interpreting field experiments (Wiens 1989a, 1989b), and well-planned comparative observations on habitat gradients may also help to validate model performance.

Sensitivity Tests

Another approach to validation that is less difficult and expensive, but perhaps also less realistic, is to conduct sensitivity tests on model components and their interactions. Do small errors in estimating or measuring a particular variable in the field have major effects on model output? Are model predictions largely insensitive to considerable variations in the values of other parameters or in the precise shapes of certain SI graphs?

The results of sensitivity tests may provide valuable guidance in designing further field studies or field validation tests; at the least, they indicate which input parameters must be estimated most accurately and which require only relatively coarse measurement. Sensitivity tests of this sort reveal which features of model operations may be affected by small changes in model functions, variable values, or the ways in which variables are combined. However, they are generally not well suited to validating some of the more general assumptions underlying the model. For example, to evaluate the assumptions that food is limiting to a particular species at a particular time, or that the HSI values obtained really do index individual and population performance in some way, requires direct field studies or analysis by other models specifically designed to explore such linkages. Sensitivity

testing will only determine relations within the specified structure of a model. Such tests can therefore diagnose assumptions that are contained within the model structure, but they cannot address assumptions that are part of the conceptual foundation of the model or are contained in the methods used to obtain data, which lie outside of the model. For example, one might construct a model of population response to habitat change based on logistic population growth. The performance of the response model could be tested by sensitivity analyses, but the assumptions contained in the logistic model itself would remain unexamined. All HSI models (indeed, any models) are built on such external assumptions.

The influences of various weighing functions in the equations used to combine SI values into an HSI (e.g., Fig. 4) may also be explored by sensitivity tests. By systematically varying these functions as well as the input values for specific parameters over a range of conditions, while holding all other aspects of the model constant, the sensitivity of model predictions may be determined. A similar approach may be used to assess model sensitivity to variations in combinations of parameters. The variations in variable input values, of course, affect model predictions only as they are standardized by the SI graphical functions, and the form of these functions may therefore be especially critical. Because virtually all of these functions are linear between specified lower and upper thresholds, the location of the thresholds may be the most important feature of these functions (Bain and Robinson 1988). The sensitivity of model predictions to the SI functions might be most directly assessed by systematically varying these thresholds for specific SI functions independently and examining the effects on model output.

Ultimately, field validations are necessary to determine whether or not a model functions as desired and to test critical model assumptions. Such field tests should be preceded by model sensitivity analyses to determine which aspects of the model should be targeted for field tests and how the field studies should be designed.

Model Predictions and Their Extrapolation

Validation must ultimately be judged by testing the accuracy of model output. It is therefore imperative that the model output be directly measurable. If model output is related to unobservable states, such as potential carrying capacity for a population or maxi-

mum habitat quality, it will be impossible to evaluate model performance, no matter how accurate the modeling procedure. Validations of models, whether accomplished by sensitivity testing or field manipulations or a combination of these approaches, will tell whether or not the model works, but not whether the underlying mechanisms are sound. If they are not, the model may have limited capacity to extrapolate beyond the boundaries of the data used to formulate the predictions. An experimental validation of model predictions in a forest area of a few hundred hectares may not necessarily hold true when extended to regions of several thousand square kilometers. A model must be developed, tested, and applied within the same range of space-time scales. Of course, it is difficult to conduct experimental validations of large-scale models. In other situations (e.g., threatened or endangered species, fragile habitats), experimentation is precluded on legal and moral grounds. This does not mean that development of models for such situations is senseless by any means, but it does mean that approaches to validation will differ depending on the scale and circumstances of model application.

The Use of Indicator Species Models

Clearly, there are many difficulties to be faced if one wishes to combine existing sets of HSI models, such as those for forest birds, into more general, multispecies HSI models. One alternative route to model generality might be through recognizing certain species as "key" or "indicator" species and then using HSI models of these species to monitor the status of wildlife–habitat relations at a broader level. This approach has a long history in wildlife management (e.g., Leopold 1933) and other areas (reviewed by Morrison 1985), and it is in fact implicit in the HSI modeling philosophy. Whether or not it is valid in a given situation depends on two considerations: (1) Are the indicator species really representative of a larger suite of species of interest, so that changes in their populations may be used to infer more general wildlife responses to habitat changes (e.g., Block et al. 1986)? (2) What does a change in population density or productivity of an indicator species really indicate? The most frequently mentioned examples of indicator species (desert quail and certain shrub species; peregrines and pesticides) involve situations in which changes in the distribution or abundance of the species can be traced to specific environmental changes. More often, variations in population dynamics and

productivity of species result from an array of interacting factors; identification of the factor responsible for changes in population attributes may be problematic (Temple and Wiens 1989). This problem, of course, is not unique to indicator species, but its effects may produce particularly severe problems when one attempts to use such species as a basis for more general conclusions. If these two considerations can be resolved, the indicator-species approach may be a useful route to generality. No departures from the current single-species HSI modeling approach are then required.

