PROCEEDINGS of the Workshop
Management of Southern Forests for
Nongame Birds

January 24-26, 1978

Atlanta, Georgia

SAG

March 1978

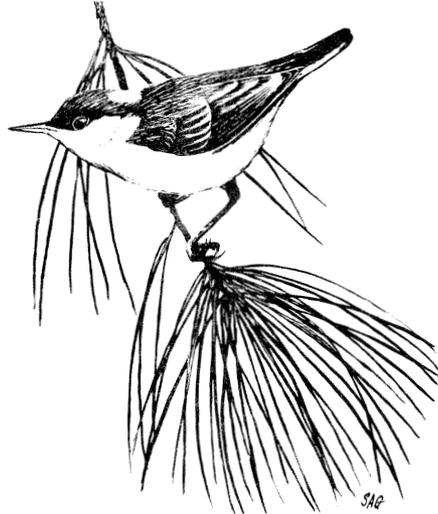Southeastern Forest Experiment Station

Asheville, North Carolina

ABOUT THE COVER:

The sketch, drawn by Dr. Sidney A. Gauthreaux, Department of Zoology, Clemson University, shows the brown-headed nuthatch, which inhabits southern pinelands.

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PREFACE

In May, 1975, a symposium was conducted in Tucson, Arizona, on the management of forest and range habitats for nongame birds. That landmark meeting opened a dialog between avian ecologists and resource managers. It was widely agreed that both groups benefitted each other, and that a series of regional workshops should be held. The objective of the series would be to insure that nongame bird habitat requirements are considered in significant land management practices, and that a diversity of natural biological communities are maintained.

To that end, the National Nongame Bird Steering Committee was formed to sponsor regional workshops to present the state of the art of nongame bird research and management in various ecoregions of the United States. The first workshop in the series was held in Portland, Oregon, February 7-9, 1977, entitled, "Nongame Bird Habitat Management in the Coniferous Forests of the Western United States".

This workshop, "Management of Southern Forests for Nongame Birds", is the second in the series, and presents bird habitat research results and management techniques for all major habitat types in the southern and southeastern United States. This workshop is jointly hosted by the USDA-Forest Service--the Southern Region; Southeastern Area, State and Private Forestry; Southeastern Forest Experiment Station; and the Southern Forest Experiment Station.

The Forest Service was joined by the National Nongame Bird Steering Committee in sponsoring this workshop. Its members include:

Forest Service, USDA
Soil Conservation Service, USDA
Fish and Wildlife Service, USDI
Bureau of Land Management, USDI
National Wildlife Federation
The Wildlife Society
Wildlife Management Institute
National Audubon Society
International Association of Wildlife
    Conservation Agencies

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Tuesday Morning, January 24

Forest Ecosystem Structure and Function and Effects on Birdlife

Moderator: Fred Kinard
Westvaco Corporation

Keynote Address:

Management of Nongame Wildlife--A Need Whose Time Has Come[1]

Michael D. Zagata[2]

Aldo Leopold and other early workers in the profession of wildlife management recognized the theoretical value of considering whole communities when making management decisions by coining the often used adage: "As the community goes, so goes the species." However, in practive the needs of game species have generally been the only needs considered or have taken priority. Grange (1949) outlined the wildlife species associated with various successional stages for a white pine climax in Wisconsin. The knowledge that the habitat for great-horned owls would be lost by setting back succession to benefit prairie chickens had little consequence.

Are we, as professional managers, to be faulted for this? Some say yes and some say no. Those who say yes feel that wildlife management should consist of the application of ecological principles that perpetuate a desired diversity. They recognize that wildlife in general has ecological, economic, educational, esthetic, historical, recreational and scientific value to the Nation and its citizens. They feel that emphasis on game species has preempted a consideration of management programs for the nonhunted species.

Those who say no look to the sources of funding for our nation's wildlife management programs, and point out that it is the hunter who has paid the bill. In addition, they stress that game management also indirectly benefits some nongame wildlife.

At this point the meaningful discussions begin to take place with the recognition that any management action benefits some species and adversely impacts others. The formerly familiar blanket statement that "good forest management is good wildlife management" illustrates the folly of a simplistic, single species approach to wildlife

management in today's world. We now recognize the importance of treating wildlife and other resources as part of an interrelated system.

It is because of the public's increased knowledge of these interrelationships that we have been prodded into giving greater emphasis to the nongame species. The habitat manipulations we have made for the benefit of game species affected other species directly or indirectly, positively or negatively. Because different wildlife species are of value to different groups in our society, concentration on one species to the detriment of others is likely to, and in fact has, alienate those whose interests have been ignored or negatively impacted.

Because of a greater recognition of the value of all wildlife to mankind by the wildlife professionals and the public, specific legislation to benefit nongame wildlife has been enacted. Examples include the Endangered Species Act, the Marine Mammals Protection Act, and the Wild and Free Roaming Horses and Burros Act. They suffer the same narrow focus as our earlier game programs and are defensive actions. They do, however, serve to point out two important factors: (1) the public is concerned about wildlife for wildlife's sake; and (2) the public can limit the professional's ability to employ sound ecological principles to manage a species, e.g., Wild and Free Roaming Horses and Burros Act. In addition, the Endangered Species Act and Marine Mammal Protection Act have illuminated our lack of basic knowledge about the ecological requirements of most listed species.

The reluctance of the professional to act on behalf of the public has prompted concerned, well-intentioned citizens to draft legislation that would mandate certain actions on behalf of wildlife. On the surface this sounds good to those of us who have fought the upward battle to gain recognition for the value of game, as well as nongame, wildlife. However, there is a real danger in this as was evidenced in a 1976 Senate bill entitled "The National

Forest Timber Management Reform Act of 1976" (S. 2926). The bill contained many "carrots" for those concerned with wildlife but could have tied the hands of the professional to exercise his skills.

The factors I have alluded to have set the stage for the title of this talk: "Management of Nongame Wildlife – A Need Whose Time Has Come." In a 1972 survey of households in the southeastern United States, nonconsumptive values of fish and wildlife were found to be greater ($12.3 billion) than combined fishing and hunting values ($11.8 billion). Results of a 1975 survey by the U.S. Fish and Wildlife Service encompassing all 50 states indicated that one-half of those persons 9 years of age and older who participated in nonconsumptive fish and wildlife-related activities also hunted, fished or did both. Membership in the National Audubon Society has grown from 41,000 in 1963 to over 400,000 today. In 1976, Missouri voters passed a referendum for a constitutional amendment to add a one-eighth of one percent sales tax for conservation that is expected to generate about $26 million in 1978 alone. Citizens in Washington, Colorado and New York have also gone on record in support of nongame programs that would include some or all of the following: (1) preserve vulnerable species; (2) establish wildlife observation areas; (3) inventory wildlife; (4) provide for management; (5) develop wildlife education material.

