

AVIAN SPECIES DIVERSITY IN RELATION TO BEAVER POND HABITATS IN THE PIEDMONT REGION OF SOUTH CAROLINA¹

by

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ABSTRACT

The seasonal structure of avian communities associated with beaver pond habitats was studied by examination of bird species diversity. Beaver pond avifaunas were highly diverse during every season but reached maximal values during the spring and summer. The importance of beaver ponds as wildlife habitat is due to a series of factors related to their structural complexity. As a result, they attract birds which are normally not associated with wetland habitats and provide excellent opportunities for multi-use wildlife management.

In recent years impoundments created by beavers (*Castor canadensis*) have become an increasingly important type of wetland habitat for wildlife in the southeastern United States. Beavers were eliminated from South Carolina in the mid-1800's (Penny 1949), but presently are distributed in at least 28 of the state's 46 counties (Woodward et al. 1976). They are currently causing substantial damage to land resources through nuisance flooding and the destruction of crops, pastures and timberlands. Effective beaver management programs are needed in many areas of the southeastern United States where damages have exceeded economic thresholds (Godbee and Price 1975). Such programs should consider multi-use wildlife management needs.

Previous research has established that beaver ponds provide excellent wildlife habitat, particularly for waterfowl (Beard 1953, Beshears 1955, Speake 1956, Arner 1964, Hodgdon and Hunt 1966, Stewart 1972). Other studies have indicated that the forest openings created by beavers were beneficial to a variety of species (Carr 1940, Swank 1949, Rutherford 1954), but to date, no quantitative research has been conducted to establish the importance of beaver ponds as habitats for both game and non-game species of wildlife.

During the fall of 1973 we initiated a series of studies on the ecology of beaver pond habitats in South Carolina. The objective of this research was to provide information for the development of a multi-use management program for beaver ponds. One important aspect was to quantify the importance of beaver ponds as a type of wetlands habitat for wildlife. To meet this objective a comparative study of differences in the structure of avian communities between beaver ponds, hardwood and pine habitats was conducted (Reese 1976). During the same period of time the avifaunas of an additional four beaver ponds in the piedmont region of South Carolina were censused. This paper reports on the structure and seasonal dynamics of avian communities associated with those ponds.

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METHODS

Four beaver impoundments of different ages, sizes and surrounding habitats (see following section) were censused monthly, excluding December, from July 1974 to July 1975. The area censused at each site was approximately 0.6 hectares (ha) and included both the pond proper and the adjacent edge (approximately 25 m wide). The four sites were, with few exceptions, visited on consecutive days within each month. Censuses were not conducted on rainy days or during periods of high winds.

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Stationary censuses were conducted, beginning at sunrise and lasting for one and one-half hours. Only birds seen or heard vocalizing within the boundaries of the census area were recorded. Birds flying over the area were excluded, with the exception of swifts, swallows, goatsuckers, and raptors which normally utilized the area from the air for either feeding or hunting (Kricher 1973).

The arrival and departure dates of most migratory species of birds were used to delineate the four seasons of the year (Reese 1976). On our study areas, the summer season included June through August, fall from September to mid-November, winter from mid-November to mid-March and spring from mid-March to the end of May.

The Shannon-Weaver Information Theory Function was used as a measure of species diversity (Shannon and Weaver 1949). The Shannon function measures the degree of uncertainty in predicting what the next species selected at random will be (Lloyd et al. 1958). It was selected over other diversity indices because it is least sensitive to sample size, more sensitive to the presence of rarer species, and has been used frequently in avian community analysis (Karr 1968, Recher 1969, Kricher 1972, *inter alia*).

The Shannon function is defined as:

$$H' = -\sum p_{ij} \ln p_{ij}$$

where p_{ij} is the proportion of the i th species in the j th habitat; natural logarithms were used.

Species diversity indices, including the Shannon function, respond to two aspects of the data: the number of species (species richness) and the equitability component (Peet 1974, Pielou 1975). Equitability refers to the evenness with which individuals are distributed among the species present.

In this study equitability was calculated by the formula:

$$J = H' / H' \max$$

where H' is as defined above, and

$H' \max$ = natural logarithm of the number of species. (Tramer 1969).

Bird species diversity (H') and equitability (J) were computed for each site for each monthly census.

