Validation of the Great Blue Heron HSI Model Reproductive Index for the Southcentral Great Plains

- Bruce A. Corley,¹ Oklahoma Cooperative Fish and Wildlife Research Unit, Department of Zoology, Oklahoma State University, Stillwater, OK 74078
- William L. Fisher, U. S. Geological Survey, Biological Resources Division, Oklahoma Cooperative Fish and Wildlife Research Unit, Department of Zoology, Oklahoma State University, Stillwater, OK 74078
- David M. Leslie, Jr., U. S. Geological Survey, Biological Resources Division, Oklahoma Cooperative Fish and Wildlife Research Unit, Department of Zoology, Oklahoma State University, Stillwater, OK 74078

Abstract: We field-tested the Reproductive Index (RI) of the great blue heron (*Ardea herodias*) Habitat Suitability Index (HSI) model in the southcentral Great Plains with the aid of Geographic Information System (GIS) technology. From January 1993 through May 1994, populations of great blue herons in 18 rookeries located throughout Oklahoma were monitored, and GIS was used to evaluate data on rookery habitat structure and surrounding landscape features. Eighteen rookeries were classified as potential nest sites and RI ratings were determined for each rookery according to model criteria. The RI identified only 3 (17%) of the 18 rookeries as suitable habitat for reproduction. After modifying the RI using habitat and landscape data from the 18 rookeries in Oklahoma, the RI more reliably characterized the habitat suitability of rookeries in the southcentral Great Plains. However, it was not significantly related to initial size of the rookery population or its size at the end of the breeding season.

Proc. Annu. Conf. Southeast Assoc. Fish and Wildl. Agencies 51:476-488

Habitat Suitability Index (HSI) models are a major part of the Habitat Evaluation Procedures (HEP) used by the U.S. Fish and Wildlife Service to assess, manage,

1. Present address: U.S. Fish and Wildlife Service, 1600 Chamberlin Parkway, Suite 8663, Fort Myers, FL 33913.

and monitor habitats of biological resources (Schamberger and Farmer 1978, Schamberger and Krohn 1982). These models are used to evaluate wildlife habitat relationships and predict species sensitivity to perturbations (Berry 1986, Van Horne and Wiens 1991). The ability of a model to predict effects of perturbations on populations and corresponding reproductive success depends on how accurately model assumptions meet species' life requisites (Van Horne and Wiens 1991). Typically, HSI models are species-specific, based on generalized physical and biological attributes of a species' habitat, and assumed to be related to carrying capacity of a particular habitat (Berry 1986, Schamberger and O'Neil 1986). Because most HSI models were developed from existing literature and professional consultations, few have been objectively field-tested, verified, and validated despite their widespread use (Brooks 1997). Model validation achieves 2 goals: model performance is tested in a particular region and model weaknesses are identified for subsequent improvement (Schamberger and O'Neil 1986).

Short and Cooper (1985) developed the great blue heron (*Ardea herodias*) HSI model to evaluate wetland habitats (i.e., herbaceous, shrub, and forested wetlands and riverine, lacustrine, and estuarine deepwater habitats) used or potentially used for foraging and nesting throughout their life cycle. Great blue herons were targeted because of their sensitivity to human disturbances during spring and summer breeding. Anderson and Hubert (1988) evaluated the Foraging Index (FI) of the model through a field verification study but did not conduct a validation study of the FI with heron population data. Furthermore, there has been no field testing of the model's Reproductive Index (RI).

We present results from a field verification and validation test of the RI of the great blue heron HSI model. Our objectives were to: 1) assign RI values to 18 active rookeries based on Short and Cooper's (1985) criteria with the aid of Geographic Information System (GIS) technology; 2) relate model output to corresponding population attributes for identification of model strengths and weaknesses; and 3) modify the model as needed for use in the southcentral Great Plains.

We thank Mark Gregory and Scott Kreiter for helping us navigate through the GIS, and Paul Balkenbush, Craig Martin, and Mike Wilkerson for their assistance. This project was funded by the U. S. Fish and Wildlife Service, RWO 13. The Oklahoma Cooperative Fish and Wildlife Research Unit is jointly sponsored by Oklahoma State University; the Oklahoma Department of Wildlife Conservation; the U.S. Geological Survey, Biological Resources Division; and the Wildlife Management Institute.