Developing General Models of Wildlife–habitat Relations

Attempts to develop general models of complex ecological systems are plagued by two problems. If one attempts to capture the complexity of the system in the model, there will be a great many parameters in the model. Errors in estimating parameter values multiply, and the model rapidly becomes unreliable (Pimm and Gilpin 1989). Attempts to simplify such models, on the other hand, may lead to a neglect of important parameters or parameter interactions.

These problems have given rise to two approaches to developing general models. The "bottom-up" method takes a series of detailed, specific models (such as existing HSI models) and aggregates them into a larger, general model. The "top-down" approach begins with a series of general statements or propositions about the system at the broadest level of analysis and incorporates more specific detail into the model, as it is needed, to address specific situations or objectives. In theory, the bottom-up approach has the advantage of building a model on known functions and mechanisms, which are validated independently. The top-down approach has the advantage of including only presumably relevant detail, but there is also a danger of developing a model that makes accurate predictions that may be based on general correlations rather than on underlying biological mechanisms. Such models often fail when they are extended much beyond the data or situations used in their development.

Evaluation of the Bottom-up Approach

The bottom-up approach is typified by Bain and Robinson's (1988) analysis of 30 riverine fish HSI

models. The approach involved 1) identifying the general components (life requisites, in this case) shared by most of the models; 2) developing a list of variables used in common for these components; 3) developing SI graphs for each variable by averaging scales and break points or thresholds for graphs from the specific models; this approach specifies minimum and maximum average suitability; 4) developing general computational rules and equations by identifying the most commonly used mathematical functions in the specific models; and 5) integrating these procedures to produce an overall HSI model. These steps are a logical approach to the problem of model aggregation. Bain and Robinson followed these procedures carefully and provided a detailed description of their analyses. When the environment occupied by a group of species imposes similar, strong limiting effects on their populations, the single-species models may share many features in common and this aggregative approach may be possible. These environmental conditions generally apply for fish in stream systems. Our analysis, however, shows that they apply rather poorly to birds occupying forested habitats. For these species, the differences among the models are considerably greater than their similarities, which makes it difficult (but not impossible) to follow the aggregation protocol outlined by Bain and Robinson (1988).

We see some areas of more general concern with this bottom-up approach. The following discussion is not a specific criticism or evaluation of the Bain–Robinson analysis, but rather is intended to emphasize these more general aspects of the bottom-up approach.

Unique Variables

This approach produces an "average" model. In so doing, it ignores key features or variables that may influence some but not most species. Thus, if unique or uncommon variables, components, or equation functions are omitted in a general model, one may fail to consider properly the species for which these are important. The model then applies to a common or average species. But frequently it is the a typical species that are endangered or particularly sensitive to habitat perturbations. Moreover, unique or uncommon variables may often be particularly strong in their limiting effects on certain species. Because the HSI approach is based on a "limiting factor" philosophy, not considering these variables may lead to incorrect predictions.

Variance

In averaging SI functions or equations, the mean values across the species are emphasized but the variance is ignored. The mean, of course, is sensitive to only those species that are included in the aggregate functions. Inclusion or deletion of one or a few species may therefore change the average functions dramatically. Furthermore, variance is what determines the confidence with which one can apply model predictions, and its omission in a multispecies model may be particularly important.

Insensitivity to Change

HSI models were developed primarily to assess the potential consequences of habitat changes. Thus, the variables included in the model should be those that are most sensitive to changes. If commonly measured variables, components, or functions are used, these may be particularly insensitive to change or have broad thresholds on SI graphs. Sensitivity analyses of individual models would help to resolve the potential severity of this problem.

Scale

Amalgamating variables and functions across species requires that the assumption that these variables and functions have similar degrees of scale dependency in time and space for the different species. If one species responds to shrub cover, say, on a scale of square meters and another responds at a scale of square kilometers, a function combining these two species may make little sense. Such differences in scales are a major source of heterogeneity in the habitat–performance relations, although the severity of this problem depends on the particular mix of scales that is aggregated. One consequence is that general models developed in this way may be sensitive to the particular models used in their construction. Steps might be taken to transform the functions and variables to a common scale, but no one yet knows how to do this (Wiens 1989c).