To meet the assumptions for statistical analyses using parametric procedures, all of the data were tested for normality by the Kolmogorov-Smirnov test and for homogeneity of variances by Bartlett's test (Ostle 1963). Analysis of variance (ANOVA), Least Significant Difference (LSD) and Pearson product-moment correlation coefficients were based on procedures outlined in Steel and Torrie (1960). Except when indicated otherwise, the 0.05 level of significance was used for all tests.

STUDY AREA

The four beaver ponds were located within 15 kilometers (km) of Clemson, South Carolina. Sites 1, 2 and 3 were in the Clemson University Experimental Forest (latitude 34°37', longitude 82°48') and within 1.1 km of one another. The fourth beaver pond was located on private land 2.3 km east of Sandy Springs, S.C., and approximately 0.5 km, north of U. S. Highway 76. The surface area of each pond was estimated by the methods used by Millar (1973) for calculating the size of small wetland habitats. The ages of the beaver ponds were determined from the records of the Clemson University Department of Forestry or from personal communication with private landowners. Analysis of the aquatic and terrestrial vegetation followed procedures detailed in Reese (1976).

Site 1 was a ten year old, 1.2 ha beaver pond located adjacent to Eighteen Mile Creek and 0.5 km from the confluence of the creek and Lake Hartwell. This pond contained 138 dead, standing trees per ha. The dominant aquatic vegetation was rice cut grass (*Leersia oryzoides*) and button bush (*Cephalanthus occidentalis*). Along the shoreline, sweetgum (*Liquidambar styraciflua*) and red cedar (*Juniperus virginiana*) were the important canopy species. Tag alder (*Alnus serrulata*) and sweetgum characterized the terrestrial understory of the area adjacent to this beaver pond.

Site 2 was a 0.2 ha, two year old beaver pond on a tributary of Eighteen Mile Creek 0.5 km north of site 1. It was surrounded by a mixed pine-hardwood forest; the pond contained 165 dead trees per ha. Pond weeds (*Potamogeton* spp.) and ludwigia (*Ludwigia*

palustris) were the dominant aquatic plants; flowering dogwood (*Cornus florida*) and sourwood (*Oxydendrum arboreum*) were the two most important understory species along the ponds edge.

The third site was approximately 1 km west of sites 1 and 2 and was surrounded primarily by shortleaf pine (*Pinus echinata*). This beaver pond was approximately eight years old, 0.4 ha in area and had 80 dead standing trees per ha. Pond weeds and sedges (*Carex* spp.) were the dominant aquatic plants; sweetgum and red maple (*Acer rubrum*) were the most important components of the understory.

Site 4 was a 0.1 ha, ten year old pond with 70 dead standing trees per ha and it was surrounded by agricultural lands and old fields. Tag alder and blunt spikerush (*Eleocharis obtusa*) were the important species of plants within the pond while sweetgum and yellow poplar (*Liriodendron tulipifera*) were the characteristic trees along the edge. In addition *Lespedeza serretia* was an important ground cover plant along the border of this beaver pond.

RESULTS

Ninety-two species of birds, representing 31 families and 2346 individuals, were recorded at the four beaver pond census sites during the period of this study (Table 1). Of this total, 28 species were categorized as annual residents, 19 as migratory breeders, 13 as wintering migrants, 17 as transient species and 15 species were irregular visitors on the study areas (Table 1). In terms of relative abundance the most important non-game species of birds were redwinged blackbirds (see Table 1 for taxonomic nomenclature and population levels), Carolina chickadees, blue jays, common grackles, cardinals, and ruby-crowned kinglets, respectively. The most important game species that utilized the beaver ponds or their edges were wood ducks, mourning doves and bobwhite quail.

There were no significant differences in species diversity (H'), equitability (J) or in the total number of birds (N) between the four beaver pond census sites during any given season. There were significant differences within seasons in the total number of species (S) recorded at each census site. These latter differences were due primarily to the presence of uncommon species, which, due to their low numbers, had little effect on the total avifauna. Since these differences were minimal, the monthly avifaunal data from the four beaver pond census sites were combined. The respective seasonal totals are given in Table 1.

Table 1. Seasonal abundance and status of all avian species recorded at four beaver pond census sites located in the piedmont region of South Carolina from July 1974 to July 1975.