Methods

Population, habitat, and landscape data were collected at 18 rookeries in Oklahoma during the breeding and post-breeding season of 1993. Rookeries occurred in 4 different ecoregions (Fig. 1), as defined by Bailey (1980), which ranged from contiguous hardwood forests in eastern Oklahoma to riparian forest patches in western Oklahoma. All rookeries were located within about 35 m of water. Rookery nest trees were predominantly (65%) sycamores (*Platanus occidentalia*) and less frequently



Figure 1. Locations of 18 great blue heron rookeries used for model validation within Bailey's (1980) vegetational ecoregions.

(all $\leq 10\%$) cottonwoods (*Populus deltoides*), baldcypress (*Taxodium distichum*), short leaf pines (*Pinus echinata*), pecan (*Carya illinoensis*), unidentifiable snags, and water oak (*Quercus nigra*). Descriptions of rookery habitats and surrounding land-scape features are presented in Corley (1995).

Eighteen active rookeries were classified as "potential nest sites" as defined by Short and Cooper (1985), and RI ratings were determined for each. This classification was done to evaluate the validity of Short and Cooper's RI variables under optimal conditions (i.e., actual nest sites). The RI variables in Short and Cooper (1985) are: distance between potential nest sites and foraging areas (V1), potential nest site characteristics (V4), disturbance free buffer zones (V5), and distance between a potential nest site and a traditional nest site (V6). Suitability indices for these variables range from 0.0 (unsuitable habitat) to 1.0 (optimum habitat). Variables V4 and V5 are binary, and variables V1 and V6 are continuous.

Distance between a potential nest site and adequate foraging areas (V1) is assigned a SI value of 1.0 if they are within 1 km of each other. An adequate foraging area is defined as a clear water body with areas ≤ 0.5 -m in depth, firm substrates, and huntable fish populations for herons (i.e., fish ≤ 25 -cm in length). For every 1-km increase in distance that the potential nest site is from an adequate foraging area, the SI is decreased by 0.1; distances ≥ 10 km receive a SI rating of 0.1. A potential nest site (V4) is assigned an SI value of 1.0 if it is a woody patch ≥ 0.4 ha in size with trees \geq 5-m in height and located within 250-m of water. If these site features are usually fulfilled, the SI value is 1.0; otherwise, it is 0.0. Variable V5 is assigned an SI value of 1.0 if there is no human disturbance (e.g., houses, roads, mechanized agriculture and silviculture, recreation) within 250 m of a potential nest site on land or within 150 m for a site surrounded by water. If these conditions do not exist, the SI value is 0.0. Variable V6 rates a potential nest site with respect to a traditional nest site. If the potential nest site is within 1 km of an active nest site, the SI value assignment is 1.0. As the distance to a potential nest site increases, the SI decreases linearly to 0.1 at 20 km and remains constant thereafter. This rate of decrease was chosen arbitrarily by Short and Cooper (1985).

We used the GIS software program Geographic Resource Analysis Support System (GRASS) 4.0 to quantify 3 of Short and Cooper's (1985) RI variables (i.e., V1, V4, and V5). Because we classified active rookeries as potential nest sites, variable V6 was not evaluated. Three digital data layers were combined to generate a landscape theme of each rookery that was used to obtain SI values for model variables. These layers were: 1) landscape-element polygons (e.g., forests, water bodies, and human dwellings), 2) linear features (i.e., dirt roads and railroad tracks), and 3) a minimum-area polygon of the rookery based on all nest trees. Descriptions of digital data acquisition procedures are presented in Corley (1995).

To obtain SI values for V1, an area within a 1-km radius around the center of each rookery was analyzed for amount of and distance to foraging areas using GRASS 4.0. The SI values for V4 were obtained by analyzing rookery habitat data collected in the field, and GRASS 4.0 generated data on the area of each rookery and its distance to water. If the criteria set by Short and Cooper (1985) for V4 were usually met, the SI value was assigned 1.0; otherwise, it was 0.0. The SI values for V5 were determined with GRASS 4.0 by generating 250-m radius areas around rookeries located over land and 150-m radius areas around rookeries surrounded by water. We circumscribed the area around each nest tree that comprised the minimum area polygon of a rookery. If no apparent human disturbance was evident within the given area, an SI value of 1.0 was assigned; otherwise, it was 0.0.