The Optimum SI Value

Much the same concern applies to the practice of basing the functions on SI graphs in which "optimum" = 1.0. What "optimum" means may differ widely among species for a particular variable and may depend on the range of circumstances considered. This problem is especially likely to occur if the models are based on an empirical rather than a theoretical optimum.

Heterogeneity of Curves

Different SI graphs reflect qualitatively different relations. If several graphs are combined to produce average SI graphs, it is important that the graphs portray the same thing in the same way. If the SI graphs depict different response variables measured in different units (with different optima), combining them may produce average curves that have no meaning. Furthermore, averaging of curves that have different response thresholds will produce new thresholds that are misleading artifacts. As Terrell and Nickum (1984) noted, "What the individual SI curves represent varies depending on how the curve was developed, the quality and quantity of the data base, and the type of response used in development of the curves. When the curves represent different responses, it is unlikely that a uniform method of aggregating curves to predict a single response exists."

Heterogeneity of Habitat Units Among Species

Just as there is likely to be heterogeneity among the SI graphs for different species, the ways in which HSI values are derived and then converted into Habitat Units (HU) may vary among species. Because HU values are derived in different ways, they are not necessarily equivalent for the different species to be aggregated in a general model. The expression of HU values as, for example, numbers per unit area may give the appearance that HU values are automatically normalized among species. Because the SI functions for different species are scaled differently with respect to area, such normalization often does not occur.

Cover-type Standardization

Although the nomenclature of cover types used in different models may be standardized, the ways in which these cover types are actually defined in the field may differ considerably among investigators. How cover types are differentiated or lumped together may also depend on the geographical scale of the analysis. If cover types are subdivided more finely for one species than for another, the aggregation of the models for these species will give misleading results unless the differences in cover-type specifications are somehow standardized. More important, species undoubtedly differ in the scales on which they perceive cover types or patches of habitat. What represents several different habitat patches to a small species may be averaged together as a single habitat patch when perceived by a larger species. Habitat suitability of cover types may therefore vary dramatically among species. Imposing on the species an average cover-type definition, or one that is derived on the basis of human perceptions of habitat patches, may produce nonsensical results when the species are aggregated into a single general model. Because management is applied at the scale of landscape elements, it is appropriate to define cover types at this scale. It is also important, however, to consider how applicable such scaling may be to the organisms of interest and to attempt to rescale cover-type definitions if necessary.

A related problem is that of nonequivalence among cover-type designations. When the cover types defined for management or mapping differ in their levels of inclusiveness, comparisons among them are difficult. Cover types may also differ substantially in the extent to which averaging of values submerges important features of habitat or wildlife characteristics. Cover types such as tundra and cottonwood–willow riparian, for example, are scarcely equivalent in the range of habitat variation they encompass.

The severity of these problems in developing a general model by means of a bottom-up approach depends on the heterogeneity of the models being aggregated. If the models are generally similar in variable specifications, SI functions, and HSI equations, the amalgamation may proceed relatively smoothly, although the problems associated with scale are likely to remain. For more disparate models, such as the set of forest bird models, the difficulties seem formidable. Nonetheless, there are some steps that may improve general models derived using a bottom-up approach.