Family/Species*	Season				Total	Status**
	S	F	W	SP		
Ardeidae						
Great Blue Heron (<i>Ardea herodias</i>)		5	2	9	16	R
Green Heron (<i>Butorides virescens</i>)	22			10	32	B
Great Egret (<i>Casmerodius albus</i>)	2				2	T
American Bitten (<i>Botaurus lentiginosus</i>)				1	1	T
Anatidae						
Mallard (<i>Anas platyrhynchos</i>)	1			15	16	R
Blue-winged Teal (<i>A. discors</i>)	1			5	6	T
Wood Duck (<i>Aix sponsa</i>)	12	32	13	25	82	R

Table 1. (Continued)

Family/Species*	Season				Total	Status**
	S	F	W	SP		
Accipitridae						
Sharp-shinned Hawk (<i>Accipiter striatus</i>)		1	1		2	I
Cooper's Hawk (<i>A. cooperii</i>)	1	2	1		4	I
Red-tailed Hawk (<i>Buteo jamaicensis</i>)		1	1	1	3	I
Phasianidae						
Bobwhite (<i>Colinus virginianus</i>)	9		1	26	36	R
Charadriidae						
Killdeer (<i>Charadrius vociferus</i>)	1				1	I
Scolopacidae						
American Woodcock (<i>Philohela minor</i>)		1			1	W
Spotted Sandpiper (<i>Actitis macularia</i>)				2	2	T
Columbidae						
Rock Dove (<i>Columbia livia</i>)				2	2	I
Mourning Dove (<i>Zenaida macroura</i>)	14	12	8	25	59	R
Cuculidae						
Yellow-billed Cuckoo (<i>Coccyzus americanus</i>)	7				7	B
Black-billed Cuckoo (<i>C. erythrophthalmus</i>)		1			1	I
Strigidae						
Screech Owl (<i>Otus asio</i>)	2	2	1		5	R
Caprimulgidae						
Whip-poor-will (<i>Caprimulgus vociferus</i>)	2				2	B
Apodidae						
Chimney Swift (<i>Chaetura pelagica</i>)	17	3		4	24	B
Trochilidae						
Ruby-throated Hummingbird (<i>Archilochus colubris</i>)					5	I
Alcedinidae						
Belted Kingfisher (<i>Megaceryle alcyon</i>)	6	8	4	3	21	R
Picidae						
Common Flicker (<i>Colaptes auratus</i>)	12	25	21	12	70	R
Pileated Woodpecker (<i>Dryocopus pileatus</i>)	6	7	1	4	18	R
Red-bellied Woodpecker (<i>Centurus carolinus</i>)	15	9	9	16	49	R
Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>)			1		1	W

Table 1. (Continued)

Family/Species*	Season				Total	Status**
	S	F	W	SP		
Hairy Woodpecker (<i>Dendropcopos villosus</i>)	2	3	6	4	15	R
Downy Woodpecker (<i>D. pubescens</i>)	10	7	12	12	41	R
Tyrannidae						
Eastern Kingbird (<i>Tyrannus tyrannus</i>)	1			1	2	I
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)	1			1	2	B
Eastern Phoebe (<i>Sayornis phoebe</i>)	2	2	1	2	7	W
Acadian Flycatcher (<i>Emidonax virescens</i>)	3			1	4	B
Eastern Wood Pewee (<i>Contopus virens</i>)	4	1			5	B
Hirundinidae						
Barn Swallow (<i>Hirundo ristica</i>)	1				1	I
Corvidae						
Blue Jay (<i>Cyanocitta cristata</i>)	24	46	46	36	152	R
Common Crow (<i>Corvus brachyrhynchos</i>)	10	12	4	10	36	R
Paridae						
Carolina Chickadee (<i>Parus carolinensis</i>)	41	43	49	39	172	R
Tufted Titmouse (<i>Parus bicolor</i>)	6	7	10	6	29	R
Sittidae						
Brown-headed Nuthatch (<i>Sitta pusilla</i>)	18		7	12	37	R
Certhiidae						
Brown Creeper (<i>Certhia familiaris</i>)			1	1	2	W
Troglodytidae						
Winter Wren (<i>Troglodytes troglodytes</i>)		1	14	3	18	W
Carolina Wren (<i>Thryothorus ludovicianus</i>)	22	21	22	11	76	R
Mimidae						
Mockingbird (<i>Mimus polyglottos</i>)	4				4	B
Gray Catbird (<i>Dumetella carolinensis</i>)	8	8		2	18	B
Brown Thrasher (<i>Toxostoma rufum</i>)	3	15	9	14	41	R
Turdidae						
American Robin (<i>Turdus migratorius</i>)	2	4	8	4	18	R
Wood Thrush (<i>Hylocichla mustelina</i>)	4	1		1	6	B
Hermit Thrush						