Suitability Index values obtained for each rookery were incorporated into Short and Cooper's (1985) RI equation: $RI = (V1 * V4 * V5 * V6)^{1/2}$. An SI value of 0.0 for any of the RI variables would subsequently result in an RI of 0.0, meaning unsuitable reproductive habitat for great blue herons. Rookery RI values were correlated with corresponding population sizes (i.e., initial and end of the breeding season) with the Spearman rank correlation test. Our null hypothesis was great blue heron rookery population sizes, both initial and at the end of the breeding season, were not related to Short and Cooper's (1985) RI values.

Results and Discussion

When applied to active great blue heron rookeries in the southcentral Great Plains, Short and Cooper's (1985) RI yielded values of 0.0 (unsuitable habitat) or 1.0 (optimum habitat); there were no intermediate values (Table 1). Variable V1 described all rookeries as optimum relative to the proximity of potential foraging areas. Variable V4 identified 17 of the 18 rookeries (94%) as optimum with respect to potential nest site characteristics. However, variable V5 classified only 3 of the 18 rookeries (17%) as optimum breeding habitats, most likely because of the overemphasis it placed on human disturbance. Thus, only 3 of the 18 rookeries (17%) were classified as optimum reproductive habitat for great blue herons, despite the fact that 14 of 18 (78%) had successful reproduction. The RI of Short and Cooper (1985) was not correlated with rookery populations, either initially or at the end of the breeding season (P > 0.10). As such, we did not falsify our null hypothesis.

480 Corley et al.

Table 1. Great blue heron population size and corresponding suitability index (SI) and reproductive index (RI) values from Short and Cooper's (1985) HSI model for 18 rookeries in Oklahoma. Variable V1 is the distance between potential nest sites and foraging areas, V4 describes nest site characteristics, V5 is the disturbance free buffer zones, and V6 is the distance between a potential nest site and a traditional nest site.

		Initial	End of the breeding season	SI variables					
Ecoregion	Rookerya	population	population size	V 1	V4	V5	V6	RI	
Tall-Grass Prairie	Province								
	1. Sweetwater 1	104	207	1.0	1.0	1.0	N/A	1.0	
	2. Sweetwater 2	14	24	1.0	0.0	0.0	N/A	0.0	
	 Fort Sill^b 	32	0	1.0	1.0	0.0	N/A	0.0	
	4. Alexandria	76	206	1.0	1.0	0.0	N/A	0.0	
	5. Walters	32	40	1.0	1.0	0.0	N/A	0.0	
Prairie Parkland P	rovince								
	6. Kubik	60	140	1.0	1.0	0.0	N/A	0.0	
	7. Terelton	160	381	1.0	1.0	0.0	N/A	0.0	
	8. Sand Springs	122	179	1.0	1.0	0.0	N/A	0.0	
	9. Ramona	18	39	1.0	1.0	0.0	N/A	0.0	
	10. Copan	104	179	1.0	1.0	0.0	N/A	0.0	
	11. Lenapah 1	54	141	1.0	1.0	0.0	N/A	0.0	
	12. Lenapah 2 ^b	24	0	1.0	1.0	0.0	N/A	0.0	
	13. Hugo	48	87	1.0	1.0	1.0	N/A	1.0	
Eastern Deciduou	s Forest Province								
	Wyandotte	80	134	1.0	1.0	0.0	N/A	0.0	
	15. Murphy	134	449	1.0	1.0	0.0	N/A	0.0	
	16. Horse Shoe	72	131	1.0	1.0	0.0	N/A	0.0	
Southeastern Mix	ed Forest Province								
	 Beavers Bend^b 	30	0	1.0	1.0	0.0	N/A	0.0	
	18. Little River ^b	28	0	1.0	1.0	1.0	N/A	1.0	

a. Rookery numbers coincide with numbers on Fig. 1.

b. Abandoned rookeries.

The use of population attributes as indices of habitat quality can be misleading (Van Horne 1983). However, data used for this study were adequate for identifying model weaknesses because herons typically use traditional rookeries. The 18 rookeries used for validation were located prior to the 1993 breeding season and confirmed to be active during the previous year through personal communication with local residents. Validation and subsequent modifications based on these populations must be viewed with caution because they may not represent populations in other regions of the country. However, modifications that we present should be representative of great blue heron rookeries in Oklahoma and the southcentral Great Plains and, therefore, can be used to aid conservation efforts in this region.