What I am saying is that there is a very solid base of support for nongame management and that the professional community should take the lead and not have to be pushed into converting that support into a program for the management of wildlife by considering whole communities. The message is clear; if we don't, it will happen in spite of us. As professionals, we can not allow that to happen.

Because of the wave of public interest in wildlife, Congress has provided the mandate, or as I view it the opportunity, to make major strides in our knowledge of wildlife, game and nongame alike. The Forest and Rangeland Renewable Resources Planning Act of 1974 (RPA), The National Forest Management Act of 1976, and the Land and Water Resources Act of 1977 afford us great opportunity to assess our fish and wildlife resource. Such an assessment, combined with greater knowledge of community associations, will permit us to base management decisions on sound data and expand our knowledge of the impacts to be expected from man-induced or natural environmental pertubations. Those of you familiar with the RPA process

know, however, that we are a long way from having the necessary wildlife data to make the kind of decisions an ever-increasing segment of the public is asking us to make.

From a selfish standpoint, we can look to the increased funding and personnel ceilings that have and will accompany this increased interest in and concern for wildlife. All that glitters is not gold, however, because the scope of our task will probably increase at a greater rate than the resources needed to do the job. There are 3,699 vertebrate species in the United States and an average of 748 species in each state. An average of 125 species per state may now be taken legally at prescribed places and times for commercial, control and recreational purposes. A survey by the U.S. Fish and Wildlife Service showed that the states want to give attention to an average of 279 fish and wildlife species in each state. It is clear that traditional funding sources are not adequate to do the job if we are going to be aggressive in recognizing the needs of nongame wildlife. In addition, we will need to develop techniques for defining habitat requirements like the one developed in the Pacific Northwest which relates wildlife-timber relationships to timber-management activities. The result was the ability to predict that "if I do this, I can expect to get that."

I have discussed briefly the history, need and justification for an expanded program of wildlife management that would include nongame and game species. The question is, how do we establish a program to fund nongame wildlife research and management when we can't completely fund the existing game management programs?

The "Federal Aid In Nongame Fish and Wildlife Conservation Act of 1977"(S. 1140) was introduced by Senator Gary Hart (Colorado) and eighteen co-sponsors on March 28, 1977. During hearings held on S. 1140 on August 3, 1977, a strong record of support was compiled for the concept of a nongame bill.

On July 28, 1977, Mr. Forsythe and Mr. Leggett introduced the "Nongame Fish and Wildlife Conservation Act of 1978" (H.R. 8606) in the House. The bill, which provides funds for both planning and implementation, also received favorable support. The Administration, as it did on S. 1140, withheld support.

The House has continued to work on a bill, and on December 7, 1977, Mr. Forsythe introduced H.R. 10255, a refined version

of H.R. 8606. It is a good bill and reflects more than 40 hours of work by the Committee legislative staff in cooperation with several conservation organizations. It provides for 90 percent matching money for planning and 75 percent for implementation. The planning portion lists 11 standards that, when adhered to, will help fill the voids in our knowledge of wildlife and its habitat requirements. Its major weakness is that it uses the authorized appropriation rather than an excise tax on certain outdoor recreational equipment and birdseed as the funding vehicle.

The momentum is there for the passage of this legislation and I feel I can truly say that nongame wildlife management is a need whose time has come. If I am right, or if I am wrong, we as professionals should consider Leopold's (1933) words of wisdom:

> Management of Other Wild Life. The objective of the game management program is to retain for the average citizen an opportunity to hunt. As already pointed out, this implies much more than the annual production of a shootable surplus of live birds to serve as targets. It implies a kind and quality of wild game living in such surroundings and available under such conditions to make hunting a stimulus to the esthetic development, physical welfare, and mental balance of the hunter.

> The objective of a conservation program for non-game wild life should be exactly parallel: to retain for the average citizen the opportunity to see, admire and enjoy, and the challenge to understand, the varied forms of birds and mammals indigenous to his state. It implies not only that these forms be kept in existence, *but that the greatest possible variety of them exist in each community.*

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The Relationship of Nongame Birds to Southern Forest Types and Successional Stages[1]

H. H. Shugart,[2] T. M. Smith,[3] J. T. Kitchings,[4] and R. L. Kroodsma[5]

Abstract.—This paper identifies general patterns of southern nongame bird species at three different spatial scales — the region, the forest stand, the microhabitat. Three hypothetical examples of nongame bird management are developed. Each example uses available information on non-game bird habitat requirements and tools used by forest managers. Possible future approaches to nongame bird management in the South are discussed.

INTRODUCTION

After several decades of research in avian ecology conducted by ornithologists in southern forests and elsewhere, we are in a position to generalize to a degree about the expected patterns of distribution of nongame birds over time and space. Two publications that may be useful for providing the reader with more detail are Slusher and Hinckley (1974) and Smith (1975). We will draw from these two volumes and current ecological literature to provide an outline of the general patterns of nongame birds and we will give some examples of approaches to managing nongame birds from our own research.

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One important aspect in considering patterns of nongame birds is to pay close attention to the time and spatial scales that are being discussed. The general patterns of variation in nongame birds over regional spatial scales may be quite different from the patterns of some smaller scale such as a forest stand. We will discuss the dominant patterns in non-game birds at three spatial scales: in the southern region, on study sites of 10 to 20 hectares in size (the forest stand), and at a microhabitat scale (less than .5 ha). Within these spatial scales, we will discuss long-term, annual and seasonal patterns of variation. The patterns are summarized on Table 1 and more detailed references are given in the discussion that follows.

DOMINANT PATTERNS OF NONGAME BIRDS IN THE SOUTHERN FORESTS

We will discuss patterns of distributions of forest bird species in four of the nine categories in Table 1.

Long-Term Regional Patterns of Nongame Birds

Over longer time scales (considering decade to decade or longer patterns of variation in bird distributions), there have been several well documented cases of range extensions into the South. For example, such northern erratic migrants as the Evening Grosbeak and the Pine Siskin now occur regularly during some winters in parts of the South in which they had never been recorded before the present decade. There have been in the somewhat more distant past — a century ago — whole-sale extinctions and regional extirpations of woodland species associated with the era of resource exploitation. Changes in species

Table 1. Dominant Patterns in Southern Nongame Forest Bird Communities Considered at Three Temporal and Three Spatial Scales. Topics in Italics are Discussed in More Detail in Text.