An averaging approach to amalgamating models is unlikely to be very useful if it is based entirely on means. But the bottom-up approach may be improved by explicitly considering variance in variable measures, SI graphs, and component relations. The data base underlying these parameters is often very coarse, so it is not likely that accurate statistical variance measures will exist for many model features, and it may not be an efficient use of field time to attempt to collect the observations that would yield variance measures. Instead, computer simulations may be used to establish ad hoc confidence limits on estimated values. SI graphs, for example, could be constructed so that they portrayed the average, expected relation, as well as some form of outer limits on the response thresholds and function (Fig. 5A). One might systematically vary individual variable values over arbitrary ranges to determine model sensitivity to parameter
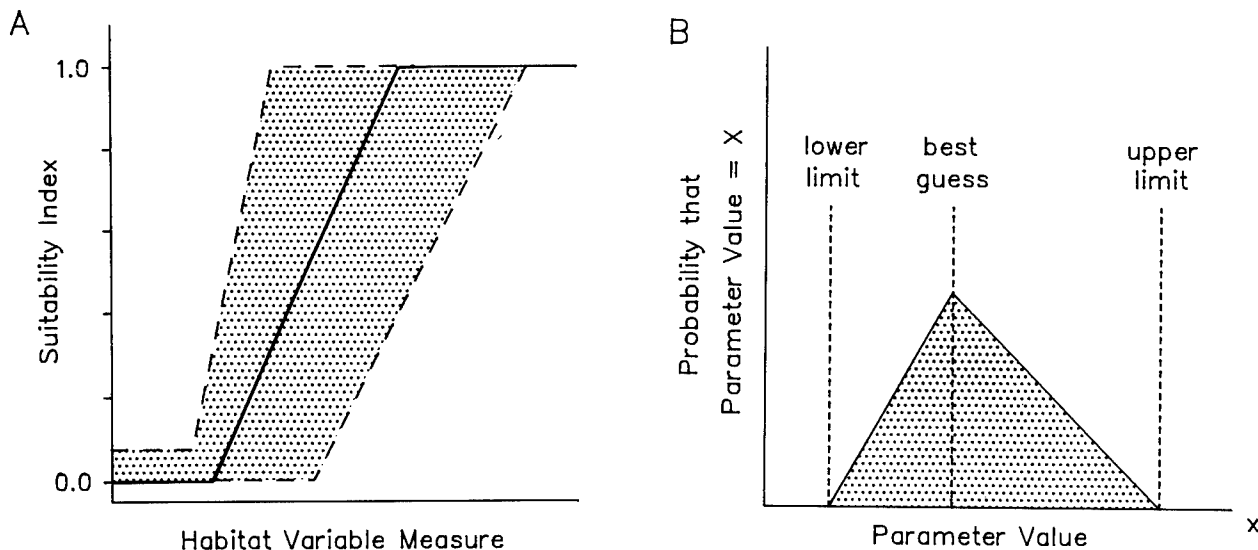
Fig. 5. A. Suitability Index (SI) graph in which variance in the SI function has been included (*shaded area*). B. One way of estimating the probability that a parameter (e.g., habitat SI) will be of a certain value for a given value of the habitat variable. Such a distribution may be used to obtain a distribution of input values for Monte Carlo computer simulations.

variation, as Bain and Robinson (1988) did. Perhaps a better way to simulate confidence limits is by Monte Carlo simulations using specified probability functions for variable values between specified extremes (e.g., Ford et al. 1982; Wiens et al. 1985; Fig. 5B). Ideally, such simulations should be conducted for individual model parameters and then for individual models before their amalgamation. If one weights variables on the basis of intuitive judgments, sensitivity tests should be conducted to determine the effects of the weighings on the HSI values derived from the model. The confidence intervals required for decisions by management or assessment of effects are often wider than those used in scientific studies (Terrell and Nickum 1984); nonetheless, attempts should be made to establish the robustness of model predictions. Such considerations are especially important if model predictions with large potential errors are being used to develop cost-benefit assessments for habitat management.

These suggested steps may improve the usefulness of specific models, but they do not solve the problem of linking together models that contain quite different sets of variables, SI graphs, or equations. In some situations, simulations may indicate that variables may be combined in various ways to enhance their uniformity among models, although scaling differences are still likely to remain. Of course, the differences among the models are consequences of the differing objectives of investigators in develop-

ing the models and the differing data bases available to them. Because the models were not developed with the intention of subsequent aggregation, it should not be surprising that they do not mesh together easily. In view of the difficulties just described, however, the approach of developing general habitat models by a bottom-up amalgamation of existing HSI models does not seem to be profitable or realistic unless the models are similar in their structure and specifications.

The Top-down Approach

An alternative to the bottom-up approach is to begin with a general model and build in the detail that is required by the nature of the ecological system (species, life functions, cover types) and modeling objectives. One might develop a guild model, for example, by first defining the general cover types and regions in which the model is intended to apply, then defining a guild or series of guilds (determined on the basis of objective criteria), and then developing statements of guild life requisites, SI graphs, and equations that would apply generally to these functionally defined groupings, rather than being averages across the component species. If scaling functions are incorporated into the definition of guilds, it might alleviate some of the difficulties of combining functions for species that scale their environments differently.

Such a hierarchical approach has two distinct advantages. First, by beginning at a general level (say,

the community of birds occupying a general habitat type such as forest) and then subdividing this according to major differences among groups (into, say, guilds occupying subsets of the forest cover types), one adds detail only so far as needed to portray critical features of the differentiated groups, with reference to the particular management objectives of interest. Of course, if this subdivision is carried out to the species level, the advantage of the top-down approach is lost. Second, because one begins with groupings of species that are progressively subdivided, critical interactions among sets or subsets of species may be retained as explicit features of the model structure. Species interactions are generally not considered in the aggregation protocol of a bottom-up approach.