Short and Cooper's (1985) HSI model did not predict suitable reproductive habitats for great blue herons in Oklahoma. Because of the mathematical and categorial limitations of the SI variables and the RI, the model failed to accurately classify the suitability of most of the 18 rookeries. Variables V1 and V4 classified >90% of the 18 rookeries as optimum reproductive habitats based on the simplified heron reproductive life requisites described in the model. However, variable V5

(and subsequently the RI) classified 83% of the rookeries as poor reproductive habitats because of its over-emphasis on anthropogenic disturbance. Thus, although Short and Cooper's (1985) model identified most of the relevant reproductive life requisites for great blue herons (Corley 1995) it failed to integrate them (i.e., individually and overall) into variables that produced meaningful results, which is not uncommon for HSI models (Van Horne and Wiens 1991).

Great blue herons are primarily piscivorous but they also eat other birds, amphibians, reptiles, and terrestrial prey (Dennis 1971, Krebs 1974, Willard 1977, Peifer 1979, Brooks and Loftin 1987). Although a versatile diet is adaptive, aquatic habitats rather than terrestrial habitats provide the primary foods for great blue herons. Short and Cooper (1985) recognized this relationship; however, because of their uncertainty about the strength of the relationship between the amount and quality of aquatic habitats and rookery size or reproductive success (Werschkul et al. 1977), they were unable to adequately quantify it. Short and Cooper (1985) did, however, incorporate a variable, V1 (distance from a potential nest site to foraging area), that attempted to describe this relationship. We found V1 to be too conservative in rating a rookery's foraging demands. Gibbs (1991) identified a positive relationship between colony size (number of nests) and the amount of available foraging habitat (ha) within a 15-km radius of 29 inland rookeries throughout Maine, which provided evidence that V1 needed modification. However, we could not synthesize information from Gibbs (1991) into a quantitative form for our model because some physiographic features (i.e., marshes, flooded meadows, estuaries, and bogs) in Maine do not occur throughout the herons' breeding range. Kelly et al. (1993) were unable to corroborate the relationship between rookery size and the amount of foraging habitat because they only analyzed the area of tidal marshes and not that of all available aquatic habitats. Nor were we able to identify a relationship between foraging area and the number of breeding birds (Corley 1995). Clarification and quantification of the interaction between great blue heron foraging areas and rookery population sizes are needed before a reliable model variable can be formulated that is representative throughout the species' breeding range.

Nesting characteristics of great blue herons are difficult to describe simply because of the species' extensive breeding range (Henny and Kurtz 1978). According to Short and Cooper (1985), potential nest site characteristics (V4) are a combination of several parameters. Furthermore, V4 is a binary variable, determined from 3 general measurements of tree height, woody patch size, and distance to water, that is optimal if potential treeland habitats "usually fulfill all of the conditions," or unsuitable if potential treeland habitats "usually do not fulfill all of the conditions" Short and Cooper (1985). We separated V4 into 2 parts: nest tree characteristics and distance from the rookery polygon to water. Nest tree characteristics were further divided into 4 variables: tree height, tree diameter at breast height (dbh), crown diameter, and crown area. Because mean number of nests per tree at each rookery was related positively to these 4 nest tree characteristics and related negatively to distance from water (Corley 1995), we incorporated these 5 variables into the model.



Figure 2. Suitability index curve for the mean nest tree height (V4A) and mean nest tree dbh (V4B) in relation to mean number of nests per rookery in Oklahoma.