	LONG-TERM	ANNUAL	SEASONAL
REGIONAL	Long-term/regional patterns are studied by biogeographers. Patterns in the South are: 1. *The number of woodland species decreases as one moves south or away from mountains. (See MacArthur, 1972).* 2. *The number of endangered species increases as one moves south and into coastal areas. (See map in text).*	Work has been done in the past decade using the data from the U.S. Bureau of Sport Fisheries and Wildlife Breeding Bird Survey. Trends of increase and decrease of common and relatively less common bird populations can be documented with fair reliability. (See C. S. Robbins' paper below). It is now possible to measure effects of regional land management policies on the regional bird populations.	Considerable information has been collected on winter and summer distributions of nongame birds as well as on migratory birds. General patterns in the South are: 1. Typical overwintering species are nonwoodland birds. 2. Migrants often display habitat selection patterns that resemble the breeding season preferred habitats. 3. Breeding bird densities in forests are on the average of 2 to 4 breeding pairs per acre but during migration densities may be several times this figure.
FOREST STAND	Long-term/forest stand patterns are often termed "avian succession studies". General patterns are: 1. *Bird diversity generally increases with successional development of an area. This increase is strongly associated with the development of diverse vegetative structure.* 2. *There is great variation among studies but bird density often increases with age of a study plot.*	*There can be considerable variation from year to year at a given forest stand in terms of populations of a given species.* The annual species composition of dominant species is constant from year to year. There can be considerable variation in the presence or absence of "rare" species from year to year.	Patterns that have emerged from studies to date indicate: 1. Variation in population size within a breeding season can be considerable due to several biotic or abiotic factors (Wiens, 1975). 2. Between seasons both the density and diversity of woodland birds is highest during migration, next highest during the breeding season and lowest in the winter.
MICRO-HABITAT	It is generally thought that microhabitat preferences of birds change relatively slowly. There are some cases of species adapting to human habitat alterations but such adaptations do not promise to be of significance as an ameliorating factor when critical habitat is altered over a region.	Very little is known about year to year changes in microhabitat selection in species. Studies with mammals have indicated that such changes can occur in rodents. Most bird studies assume that year to year microhabitat preferences are reasonably constant. (See James, 1971 for niche gestalt concept).	*Studies using discriminant function analysis and other multivariate techniques show promise as a management tools. Such studies may allow the development of habitat management for nongame birds. Information on microhabitat can be used to incorporate bird habitat projections in forest stand simulators.*

ranges and the extinction (or potential there-
of) of species can be summarized in two ways:
(1) We can consider the patterns of overlap
of species ranges to form a regional pattern
of species richness (viz. areas in which many
ranges overlap are species rich). We can
then consider patterns of species richness
over the South. (2) We can map the ranges of
species that are considered to be in danger
of extinction.

Species Richness

Several factors influence the richness
(measured in terms of the number of species)
of the South's regional breeding avifauna.
Regions that have considerable topographic
relief or great heterogeneity of habitat
types tend to have more species than other-
wise comparable areas. Florida is depauperate
(has less species than one would expect) for
a region with both temperate and tropical
habitats. This relative lack of species is
due to the fact that Florida is a peninsula
and is isolated by the Gulf of Mexico from
the sources of tropical species that might
otherwise occur there (Cook 1969). It is the
depauperate nature of Florida that has allowed
it to be a "staging area" for the invasion of
exotic species onto the North American conti-
nent.

In general, the greatest richness of non-
game bird species is in the Appalachian
region of the South. This richness is due
in part to the altitudinal changes in the
region and in part because the region is in a
zone in which several species with northern
affinities extend their ranges into the South.
Table 2 provides a list of species occurring
in these forests along with a general descrip-
tion of the species habitat preferences and
nest site characteristics.

Endangered Species

If one maps the joint ranges of all of
the so-called endangered bird species that
occur in the South (Fig. 1) the resultant pat-
tern is the inverse of that for species rich-
ness. The endangered species tend to be
distributed in coastal areas (or on the
coastal plain) and in the southern part of
the region. Of these endangered species, most
are not directly associated with forest habi-
tats, but the Red-Cockaded Woodpecker (which
is an old-age pine-forest endemic species) is
often associated with areas that are managed
for wood products. The management of land on
which an endangered species occurs is a very
difficult endeavor both from a legal stand-
point and in terms of the practical management
aspects. Many of the endangered species are
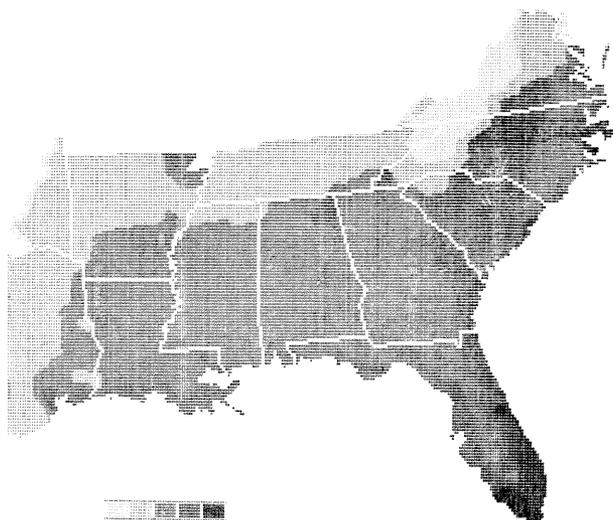
Figure 1.--Overlaps in ranges of endangered
species in the South. The darkest shading
on the map indicates areas in the range of
five rare or endangered bird species, the
lightest shading indicates areas in the range
of only one rare or endangered bird species.
Intermediate shadings indicate 2, 3, or 4
species increasing with intensity of map
shading.

rare birds that are associated with an ecologi-
cally unique habitat type (e.g., Cape Sable
Seaside Sparrow) and management for these spe-
cies is often a matter of avoiding any altera-
tion in the habitat in which the species occur.
Species such as the Red-Cockaded Woodpecker and
perhaps the Bachman's Warbler are rare but also
occur in transient habitats (respectively, old-
growth pine stands, and disturbed southern
swamp-forests). One cannot manage land for
such species simply by leaving areas alone that
appear to be suitable habitat. Natural succes-
sion will transform the habitat in time to some
other habitat type. The management for these
species would have to include the creation of
new habitat in adjacent areas. The management
of southern forests to include as an objective
the perpetuation of transient-habitat endemics
such as the Red-Cockaded Woodpecker may be one
of the most difficult tasks that the regional
manager ever has to tackle.