Another advantage of a top-down approach is the compatibility of such hierarchically structured models with GIS-based habitat analysis (e.g., Scott et al. 1987). When moving from general to more specific models, the spatial scale can be varied in a way that retains known relations with cover-type map data. The map images may then be varied in concert with the HSI models in simulations to project the possible consequences of habitat or landscape modifications on model predictions.

There are also difficulties with a top-down approach to developing general models, however. Several of these (unique variables, scale, the "optimum" SI value, heterogeneity of habitat units among species) are the same as those characterizing the bottom-up approach; others are more evident in the top-down approach.

Community or Guild Definition

The bottom-up approach begins with the species and aggregates as far as compatibility of the species-level models permits. In the top-down approach, one must specify the most general level at the outset. This level is arbitrary, based on the objectives of the modeling exercise. For some purposes, a broadly defined community may be the focus, whereas for others a more narrowly defined community or series of guilds, or perhaps a single guild, may be more appropriate. Whatever the level, the criteria used to define it must be clearly specified. This is especially true for guilds, which may be defined using a variety of procedures and criteria, some more objective than others (Jaksić 1981; Wiens 1989a). The definition of the community or guild should be accompanied by a statement of the time and space scales of model application. For example, the wildlife–habitat relations of organisms may

be quite different when considered over a month in summer, the entire summer, the entire year, or a sequence of years. Patterns that are evident at a local spatial scale may disappear or even be reversed at a broader, regional scale (e.g., Wiens et al. 1987). All of these definitional decisions are more equivocal than those involved in species-level models.

Output Parameters

In traditional HSI models, some measure of species or population performance (e.g., density, biomass, productivity) is the criterion of interest predicted by the models. By contrast, with guild or community models such measures may be less relevant to management objectives. Species richness or diversity is often identified as the most important attribute of communities, but other features (e.g., guild composition, food-web complexity, total community niche space, species packing) may also be relevant to particular objectives. Guild structure, for example, may provide a more sensitive indicator of overall community response to habitat changes than species richness alone, which may not change because invading or edge species can substitute for other species more characteristic of the habitats. Which measures are most appropriate depends on the specific management objectives, so these objectives must be clearly specified at the outset of any modeling exercise.

Area Effects

In traditional HEP models, HSI values are assumed to be independent of area when HU values are calculated. Area, however, is an important component of community-level attributes such as species richness. As Schroeder (1986) observed, multiplying an HSI that contains area effects by habitat area to derive HU values has the effect of double-counting area and is not a logical mathematical operation. This operational problem may be especially severe in models that take the community as the general frame of reference because many community-level features are area-dependent.

System Openness

The capacity of any model to produce accurate predictions of species or community features from specified input variables depends on how much the features of interest are influenced by those variables alone. The boundaries imposed on the system in space and time (e.g., a particular location during the breed-

ing season) are usually assumed to include all of these influential or limiting variables. If a system is open to external influences (i.e., it has been incorrectly bounded), the factors that actually influence population or community dynamics may not be included in the model and the model predictions may therefore be of little value. With a single species as the focus, this problem may be reduced by careful design and planning. In multispecies assemblages such as guilds or communities, however, the number of species may be large. Because these species probably operate on different scales in space and time (e.g., residents versus migrants, short-lived versus long-lived), the likelihood that the guild or community features will be influenced by factors beyond the specified boundaries increases dramatically as species number and variety increase.

A Logical Foundation for Model Development

A major difficulty in developing species-specific HSI models, or bottom-up or top-down general models, is in specifying the variables that may influence a feature of interest (e.g., a life requisite) and interrelating these correctly. The envirogram approach of Andrewartha and Birch (1984) and Niven (1987, 1989) offers a way to develop a logical foundation for specifying and relating variables in models. Using formal logic, one can distinguish environmental features that influence organisms directly—elements of the "centrum"—from those that influence organisms indirectly, by way of the centrum; these are elements of the "web." The centrum comprises four classes of environmental factors, distinguished by the kinds of effect they have on organisms (positive or negative) and the reciprocal effects of the organisms on those factors (positive, negative, or neutral). Thus, resources are defined as objects or factors that have a positive influence on the organism and that are decreased or unchanged by the actions of the organisms. Mates are defined by a positive-positive set of influences, whereas predators are objects that have negative effects on the organism and are in turn positively influenced (e.g., nourished). Malentities are factors that negatively influence the organism but do not in turn benefit from the interaction (e.g., drought). Such distinctions may seem clear and somewhat trivial, but they function to classify environmental factors formally according to the specific form of their effects and conse-

quences. They represent an alternative categorization to life requisites that may avoid problems in defining logical relations among the latter.