We devised potential nest site suitability curves from frequency distributions of nest tree characteristics. To generate the suitability curve for each of the variables, we connected midpoints of the ascending portion of frequency histogram bars until the asympote was reached (SI = 1.0); beyond the asympote, the curve remained at 1.0 over all values within the range of the variable (Figs. 2, 3, 4). We overlaid the curve on the scatterplot of rookery values to compute actual suitability index values (Table 2). We used 2 equations to obtain a new SI value for potential nest sites (V4): 1) NT = (V4A * V4B * V4C * V4D)^{1/4}, where: V4A is the average height (m) of potential nest trees, V4B is the average dbh (cm) of potential nest trees, V4C is the average crown diameter (m) of potential nest trees, V4D is the average crown area (m²) of



Figure 3. Suitability index curve for the mean nest tree crown diameters (V4C) and mean nest tree crown area (V4D) in relation to mean number of nests per rookery in Oklahoma.

potential nest trees; and 2) $V4 = (NT * V4E)^{1/2}$, where: NT is the nest tree characteristics derived from equation 1, and V4E is the distance from the patch of potential nest trees to a water source. We developed these 2 equations for determining potential nest site characteristics because NT dictates the number of nest placement opportunities available for herons and deserves equal weight in the computation of V4 (U.S. Fish and Wildl. Serv. 1981). Because of close association between nesting herons and water sources, V4E targets areas for ground-truthing to locate potential nest trees that may be used by herons.

Great blue herons are wary of humans especially during early phases of nesting, and human disturbances can cause partial or complete rookery abandonments



Figure 4. Suitability index curve for the distance of rookeries to water (V4E) in relation to mean number of nests per rookery in Oklahoma.

(Thompson 1979, Custer et al. 1980, Kelsall and Simpson 1980). However, several rookeries in our study may have habituated to certain forms of disturbance (Corley 1995). We believe that less emphasis should be placed on anthropogenic disturbance when evaluating potential nesting habitats, at least in the southcentral Great Plains. Variable V5 was separated into 3 components (Fig. 5): 1) passive disturbance (e.g., pre-existing agricultural activities, vehicular transportation, and cattle management activities) was indexed by unimproved dirt roads, 2) intermediate disturbance (e.g., residential areas and recreational activities) was indexed by human habitation, and 3) critical disturbance was indexed by newly created landscape alterations.

We developed suitability curves for passive (V5A) and intermediate (V5B) disturbance types based on regressions of minimum distances that herons nested from a disturbance type and total nests per rookery (Fig. 5). The regression equation for the ascending portion of V5A was: number of nests = $2.73 - 64.62 \times$ disturbance distance ($R^2 = 0.287$, P = 0.640, N = 3). The regression equation for the ascending portion of V5B was: number of nests = $7.48 - 1515.17 \times$ disturbance distance ($R^2 =$ 0.826, P = 0.033, N = 5). Because of limited observations of great blue herons in association with critical disturbances, we based the V5C curve on Short and Cooper's (1985) variable V5. The equation for obtaining a new SI value for V5 was: V5 = (V5A * V5B * V5C)^{1/2}, where: V5A = distance (m) to passive disturbance, V5B = distance (m) to intermediate disturbance, and V5C = distance (m) to critical disturbance. Variables V5A and V5B are continuous, and V5C is binary.

No distinction was made between rookeries located on land versus those surrounded by water with respect to human disturbance because no rookeries on islands were studied. In the southcentral Great Plains of Oklahoma, we observed that heron rookeries were typically located in trees within riparian areas along water features (e.g., reservoirs, rivers, or streams) on the side of the water opposite of human disturbances. Therefore, we presumed that nesting herons used natural landscape features

Table 2. Revised SI and RI values for 18 great blue heron rookeries in Oklahoma. Nest site variables (V4) are nest tree (NT) characteristics of tree height (V4A), tree diameter at breast height (V4B), tree crown diameter (V4C), and tree crown area combined with distance of nest trees from water (V4E). Disturbance variables (V5) are passive disturbances (V5A), intermediate disturbances (V5B), and critical disturbances (V5C) to the rookery.