Table 2. Habitat preferences of birds that breed in woodlands of the eastern United States[a], and their abundance in eastern mountain hardwood forests[b] during the breeding season

Species	Forest type(s) preferred[c]					Density--pairs per 100 acres (or frequency in all stands[b])[c]				Nest site preferred[d]
	1	2	3	4	5	6	7	8	9	
Occurring primarily in forest interior										
Cooper's Hawk		X					(2)[b]			B
Sharp-shinned Hawk		X					(1)			C
Broad-winged Hawk		X					(8)			B
Ruffed Grouse			X			1	+	+	+	G
Yellow-billed Cuckoo	X					+	1	1	1	U
Black-billed Cuckoo	X					+	2	+	+	U
Barred Owl	X						(7)			D
Saw-whet Owl		X					(0)			O
Chuck-will's-widow		X					(0)			G
Whip-poor-will		X					(8)			G
Pileated Woodpecker			X			+	+	+	1	O
Red-bellied Woodpecker			X			1	+	+	1	O
Yellow-bellied Sapsucker			X			+	0	0	1	OD
Hairy Woodpecker			X			+	+	+	1	OD
Downy Woodpecker		X				3	1	+	2	O
Great Crested Flycatcher			X			2	1	2	2	OD
Acadian Flycatcher	X					4	2	3	28	D
Least Flycatcher			X			4	0	0	1	B
Eastern Wood Pewee			X			5	5	5	5	D
Black-capped Chickadee		X				1	4	1	2	OD
Carolina Chickadee		X				3	1	+	4	O
Tufted Titmouse	X					3	2	4	9	OD
White-breasted Nuthatch	X					5	2	6	15	OD
Red-breasted Nuthatch	X						(1)			
Brown Creeper		X					(1)			between bark and trunk exposed roots
Winter Wren		X				0	0	0	+	U
Wood Thrush	X					5	2	6	15	U
Hermit Thrush				X			(2)			G
Veery	X					8	5	4	3	G
Blue-gray Gnatcatcher	X					3	2	6	9	
Golden-crowned Kinglet	X						(0)			C
Solitary Vireo				X		+	+	2	2	CU
Red-eyed Vireo	X					18	23	21	37	U
Black-and-white Warbler	X					9	6	9	5	G
Swainson's Warbler	X					0	0	0	+	U
Worm-eating Warbler	X					2	+	+	9	G
Nashville Warbler		X					(0)			G
Parula Warbler		X				+	0	+	1	B
Magnolia Warbler	X					1	+	+	2	CU
Black-throated Green Warbler				X		3	5	5	7	CU
Black-throated Blue Warbler				X		8	4	6	4	U, CU
Cerulean Warbler	X					2	0	3	17	D
Yellow-throated Warbler		X				0	+	0	0	B
Blackburnian Warbler		X				1	+	1	3	C
Pine Warbler	X					+	3	+	+	C
Ovenbird	X					14	11	17	17	G
Kentucky Warbler	X					3	0	7	5	G
Hooded Warbler	X					14	5	4	6	U
Canada Warbler			X			1	+	8	3	G
Scarlet Tanager			X			7	+	3	7	D
Rose-breasted Grosbeak	X					1	3	1	2	U
Occurring primarily in forest edge, brush, and areas with scattered trees										
Sparrow Hawk (American Kestrel)		X					(0)			O
Bobwhite		X					(1)			G
Mourning Dove		X					(2)			B
Common Flicker		X				2	+	1	1	O
Eastern Kingbird	X						(0)			D
Willow Flycatcher		X					(0)			U
Olive-sided Flycatcher				X			(0)			C
House Wren	X					0	0	0	+	O
Mockingbird		X					(0)			U
Brown Thrasher		X				0	0	+	0	U
Robin		X				+	1	1	1	B
Eastern Bluebird		X					(0)			O
Cedar Waxwing		X					(9)			B
White-eyed Vireo		X				+	0	0	0	U
Yellow-throated Vireo	X					2	1	1	3	D
Warbling Vireo	X						(0)			D
Prothonotary Warbler	X						(0)			O
Golden-winged Warbler		X				6	+	0	0	G
Blue-winged Warbler		X				0	0	0	+	U
Yellow Warbler	X					0	1	0	+	U
Chestnut-sided Warbler	X					19	2	1	4	U
Prairie Warbler		X				3	1	+	+	U
Louisiana Waterthrush	X					2	+	+	1	stream banks
Yellow-breasted Chat		X				4	+	+	+	U
Mourning Warbler		X				4	+	0	1	G
American Redstart				X		3	+	+	16	U
Orchard Oriole	X						(0)			D
Blue Grosbeak		X					(0)			U
Indigo Bunting		X				13	8	1	2	U
Rufous-sided Towhee		X				19	2	9	7	G
Slate-colored Junco		X				4	+	6	3	
Chipping Sparrow		X					(1)			U
Song Sparrow		X				1	+	0	0	G
Occurring in forest interior and edge, brush and areas with scattered trees										
Turkey Vulture		X					(2)			G
Black Vulture		X					(0)			G
Red-tailed Hawk		X					(2)			B
Red-shouldered Hawk		X					(3)			B
Screech Owl		X					(2)			O
Great-horned Owl		X					(1)			B
Ruby-throated Hummingbird		X				1	1	+	+	U
Red-headed Woodpecker	X						(0)			OD
Blue Jay		X				+	+	+	1	B
Common Crow		X					(26)			B
Carolina Wren		X				0	+	0	4	U,O
Catbird		X				1	+	1	1	U

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Species	Forest type(s) preferred[c]					Density—pairs per 100 acres (or frequency) in all stands[b][c]				Nest site preferred[d]
	1	2	3	4	5	6	7	8	9	
Cardinal		X	X			4	1	2 (0)		U
White-throated Sparrow								8		

Species	Forest type(s) preferred[c]					Density—pairs per 100 acres (or frequency) in all stands[b][c]				Nest site preferred[d]
	1	2	3	4	5	6	7	8	9	
Northern (Baltimore) Oriole		X				1	(4) +			D
Summer Tanager					X			+	2	B

[a]All species that breed east of a line from western Louisiana to western Minnesota are included except species that are rare or have very small breeding ranges within this area.