An envirogram is simply a diagram of the logical formulations that link components of the web and the centrum to the well-being of organisms over a specified time and area. As an example, we have developed an envirogram for the pileated woodpecker (Fig. 6). Because this envirogram is based only on the information contained in the HSI model report for this species, it contains only two of the four components of the centrum: resources and predators. A complete envirogram for this species would include other factors related to the mates and malentities components of the centrum. There are clear differences between the logical and structural interrelations of factors influencing this species when portrayed by the envirogram compared with the descriptive categories in the HSI model (Fig. 6). In the HSI model, measures relating to snags, tree stumps, and logs, trees, and tree canopy collectively influence the life requisite of food plus cover plus reproduction. In the envirogram, these factors are interrelated in a logical fashion through a hierarchy of direct and indirect effects. Thus, one sees that water availability influences the growth and occurrence of large, live trees, which in turn produce snags (when they die) and logs and stumps (when they fall). Logs and stumps are important to the woodpeckers by providing a resource, insect food. The water $\rightarrow$ large live tree$\rightarrow$ snag linkage is also important in providing another resource, nest sites (which, in the envirogram terminology, are regarded as a token; Andrewartha and Birch 1984). The same linkage also relates to the predator portion of the centrum, in that snags provide roosting sites that afford woodpeckers protection from predators.

We see several advantages to the envirogram approach for specifying wildlife–habitat interrelations: 1) it provides a logically consistent ordering of relations among environmental factors, as defined by the nature of their influences on organisms; 2) these relations can be supported by formal logical expressions (Niven 1987); 3) it provides a standard framework that can be applied to all species, facilitating model consolidation; 4) by arranging environmental factors according to the form and directness of their influences, attention can be focused on especially important sets of variables ; and 5) in the process of constructing an envirogram, attention may be drawn to variables that might otherwise be overlooked.

The envirogram and the logical structure that underpins it represent a way of portraying relations
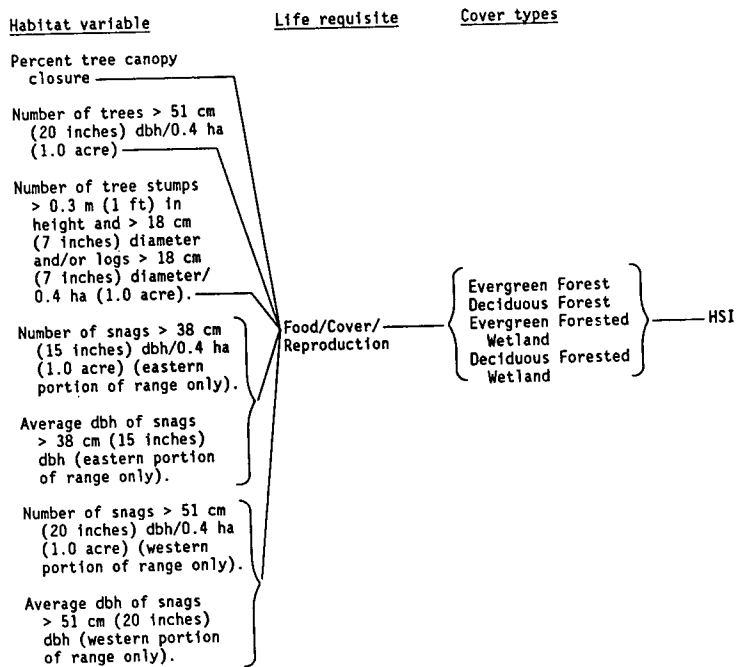
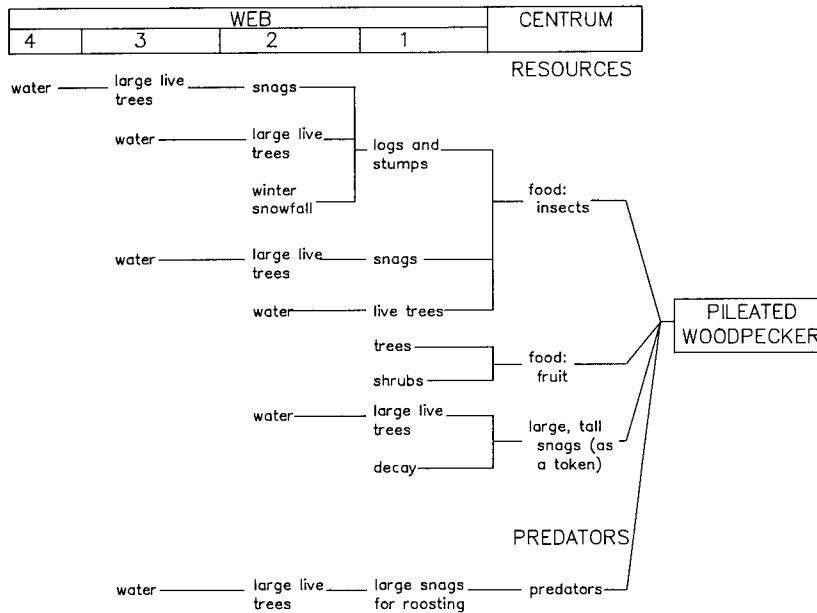**Fig. 6.** A. Relations among variables contained in the Habitat Suitability Index (HSI) model for pileated woodpeckers, as contained in the HSI model structure. B. An envirogram based on the same information, in which the relations among variables are portrayed in a more logical fashion.