	Nestsite variables					Disturbance variables						
Rookery ^a	V4A	V4B	V4C	V4D	V4E	NT	V4	V5A	V5B	V5C	V5	RI
1. Sweetwater 1	0.1	0.2	0.2	0.2	1.0	0.2	0.4	1.0	1.0	1.0	1.0	0.6
2. Sweetwater 2	0.1	0.2	0.3	0.5	1.0	0.2	0.5	1.0	0.1	1.0	0.3	0.4
 Fort Sill^b 	0.7	0.7	0.6	0.8	0.4	0.7	0.5	1.0	1.0	0.0	0.0	0.0
 Alexandria 	0.8	0.5	0.7	0.5	0.5	0.6	0.6	1.0	0.2	1.0	0.4	0.5
5. Walters	0.8	0.4	0.2	0.1	0.7	0.3	0.4	0.5	1.0	1.0	0.8	0.6
Kubik	1.0	0.5	0.5	0.4	0.9	0.6	0.7	1.0	1.0	1.0	1.0	0.8
7. Terelton	1.0	0.1	1.0	0.8	1.0	0.5	0.7	0.7	0.6	1.0	0.7	0.7
8. Sand Springs	0.8	0.9	1.0	0.8	1.0	0.9	0.9	0.4	1.0	1.0	0.7	0.8
9. Ramona	0.6	0.9	0.7	0.9	0.9	0.8	0.8	1.0	1.0	1.0	1.0	0.9
10. Copan	0.7	0.3	0.5	0.4	0.9	0.5	0.6	1.0	1.0	1.0	1.0	0.8
11. Lenapah 1	0.9	0.6	0.9	0.7	0.6	0.8	0.7	0.9	1.0	1.0	1.0	0.8
12. Lenapah 2 ^b	0.8	0.4	0.4	0.3	1.0	0.4	0.7	0.8	1.0	0.0	0.0	0.0
13. Hugo	1.0	0.8	0.2	0.6	0.7	0.6	0.6	1.0	1.0	1.0	1.0	0.8
14. Wyandotte	0.8	1.0	0.7	0.9	0.7	0.8	0.8	1.0	0.1	1.0	0.3	0.5
15. Murphy	0.8	0.9	0.7	1.0	0.5	0.8	0.6	0.5	0.9	1.0	0.8	0.7
16. Horse Shoe	0.9	0.7	0.6	0.8	0.4	0.7	0.5	1.0	1.0	1.0	1.0	0.7
17. Beavers Bend ^b	0.7	0.2	0.2	0.4	0.1	0.3	0.2	1.0	1.0	1.0	1.0	0.4
18. Little River ^b	0.9	0.4	0.9	0.9	1.0	0.7	0.9	1.0	1.0	1.0	1.0	0.9

a. Rookery numbers coincide with numbers on Fig. 1.

b. Abandoned rookeries.

to buffer themselves from human activities. However, regardless of the natural buffer size or degree that the rookery had adapted to human structures and activities, birds flushed when we intruded into the buffer.

The RI value for a potential nest site was derived by incorporating results of potential nest site characteristics (V4) and distance (m) to human disturbance (V5) into the following equation: $RI = (V4 * V5)^{1/2}$. This equation generated a value of 0.0 when a human disturbance was within 25 m to 250 m (depending on disturbance type) of nesting herons.

Values for modified variables and the resulting RI ranged from 0.0 to 0.9 (Table 2). However, values for the critical disturbance variable (V5C) were either 0.0 or 1.0 with no intermediate values because of the small sample of rookeries subjected to critical disturbances. Variable V5C was 0.0 at only two rookeries (i.e., Lenapah 2 and Fort Sill) where abandonment resulted from a critical disturbance; the RI values for these rookeries were 0.0. There was no relationship (P > 0.05) between SI variables and rookery population size (initial or at the end of breeding season). Similarly, no relationships (P > 0.05) existed between nest tree characteristics (NT) or human disturbance (V5) and rookery population sizes (initial or at the end of breeding season), or between the modified RI and initial rookery population sizes and rookery population sizes at the end of the breeding season.



Figure 5. Suitability index curve for rookery proximity to a passive disturbance (V5A), rookery proximity to an intermediate disturbance (V5B), and rookery proximity to critical disturbance (V5C) in relation to total number of nests per rookery. Open circles in V5A and V5B signify values used in regression analysis to develop ascending portion of suitability curve.

The modified RI can be used to identify areas that may be potential nesting sites if a nearby traditional rookery needs to relocate. However, to meet modification assumptions, it is important to identify primary nest tree species used by herons that are relocating because herons are likely to seek out familiar nesting substrates (Corley 1995). After the primary nest tree species is identified, trees species in an area of ≥ 0.4 ha need to be measured for potential nest site characteristics. Additionally, evaluations should be limited to areas within a 1-km radius of a traditional rookery because heron rookeries sometimes split up into satellite rookeries within this distance from traditional rookeries (Custer et al. 1980, Kelly et al. 1993). We recommend that areas meeting the prescribed criteria with RI values ≥ 0.5 should be protected from landscape alterations because the majority (78%) of successful rookeries in our study generated modified RI values ≥ 0.5 .