[b]The four density estimates for each species represent the average number of breeding bird pairs per 100 acres in the following four types, respectively, of mountain hardwood forests from North Carolina to New York: cutovers (N = 7 stands); stands of young forest with average canopy height = 25-30 feet (N = 5); stands of medium-aged forest with average canopy height = 35-45 feet (N = 7); and stands of mature forest with average canopy height > 50 feet (N = 11). Plus signs (+) indicate densities between zero and one pair per 100 acres. Each single number in parenthesis represents the number of stands (out of a total of 30 stands) in which the particular species was noted as a visitor or occurred too infrequently to allow density estimation. Data were obtained from census reports in American Birds, many of which were contributed by the Brooks Bird Club.

[c]1 - coniferous, 2 - deciduous, 3 - deciduous and coniferous, 4 - deciduous and deciduous-coniferous, 5 - coniferous and deciduous-coniferous, 6 - cutovers, 7 - young, 8 - medium-aged, and 9 - mature.

[d]Abbreviations for nest sites are as follows: D = deciduous trees, C = coniferous trees, B = both deciduous and coniferous trees, O = cavities, OD = cavities in deciduous trees, U = broadleaf undergrowth (sometimes low tree branches), CU = coniferous undergrowth, and G = ground.

Long-Term Patterns of Nongame Birds at the
Scale of the Forest Stand

Patterns in Breeding Bird Diversity

Diversity indices as used by most ecolo-
gists (see MacArthur and MacArthur 1961;
Patten 1962; Lloyd and Ghelardi 1964; Monk
1967; for various uses of diversity indices
with different sorts of organisms) can be
thought of as having two components:

Richness — the number of species in a
given community.

Equitability — the evenness of numeri-
cal abundance of the populations
in a given community.

For breeding bird communities the diver-
sity is mostly due to the number of species
(richness) (Tramer 1969; Kricher 1972) so
that for studies of similar sampling intensity
and size, diversity (often calculated as $H' =$
$\Sigma p_i \text{Log} p_i$, where H' is the diversity index and
p_i is the frequency of occurrence of the ith
bird species) varies directly with species
richness. The diversity index is not as
strongly influenced by rare species as is a
species list, and is useful in comparing
studies of differing sample intensity (Buzas
and Gibson 1969).

There is a general theory that species
diversity of organisms should increase through
succession with a decline in diversity in the
last successional stages (Margalef 1958).
This pattern has not been uniformly noted in
studies of breeding birds and is almost
certainly not the case in winter bird popu-
lations. Adams (1908) listed species of birds
characteristic of successional stages (aquatic
communities to bogs to climax forests) on Isle
Royale, Michigan. Adams found a greater
variety of bird life (species richness) in the
intermediate stages of succession. Figure 2
(from Smith 1975) shows the pattern for three
more recent studies. In no case is a decline
in species diversity toward the end of succes-
sion particularly evident, but there is a tend-
ency for diversity to increase through succes-
sion. There is considerable variation in
pattern among the three studies.

Patterns of Breeding Bird Density

An increase of avian density through a
progression of successional communities has
been documented by Saunders (1936) in New
York, Kendeigh (1948) in Michigan, Odum
(1950) in North Carolina, Johnston and Odum
(1966) in Georgia, Haapanen (1965) in Finland,
Karr (1968) in Illinois, Karr (1971) in
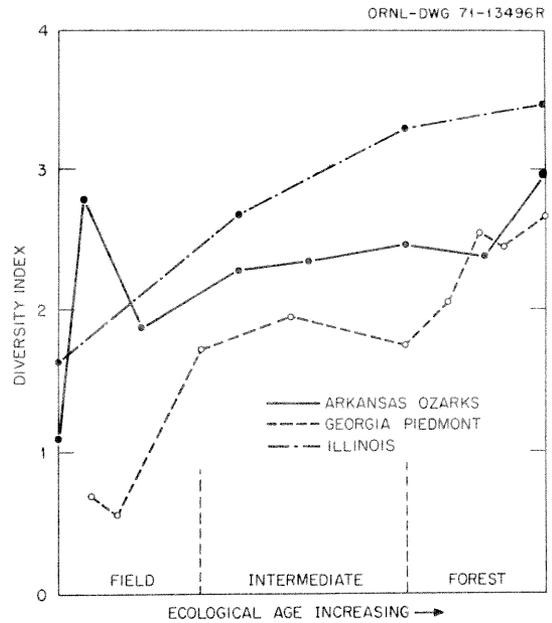Panama, Shugart and James (1973) in Arkansas.

Figure 2.—Changes in the species diversity
index (H') for bird communities during eco-
logical succession. The Arkansas data are
from Shugart and James (1973); Georgia data
from Johnson and Odum (1950); Illinois data
from Karr (1971). Figure modified from
Shugart and James (1973).

These findings drawn from diverse regions are
in general agreement. There are notable
exceptions to this general pattern [e.g.,
Kendeigh (1947) found highest bird densities
in shrubby seral stages of communities in the
Helderberg Plateau region of New York]. How-
ever, there is an expected pattern of higher
densities of birds in mature forests.

Annual Changes in Bird Communities at the
Scale of the Forest Stand

A second time scale important at the level
of the forest stand is that of annual or year-
to-year variation in the composition of avian
communities. This annual variation can take
two forms: variation in the population of a
given species, and annual variation of the spe-
cies composition of the community as a whole.
Figure 3 shows the annual fluctuations in the
number of breeding pairs of selected bird spe-
cies in an Illinois woodland over a period of
years.

The actual causes for such yearly fluc-
tuations in species abundance are for the most
part unknown. Wiens et al. (1974) found no
clear relationship between fluctuations in
population size of avian species and climatic
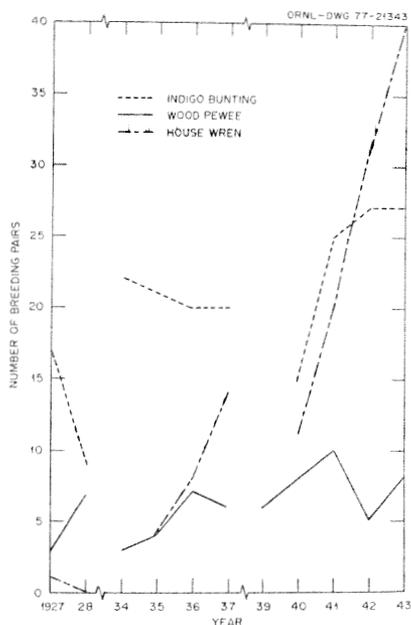variation. The problem of identifying causal

Figure 3.--Number of pairs of selected species of breeding birds in Trelease Woods, Urbana, Illinois (55 acres). Data from Kendeigh (1944).

factors is confounded by the fact that many of the breeding species in an area are migratory species whose densities may be a result of factors taking place in other areas of their range. Fluctuations may also be a result of changes in dispersal (distributional) patterns rather than absolute numbers. Territory size in avian species has been found to be negatively correlated with abundance of food within the territory (Stenger 1958; Schoener 1968). As a result of this, annual variations in the number of breeding birds of a particular species in a given stand might be a result of varying territory size resulting from variations in the food supply (i.e., insect biomass).