Table 1. (Continued)

Family/Species*	Season				Total	Status**
	S	F	W	SP		
<i>(Catharus guttata)</i>			1		1	W
Eastern Bluebird <i>(Sialia sialis)</i>	3			5	8	B
Sylviidae						
Blue-gray Gnatcatcher <i>(Polioptila caerulea)</i>	7			12	19	B
Golden-crowned Kinglet <i>(Regulus satrapa)</i>		1	32	12	45	W
Ruby-crowned Kinglet <i>(R. calendula)</i>		7	67	17	91	W
Bombycillidae						
Cedar Waxwing <i>(Bombycilla cedrorum)</i>			3	7	10	I
Sturnidae						
Starling <i>(Sturnus vulgaris)</i>	8	15	2	5	30	R
Vireonidae						
White-eyed Vireo <i>(Vireo griseus)</i>	5	1		7	13	B
Yellow-throated Vireo <i>(V. flavifrons)</i>				1	1	T
Solitary Vireo <i>(V. solitarius)</i>		1			1	T
Red-eyed Vireo <i>(V. olivaceus)</i>	1			1	2	B
Parulidae						
Black-and-white Warbler <i>(Mniotilta varia)</i>		1		1	2	T
Prothonotary Warbler <i>(Protonotaria citrea)</i>	3			3	6	B
Magnolia Warbler <i>(Dendroica magnolia)</i>		1		1	2	T
Cape May Warbler <i>(D. tigrina)</i>		1		5	6	T
Black-throated Blue Warbler <i>(D. caerulescens)</i>		1			1	T
Yellow-rumped Warbler <i>(D. coronata)</i>			15	15	30	W
Bay-breasted Warbler <i>(D. castanea)</i>		1			1	T
Blackpoll Warbler <i>(D. striata)</i>				3	3	T
Pine Warbler <i>(D. pinus)</i>	3	13	6	5	27	R
Louisiana Waterthrush <i>(Seiurus motacilla)</i>	1			3	4	T
Common Yellowthroat <i>(Geothlypis trichas)</i>	21	3		16	40	B
Yellow-breasted Chat <i>(Icteria virens)</i>				1	1	T
Hooded Warbler <i>(Wilsonia citrina)</i>	1				1	B

Table 1. (Continued)

Family/Species*	Season				Total	Status**
	S	F	W	SP		
Wilson's Warbler (<i>W. pusilla</i>)		1			1	T
Icteridae						
Eastern Meadowlark (<i>Sturnella magna</i>)				2	2	I
Redwinged Blackbird (<i>Agelaius phoeniceus</i>)	28	79	25	110	242	R
Orchard Oriole (<i>Icterus spurius</i>)	2				2	B
Rusty Blackbird (<i>Euphagus carolinus</i>)			1	22	23	T
Common Grackle (<i>Quiscalus quiscula</i>)	31	42	20	17	110	R
Brown-headed Cowbird (<i>Molothrus ater</i>)	5		4	19	28	R
Thraupidae						
Summer Tanager (<i>Piranga rubra</i>)	4				4	B
Fringillidae						
Cardinal (<i>Cardinalis cardinalis</i>)	27	18	14	33	92	R
Blue Grosbeak (<i>Guiraca caerulea</i>)				2	2	I
Indigo Bunting (<i>Passerina cyanea</i>)	4			3	7	I
Purple Finch (<i>Carpodacus purpureus</i>)		48	11		59	W
American Goldfinch (<i>Spinus tristis</i>)	6	3	22	21	52	R
Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)	17	7	17	15	56	R
Bachman's Sparrow (<i>Aimophila aestivalis</i>)				1	1	I
Field Sparrow (<i>Spizella pusilla</i>)	1		4	2	7	I
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)		2			2	T
White-throated Sparrow (<i>Z. albicollis</i>)			51	19	70	W
Swamp Sparrow (<i>Melospiza georgiana</i>)		15	35	8	58	W
Song Sparrow (<i>M. melodia</i>)		8	27	12	47	W

* Taxonomic nomenclature follows A. O. U. 1957, 1973

**Seasonal status

R = permanent resident

B = migratory breeder

W = wintering migrant

T = transient, migrates through area

I = irregular visitors

To evaluate temporal changes in the structure of the avian communities associated with beaver pond habitats, the seasonal values of H' , J , S , and N were compared by ANOVA and LSD tests. Bird species diversity (H') decreased significantly from summer to winter and increased significantly in spring (Table 2). Equitability (J), a measure of the evenness

Table 2. Seasonal values (mean \pm standard deviation) of avian diversity (H'), equitability (J), species richness (S) and number of individuals (N) birds recorded at four beaver pond census sites located in the piedmont region of South Carolina.