Literature Cited

- Anderson, S. H. and W. A. Hubert. 1988. Evaluation of habitat suitability models for use on the Platte River, Nebraska. Annu. Rep., U.S. Fish and Wildl. Serv., Wyo. Coop. Fish and Wildl. Res. Unit, Laramie. 60pp.
- Bailey, R. G. 1980. Description of the ecoregions of the United States. U.S. Dep. Agric. Misc. Publ. No. 1392. 77pp.
- Berry, K. H. 1986. Introduction: development, testing, and application of wildlife-habitat models. Pages. 3-4 in J. Verner, M.L. Morrison, and C.J. Ralph, eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. Wis. Press, Madison, Wis.
- Brooks, J. and R. W. Loftin. 1987. Great blue heron eats grey squirrel. Fla. Field Nat. 15:107-108.
- Brooks, R. P. 1997. Improving habitat suitability index models. Wildl. Soc. Bull. 25:163-167.
- Corley, B. A. 1995. Habitat and population characteristics of great blue heron rookeries in the south central great plains: partial validation of the great blue heron habitat suitability index model. M. S. Thesis, Okla. State Univ., Stillwater, Okla. 73pp.
- Custer, T. W., R. G. Osborn, and W. F. Stout. 1980. Distribution, species abundance, and nesting-site use of Atlantic coast colonies of herons and their allies. Auk 97:591–600.
- Dennis, C. J. 1971. Observations on the feeding behavior of the great blue heron. Passenger Pigeon 33:166–172.
- Gibbs, J. P. 1991. Spatial relationships between colonies and foraging areas of great blue herons. Auk 108:764-770.
- Henny, C. J. and J. E. Kurtz. 1978. Great blue herons respond to nesting habitat loss. Wildl. Soc. Bull. 6:35–37.
- Kelly, J. P., H. M. Pratt, and P. L. Greene. 1993. The distribution, reproductive success, and habitual characteristics of heron and egret breeding colonies in the San Francisco Bay area. Colonial Waterbirds 16:18–27.
- Kelsall, J. P. and K. Simpson. 1980. A three-year study of the great blue heron in southwestern British Columbia. Proc. 1979 Conf. Colonial Waterbird Group 3:69–74.
- Krebs, J. R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the great blue heron. Behavior 51:99–134.
- Peifer, R. W. 1979. Great blue herons foraging for small mammals. Wilson Bull. 91:630-631.
- Schamberger, M. and A. Farmer. 1978. The habitat evaluation procedures: their application in project planning and impact evaluation. Trans. North Am. Wildl. and Nat. Resour. Conf. 43:274–283.
- and W. B. Krohn. 1982. Status of the habitat evaluation procedures. Trans. North Am. Wildl. and Nat. Resour. Conf. 47:154–164.
- and L. J. O'Neil. 1986. Concepts and constraints of habitat-model testing. Pages 5–10 in J. Vermer, M.L. Morrison, and C.J. Ralph, eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. Wis. Press, Madison.
- Short, H. L. and R. J. Cooper. 1985. Habitat suitability index models: great blue heron. U.S. Fish and Wildl. Serv. Biol. Rep. 82(10.99). 23pp.

488 Corley et al.

- U.S. Fish and Wildlife Service. 1981. Standards for the development of habitat suitability index models. U.S. Fish and Wildl. Serv., Div. Ecol. Serv., Washington, D.C. 174pp.
- Thompson, D. H. 1979. Declines in populations of great blue herons and great egrets in five midwestern states. Proc. 1978 Conf. Colonial Waterbird Group 2:114–127.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47:893–901.

and J. A. Wiens. 1991. Forest bird habitat suitability models and the development of general habitat models. U.S. Fish and Wildl. Serv., Fish Wildl. Res. 8, 31pp.

- Willard, D. E. 1977. The feeding ecology and behavior of five species of herons in southeastern New Jersey. Condor 79:462–470.
- Werschkul, D., E. McMahon, M. Leitschuh, S. English, C. Skibinski, and G. Williamson. 1977. Observations on the reproductive ecology of the great blue heron (*Ardea herodias*) in western Oregon. Murrelet 58:7–12.