Annual turnover of species in a stable vegetation type is rather insignificant in mainland regions and usually reflects the presence of "rare species" encountered during censuses. The actual species composition of the dominant segment of the avifauna changes little from year to year for a given site.

Seasonal Patterns in Bird Microhabitat Selection

One of the more interesting lines of research to develop over the past decade has been the use of multivariate statistical techniques to quantify the microhabitat selection patterns of select nongame bird species usually within a season. Schoener (1974) has reviewed the manner in which similar species utilize their environments and has noted the following general patterns:

1. The important variables involved in resource partitioning are typically habitat variables, followed in importance by food variables.

2. As the number of species considered in a community increases, the number of variables needed to separate the ecological roles of the species increase.

Recently, there have been multivariate statistical analyses (James 1971; Shugart and Patten 1972; Anderson and Shugart 1974; Whitmore 1975) directly applied to determine the influence of a number of habitat variables on the distributions and microhabitats of entire avian communities. These studies indicate that the simple relationship between bird species diversity and foliage height diversity first presented by MacArthur and MacArthur (1961) is neither as direct nor as universally applicable as it was first thought. The application of multivariate analysis to the habitat selection problem in birds also seems to reduce problems in data interpretation.

For example, one application of discriminant function analysis has been proposed by Conner and Adkisson (1976) to determine potential woodpecker inhabitation by measuring variables in the structural vegetation. Discriminant function analysis can also be applied to the entire woodpecker community in order to identify differences in structural niche requirements among species. Using data collected by R. Bunnell on a study area on the Department of Energy Oak Ridge Reservation, a discriminant function was computed so that given the vegetational structure at a given point in space, the probability of the point being utilized by a given woodpecker species could be determined. Vegetative data that corresponded to the parameters used in the woodpecker habitat analysis had been collected for a number of inventory plots on the Oak Ridge Reservation (Bunnell et al. 1978) where no survey of woodpecker species have been made. These data were fed into the discriminant function and the most probable woodpecker species associated with each inventory plot was computed. The resultant map (Fig. 4) made with Symap (Dougnik and Sheeham 1975) shows the potential woodpecker feeding habitats by species for a site called the Haw Ridge Site. Such a map could be used by a resource manager to avoid the areas that might be used by a given woodpecker species or it might allow the placement of a nature trail so that a visitor could expect to see all the indigenous woodpecker species with minimum effort. The idea of coupling microhabitat analysis with the
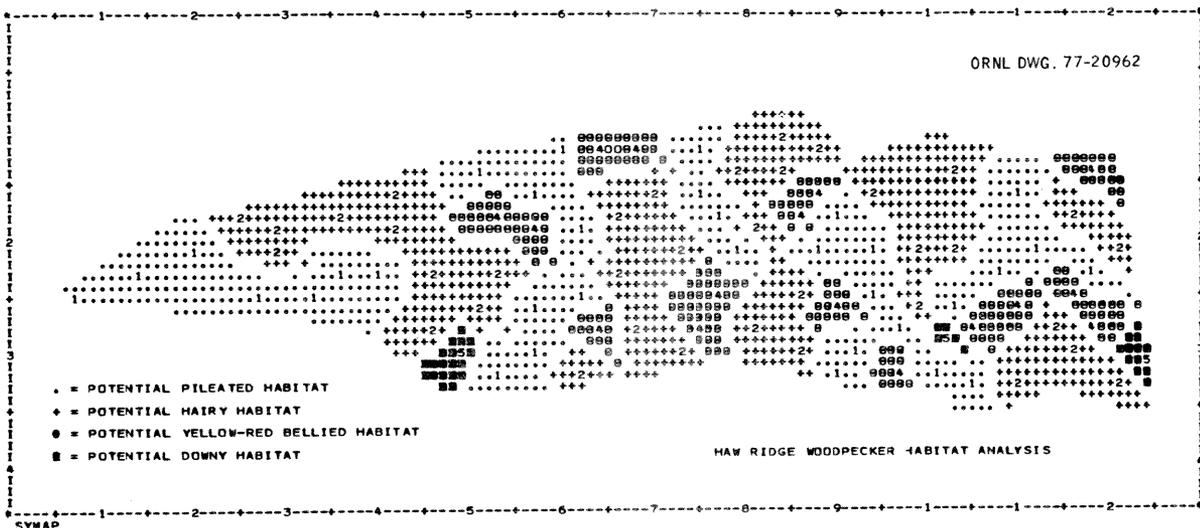
Figure 4.—A Symap map of potential woodpecker habitat on a study site called Haw Ridge on the Department of Energy Oak Ridge Reservation. The map was drawn using a discriminant function (calculated on a base data set) to determine the expected woodpecker species at each of the forest inventory plots on Haw Ridge. Yellow-bellied Sapsucker and Red-bellied Woodpecker habitats are similar and are lumped together.

forest inventory sample plots used by resource managers creates the potential for nongame management comparable to those used for many game species.

POSSIBLE NEW METHODOLOGIES FOR NONGAME BIRD MANAGEMENT

Regional Modeling of Nongame Bird Management

Shugart et al. (1973) formulated a rationale and methodology for constructing models of forest succession over large land areas (10^8 - 10^{10} acres). In developing this methodology an example model was used to simulate changes in amounts of forested land of various successional stages in the State of Michigan. Models of this type allow for long-term predictions to be made concerning the areas of land covered by a particular forest type. For species in which the preferred habitat can be easily associated with a forest type (as opposed to species that have specific microhabitat preferences — discussed below), such simulators can be used to project the long-term regional consequences of different management strategies.

As a purely hypothetical example of how one might couple a regional-inventory projection model to the habitat selection patterns of a given species, we will consider

how the habitat available to the Kirtland's Warbler might change in the face of two different management schemes. We will use the Shugart et al. (1973) example model as a succession simulator and will consider only the gross habitat selection patterns of the Kirtland's Warbler. Kirtland's Warbler is an endemic of the Jack Pine forests of northern Michigan. It is restricted to the fairly dense stands of young Jack Pines that spring up after forest fires (Bent 1963). As a result of current fire prevention practices, the Jack Pine forests, being an early successional forest type, are quickly declining in area. Subsequently the population of Kirtland's Warbler has declined drastically to the point at which today it is an endangered species.