among variables influencing organisms. An envirogram does not specify the quantitative state of these variables (e.g., specific size of snags) or area-dependent relations such as density. The approach provides a framework within which such states may be specified, however. We believe that the approach has potential as a way of placing the structure of HSI models on a firmer and more consistent logical foundation. Although our example is focused on a single species, multiple envirograms for sets of species that occur together could be constructed to show the common elements useful for developing logically derived multispecies habitat-response models.

The Importance of Habitat Landscapes

In nature, cover types occur in patches that are interspersed among patches of other types. The overall landscape is a complex mosaic of patches. The HEP approach to modeling wildlife–habitat relations has usually dealt with the mosaic structure of landscapes by classifying the cover types, calculating the area of each, and using this area to convert HSI values to HU values. The HEP approach assumes that habitat suitability in a given patch is not influenced by the size or shape of the patch or by the nature of adjacent habitat patches (the treatment of the distance variables in the models we considered here represent exceptional cases). Evidence is accumulating, however, that these aspects of landscape mosaic structure have important effects on wildlife populations (Forman and Godron 1986; Verner et al. 1986). The shape of a habitat patch, for example, influences the ratio of patch edge to patch interior (Temple 1986; Wiens 1989a), which in turn may determine how susceptible populations are to predators (Wilcove 1985). When a single species or a community occupies several cover types, the arrangement of the mosaic may be important. A particular habitat patch, for example, may be unsuitable if it is bordered by one cover type but used extensively if adjacent to some other type. To the extent that landscape patterns are important, area alone will be an inadequate measure of the effects of habitat changes on wildlife populations. Modifications of the overall landscape mosaic, as well as changes in individual habitat patches, make it especially important to consider wildlife responses in the context of landscapes.

Landscape mosaic effects on wildlife–habitat relations should be considered as a central element of future model development. The present HSI models generally ignore such effects, and bottom-up attempts to develop more general models based on these single-species models would also ignore landscape effects. Top-down models can consider landscape effects, but only if they are included at the outset of model design. Sensitivity tests cannot be used to measure such effects with the existing models because the models lack functions that interrelate cover types or assess area effects. Despite the scarcity of empirical data to use in landscape mosaic models, some of the existing concepts and ideas of landscape ecology could be synthesized specifically to apply to modeling wildlife habitat relations.

Summary and Conclusions

Our review of woodland bird HSI models and our more general evaluation of the HSI modeling approach leads us to certain conclusions. We list these in the sequence that they appear in the report rather than by any particular priority:

1. At present, HSI models should be viewed as working, quantitative hypotheses of wildlife–habitat relations. The models were developed as management tools, but they may actually be more useful in identifying basic topics for research and in assisting in experimental designs to test the effects of specific perturbations. Their use as predictive tools in management and planning depends on the level of understanding incorporated in the models and their functions, but at this time it is risky to predict from most of the models in the absence of general validation.