Season	n^*	H'	J	S	N
Summer	12	2.74(.21) bc**	.94(.02) b	19(4) a	40(12) a
Fall	8	2.49(.2) ab	.85(.08) a	19(5) a	70(42) c
Winter	16	2.39(.30) a	.86(.08) a	17(3) a	54(22) ab
Spring	11	2.83(.19) c	.89(.04) ab	25(4) b	64(10) bc

* n = number of censuses per season

**Seasons with different letters were judged to be significantly different ($p < .05$) through analysis of variance and LSD tests.

with which individual birds were distributed among the species present, was highest during the summer and decreased significantly during fall and winter. There were no significant differences in the number of species (S) between the summer, fall, and winter seasons, but there were significantly more species that utilized the beaver ponds during the spring. The number of individuals present on the study area were at their lowest levels during the summer and winter and highest in the fall and spring respectively.

During the spring and summer, there were significant correlations between H' and S (spring $r = .94$, $p < .05$; summer $r = .93$, $p < .05$) but not between H' and N . The regression of H' against S demonstrated that changes in avian diversity of the beaver ponds during spring and summer were closely related to variations in species richness (Figure 1). An obvious consequence of this is that during the spring and summer seasons the importance of the beaver pond habitats that we censused, in terms of their avian diversity, could be adequately described by merely counting the number of species present; i. e., their relative abundances could be disregarded. This suggests that the factors which regulated bird species diversity during these two seasons did so by determining the number of species which coexisted in a given beaver pond. For our data there are probably two important factors responsible for producing these results. First, the significantly higher number of species and individuals in the spring corresponded in general, to the period of northward migration through our study area. Therefore, the relationship between H' and S during the spring probably reflects a seasonal change (that resulted from migration) in the structure of the avian communities of beaver ponds and may not necessarily have been related to mechanisms of local population regulation. However, this is also the time of the year when territorial activities associated with breeding and nesting are being initiated. The net effect of this territorial behavior is to regulate the number of birds that can coexist in a given area. Results from previous studies have revealed that the influences of territorial behavior were most evident during the summer season (Tramer 1969, Kricher 1972, *inter alia*). On our study areas, this apparently accounted for the reduction in the number of species of birds that utilized the beaver ponds during the summer and resulted in a high equitability of distribution.

In comparison, during the period of fall migration, although the mean number of individuals were at their highest levels for the entire year, the fall values for equitability (J) were significantly lower than they were for the preceding summer period. This reflects, in part, the presence of flocks of migratory birds and the absence of territoriality associated with nesting activities. Consequently there were no significant intercorrelations between H' , S and N during the fall and winter seasons. During those periods,

bird species diversity of the beaver ponds could not be adequately predicted solely on the basis of species richness.