Results of a 250-year simulation of the Jack Pine forests of Michigan under conditions both of natural succession (in the absence of natural or man-made disturbance) and of harvesting with a rotation age of 50 years, is shown in Fig. 5. Under conditions of natural succession Jack Pine decreases to 1/10 of its original area (of 671.5 X 10^4 acres) within 100 years and continues to decrease to 1.09 X 10^4 acres by the end of the 250-year simulation. When timber harvest and replanting is introduced to the model, equilibrium occurs for Jack Pine at the onset of the simulation with total area covered varying by less than 2% over the 250 years.
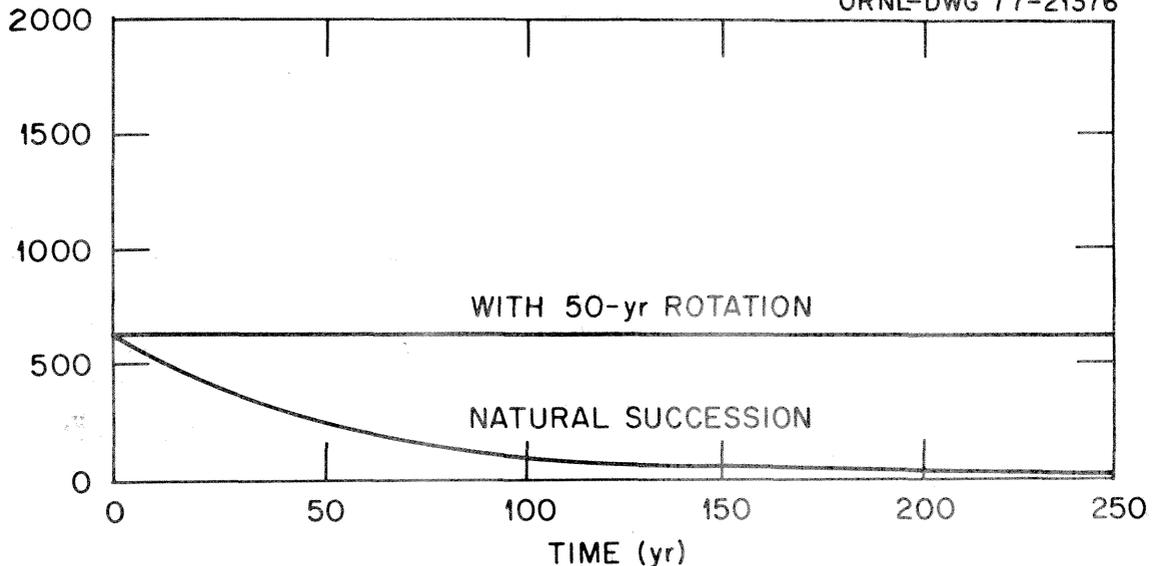
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Figure 5.--Total acreage of Jack Pine in Michigan through 250 years of simulated succession with and without forest management. (Vertical axis in acres X 10^3)

In actual fact, to deal with this prob- lem of declining habitat availability for Kirtland's Warblers under present conditions, selected areas of Jack Pine forest are being set aside and periodically burnt to make available young stands of suitable habitat. The value of models such as the one above, is in their ability to predict long-term trends in the availability of habitat types under various management practices. In the above simulation, the harvesting of Jack Pine using the equivalent of a fifty-year rotation period appears to maintain the present status of Jack Pine as a forest type and thus halt the decline of available Kirtland's Warbler habitat.

In this hypothetical example we have coupled a computer model (that projects the regional inventory of different forest types into the future) to the gross habi- tat preferences of a nongame bird species. Models which project future forest cover are being used and developed for forest systems for many regions of the United States. Some of these models even take into account economic feedbacks that might alter the harvest and site preparation options (for example) that are used (see Shugart et al. 1977 for a review of some of the more ecologically oriented models of this sort). Given the existence of regional "habitat projection models" — which is what the models used to project state forest inven- tories really are — we are in a position to incorporate bird habitat preferences into these models and to manage nongame bird habitats.

Stand Modeling of Nongame Bird Management

Just as we can use regional inventory pro- jection models to predict the changes of suit- able habitat for species over an entire state, we can also use stand simulators to assess effects of alternate management strategies on selected bird species or for entire bird com- munities. Stand simulation models are reviewed in Horn 1977; Shugart et al. 1977. These models are quite varied in the types of mathe- matics used but they typically function by con- sidering the tree by tree changes over time for an area that corresponds to that of a canopy tree or to some sampling unit. The spatial scale of these models corresponds to the scale of what we earlier, termed the microhabitat spatial scale for birds.

As a hypothetical example, we took the stand simulator (FORET) that has been devel- oped for East Tennessee (Shugart and West 1977) and used the model to simulate 1000 years of natural succession on 100 plots of forested land each of which is 1/12 ha (∿ 1/5 acre). This particular model functions by keeping track of the diameter and species of each individual tree occurring on the simulated plot. Each year, a probability of mortality for each indi- vidual tree is determined and a random number is drawn to determine if a given tree should be killed. Similarly, according to conditions on the forest plot, trees of different species become established either by seeding in or by sprouting. Each year the diameter of each tree is increased according to the species and size of the tree and taking into account shading, crowding and climate. The output from the model is in the form of lists of tree diameters by species per 1/12 ha. This output looks like a stand tally sheet and is provided each year

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for each simulated plot. By combining the output from several replicate runs (usually 100) we can see the dynamics of a forest. Output from the model, and a discussion of the validation of this model are in Shugart and West 1977.