2. Several assumptions are central to HSI models and therefore merit careful evaluation. Among the most important are the following:

- Life requisites are correctly identified and interrelated and are indeed limiting to individuals and populations of the species of interest. (We recommend that the response variables of reproduction and of mortality and survival be separated in the model structure from the measured environmental variables such as food and cover, rather than being lumped as life requisites).
- The seasons contained in the model are in fact the periods of limitation. For models restricted to the breeding (or wintering) season, one must assume that the populations are not open; that is, their densities are influenced only by events occurring at times or places included in the model.

- The equations used to combine SI values into HSI's may involve simple additive functions or more complex weighing. As these equations become more complex, they are likely to contain more hidden assumptions and unanticipated behaviors, and errors in specifying the SI functions may be amplified. By specifying optimum values for SI relations in different ways and then combining them in such equations, the meaning of the HSI values produced may be unclear.
- In deriving an overall suitability index for a given location, it is usually assumed that the limiting effects of variables are not area-dependent (except as defined by a sometimes ambiguous specification of the minimal area requirements of the species), that the context of cover types in a landscape mosaic has little effect on habitat values within a cover type, and that any landscape-context effects that do occur are not scale- or area-dependent. These assumptions are not warranted.

3. Model validation efforts should focus on (in order of priority): (a) testing these and other assumptions, especially regarding the limiting effects of particular environmental factors; (b) determining the sensitivity of model predictions to the structure of the HSI equations and the estimation of variables; and (c) evaluating the accuracy of model predictions under field conditions. Often, carefully designed experimental manipulations of key variables may yield greater insights than broad-scale, multifactor comparisons. Costs of field validation can be reduced by using computers to test sensitivity of model structure and assumptions before field tests.

4. The bottom-up approach of combining single-species HSI models into general, multispecies HSI models may not be feasible unless the models (species) are similar in their structure and variable specifications. The forest bird models we reviewed do not have these similarities. Aggregating specific HSI models into more general models is complicated by different specifications of minimal area, life requisites, and optimum in SI graphs, dissimilar ranges of cover types, a lack of shared variables among the models, different functions to derive SI values for variables that are shared, and differences in the scale-dependency of wildlife–habitat responses among species.

5. The top-down approach for deriving general models begins at the community or guild level and defines appropriate variables and functions. This approach restricts attention to those variables needed to define relations pertinent to a particular management objective. It also retains important elements of species interactions that are difficult to build into general models composed of independent single-species models. The approach is hampered by difficulties that characterize the bottom-up approach, as well as by the problems of consistently defining the appropriate level of interest, specifying what measure of system performance is most suitable, and incorporating area effects on these community parameters. As additional species are included in a general model, problems of system openness to extrinsic limiting influences also become more severe.

6. We note two possibilities for developing HSI models in new directions. One involves developing a firmer logical framework for organizing the relations among environmental factors and organisms. The second emphasizes the importance of the landscape mosaic context of cover types or habitat patches used by the species or groups of species to be modeled. Each of these foci will require a new form of models rather than additional variations on the present HSI themes.

Acknowledgments

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1. Life History and Status of the Endangered Cui-ui of Pyramid Lake, Nevada, by G. Gary Scoppettone, Mark Coleman, and Gary A. Wedemeyer. 1986. 23 pp.
2. Spread, Impact, and Control of Purple Loosestrife (*Lythrum salicaria*) in North American Wetlands, by Daniel Q. Thompson, Ronald L. Stuckey, and Edith B. Thompson. 1987. 55 pp.
3. Taxonomy, Life History, and Ecology of a Mountain Mahogany Defoliator, *Stamnodes animata* (Pearsall), in Nevada, by Malcolm M. Furniss, Douglas C. Ferguson, Kenneth W. Voget, J. Wayne Burkhardt, Arthur R. Tiedemann, and John L. Oldemeyer. 1988. 26 pp.
4. Demographic Characteristics of a Maine Woodcock Population and Effects of Habitat Management, by Thomas J. Dwyer, Greg F. Sepik, Eric L. Derleth, and Daniel G. McAuley. 1988. 29 pp.
5. Premigrational Movements and Behavior of Young Mallards and Wood Ducks in North-central Minnesota, by Ronald E. Kirby, Lewis M. Cowardin, and John R. Tester. 1989. 25 pp.
6. Water and Habitat Dynamics of the Mingo Swamp in Southeastern Missouri, by Mickey E. Heitmeyer, Leigh H. Fredrickson, and Gary F. Krause. 1989. 26 pp.
7. Chironomidae of the Southeastern United States: A Checklist of Species and Notes on Biology, Distribution, and Habitat, by Patrick L. Hudson, David R. Lenat, Broughton A. Caldwell, and David Smith. 1990. 46 pp.

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