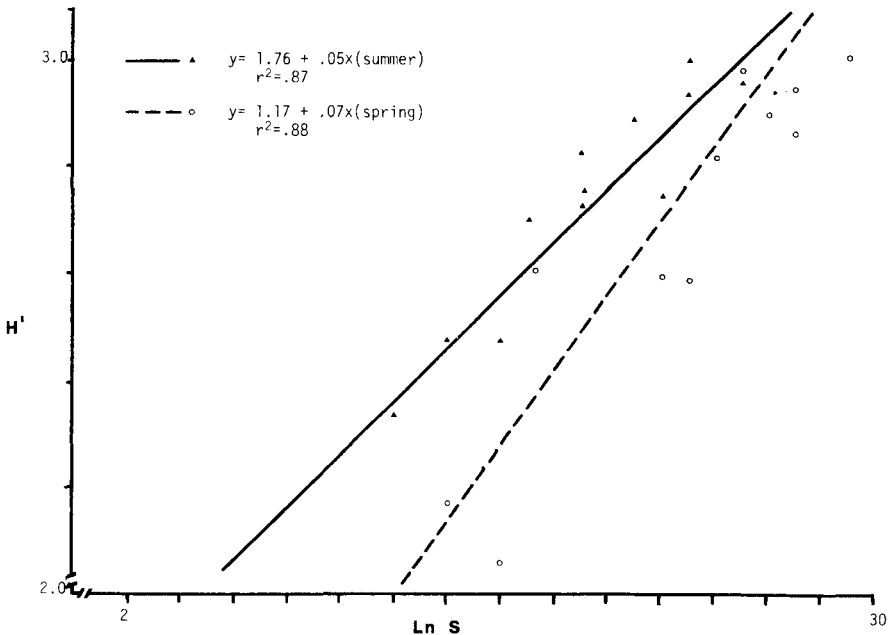


Figure 1. Regression of diversity (H') against the number of species (S) of birds recorded during the spring and summer at four beaver ponds in the piedmont of South Carolina.

DISCUSSION

The study of ecological communities is currently providing much insight into how interactions between species over time and space could influence resource allocation (Yeaton 1974). The results of this study could be broadly applied to multi-use wildlife management programs. Our research has also demonstrated that the widely recognized value of beaver ponds for migratory waterfowl is minor compared to the high year round use by non-game species.

Many workers have drawn attention to the relation between habitat structure and faunal diversity. For example, the correlation between increases in the diversity of breeding bird species in a community with increasing habitat complexity has been demonstrated by a number of previous studies (MacArthur and MacArthur 1961, MacArthur 1965, Tramer 1969, Kerr and Roth 1971, Cody 1974, Wiens 1974, Willson 1974). Diversity of some small mammal communities also may be closely tied to the structural heterogeneity of the environment (Rosenzweig and Winakur 1969).

Previous research on the structure of avian communities has dealt primarily with terrestrial habitats (see references listed above). As a result, the influence of the presence of water on bird species diversity is relatively unknown. Karr (1968) and Ferguson et al. (1975) have suggested that the addition of ponds or streams to an area adds an important structural component to the habitat. This effectively increases the heterogeneity of the habitat which in turn allows increases in the distribution and abundance of avian wildlife.

The research summarized here, and detailed for an additional beaver pond complex in Reese (1976), has established objectively that beaver ponds provide excellent habitat for highly diverse avian communities throughout the entire annual cycle. For example, annual mean values for avian diversity were highest at beaver ponds ($H' = 2.61$; this study) and, as detailed in Reese (1976) decreased along a gradient from unimpounded creek bottomlands ($H' = 1.69$) to upland hardwoods ($H' = 1.60$) to pine habitats ($H' = 1.36$). The numbers of species and individuals followed the same trends (i.e. $\bar{S} = 20, 7, 7, 5$; $\bar{N} = 57, 15, 17, 13$, respectively for the above mentioned habitat types). The presence of water at the beaver pond sites altered the normal land-use pattern for the areas we studied. This apparently provided increased structural complexity and potential for production of important avian food items. As a result, through ecological mechanisms of resource partitioning (Schoener 1974), birds which may not normally be considered to be associated with wetland habitats were attracted to the beaver pond and/or their adjacent edges.

The apparent direct relationship between diversity of the beaver pond habitat is in general agreement with reports in the literature for avian species diversity for other types of non-aquatic habitats. However, since the general parameters of foliage height diversity, vertical strata diversity, percent volume cover etc., do not apply particularly well to beaver ponds (particularly those over 5 years old), there must be a different set of structural factors that are important. Collectively, these probably include a complex of factors such as, (1) increased habitat interspersion, (2) the presence of several seral stages in close proximity to one another, (3) creation of forest openings, (4) presence of dead, standing trees for insectivorous and cavity nesting species, (5) high aquatic insect populations which serve as important avian food items, (6) abundant small seed crops for foods, and (7) a constant source of water.

The results of this study suggest several considerations for managing beaver pond habitats. First, we clearly recognize that for certain nuisance situations, the most effective beaver management program may dictate animal removal. However, the detrimental effects associated with many beaver ponds are below current economic land-use thresholds. In addition, these detrimental effects may be offset by opportunities for multi-use wildlife management at little or no additional costs to the landowner. As mentioned previously, beaver ponds provide excellent waterfowl habitat, particularly in the southeastern United States for resident populations of wood ducks. With increased attention being given to the non-consumptive utilization of wildlife resources beaver ponds also should be recognized as providing opportunities for natural resource education, nature trails, bird watching, photography etc.

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