The model output from 100 plots for 1000 years of natural succession was converted to biomass (in metric tons ha^{-1}). We then apportioned this biomass between thin-barked tree species and thick-barked species. The thin-barked trees were the species that the Yellow-bellied Sapsucker might use for feeding. The Yellow-bellied Sapsucker (occurring in winter throughout the South) feeds on the inner bark, tree sap and the insects drawn to the holes that the bird maintains in selected trees. Figure 6 shows the percentage of trees that
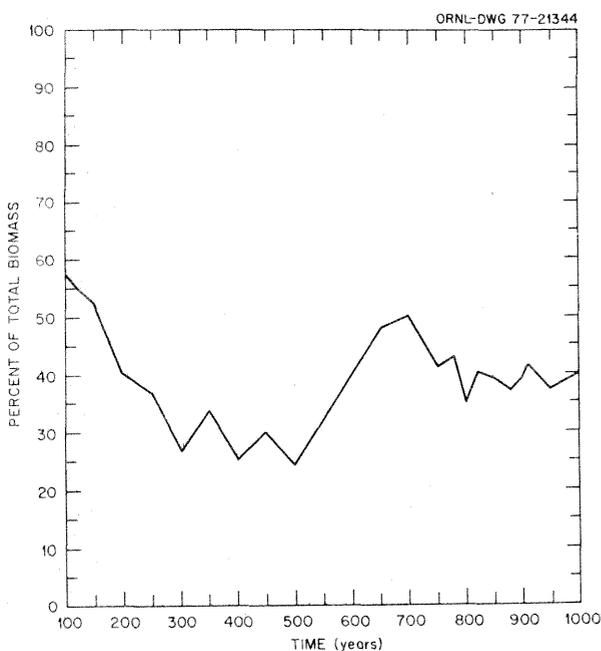

Figure 6.--Thin-barked tree species suitable for feeding by Yellow-bellied Sapsuckers as a percentage of the total biomass through 1000 years of simulated stand development on 100 1/12 ha circular plots.

might be fed upon by Yellow-bellied Sapsuckers during 1000 years of natural succession in East Tennessee. There are two periods early and late in the succession in which sapsucker trees are particularly available but in no case is there a shortage of potential feeding sites during natural succession in the East Tennessee forests.

There are several logical extensions of this sort of habitat modeling. We could have increased the mortality probability for trees utilized by sapsuckers to obtain an estimate of the effect of this bird on the patterns of forest succession. We could harvest trees from the simulated stands and assess the effect of any stand management scheme on the availability of sapsucker feeding sites. Using multivariate statistical descriptions of habitat structure associated with different bird species, we could simulate bird community changes under natural succession or under various management options. What is needed in this case is a stand projection model and a knowledge of species habitat preferences.

FUTURE PROBLEMS IN NONGAME BIRD MANAGEMENT

Through this discussion we have focused on the habitat preferences of southern nongame birds at different spatial and temporal scales. We have provided some general rules-of-thumb for patterns of bird populations and we have given three examples of what we feel will be the nature of future nongame bird management. It is imperative for the development of nongame bird management as a scientifically sound system of management practices that we learn more about the habitat requirements and niche relationships of nongame birds. Many temperate bird species (at least within a given season) seem to be closely tied to certain microhabitat features. This probably is not the case with all temperate species and seems not to be the case in general in tropical birds (Able and Noon 1976). We must know which species are associated with which habitat elements and we must know which species cannot be managed by simply managing for habitat.

It is probable that management for nongame species will be practiced in the less-economically important mountain forests of the Arkansas and Missouri Ozarks and in the Southern Appalachians due to several ecological and economic factors. These forests are already used in a primary fashion for outdoor recreation so that the political pressures and incentives may be greatest in these regions for a concerted effort to manage song birds. Also these forest systems have a rich avifauna. The economically important pine-dominated forests of the coastal plain should not be overlooked in terms of their potential for nongame bird management. The richer bird communities may be in forests of the southern mountains, but not all species occur in abundance in these regions and some species are more or less endemic to the coastal plain and piedmont ecosystems. There is a potential for ignoring nongame bird populations in the pine forests that could create shortages in critical habitat for some species in the future. This potential problem should be recognized and avoided.

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We have identified two areas in which tools and data familiar to the forest manager could be used to attempt to optimize birds and other uses of forests. The first area involved the use of forest inventory data as habitat potential data for nongame species. The second area involved using stand and regional forests simulators to project bird habitat availability into the future. There is undoubtedly more to nongame bird management than simply habitat management but much work needs to be done in this area. The insights of the forest-entomologist would be invaluable in studying food availability for nongame birds, for example. The richest research area in nongame bird management in the future may well be the combining of the present understanding of avian ecology with the experience in managing forests.

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The Structure and Organization of Avian Communities in Forests

Sidney A. Gauthreaux, Jr.[1]

Abstract.--The structure of bird communities is presented in the context of Southwood's schema of ecological strategies and the habitat templet. Heterogeneity in space and time and their effects on the gradients of durational stability and of resource level and constancy are considered the underlying factors in community organization. These gradients are used in discussing species strategies and life forms, community process (succession), and community characters (spatial complexity, trophic complexity, niche breadth, standing crop, turnover, and diversity).

INTRODUCTION

The concept of community as an aggregate of organisms which form a distinct ecological unit defined in terms of flora and fauna is widely accepted, but it is also obvious that the concept includes complex dynamic interactions and properties of the component species. In this presentation I will give a broad overview of the structure of avian communities in forests. In discussing avian community ecology I should mention that it is a bit naive to speak of "avian" community ecology, because birds represent but a part (and some would say a rather insignificant part) of the total community structure. Nonetheless, work on birds has contributed greatly to our knowledge of the structure and dynamics of ecological communities, and it is this contribution I wish to stress in this paper.

The ultimate objective in studying community ecology is to determine the nature and the relative importance of the factors controlling its composition; also, whether, to what extent, and why the community is changing with time (Pielou 1974). In order to achieve this objective it is necessary to define some measurable properties of the community as a whole and in so doing make possible comparsons of the quantitative properties among several communities. As Pielou (1974) points

out, this is a necessary first step toward an understanding of how communities function. Thus, the study of bird communities is the search for relations among measurable aspects of sets of bird species such as patterns of size or relative abundance among the species within a community and patterns of numbers of species that vary regularly from community to community (MacArthur 1971).

Southwood (1977) has recently stressed the importance of time and space in terms of ecological strategies of species in communities and emphasized that the strategies of the species have evolved to maximize the numbers of their descendents in the community. He has generated a schema in which various features of communities have been arranged against the axes of space and time (fig. 1). Southwood's schema will be used as a guideline in my treatment of avian community ecology. It should be noted that any consideration of avian communities involves treatment of component species' strategies, community process (succession), and community characters (spatial complexity, trophic complexity, niche breadth, standing crop, turnover, and diversity), and these considerations will serve as the outline for my presentation.

COMPONENT SPECIES STRATEGIES

A number of recent studies have addressed life history strategies from many different viewpoints. In a theoretical examination of optimal reproductive efforts, Schaffer (1974a) has relaxed the general assumption of environmental constancy, and Schaffer (1974b) and Schaffer and Rosenzweig (1977) have investigated

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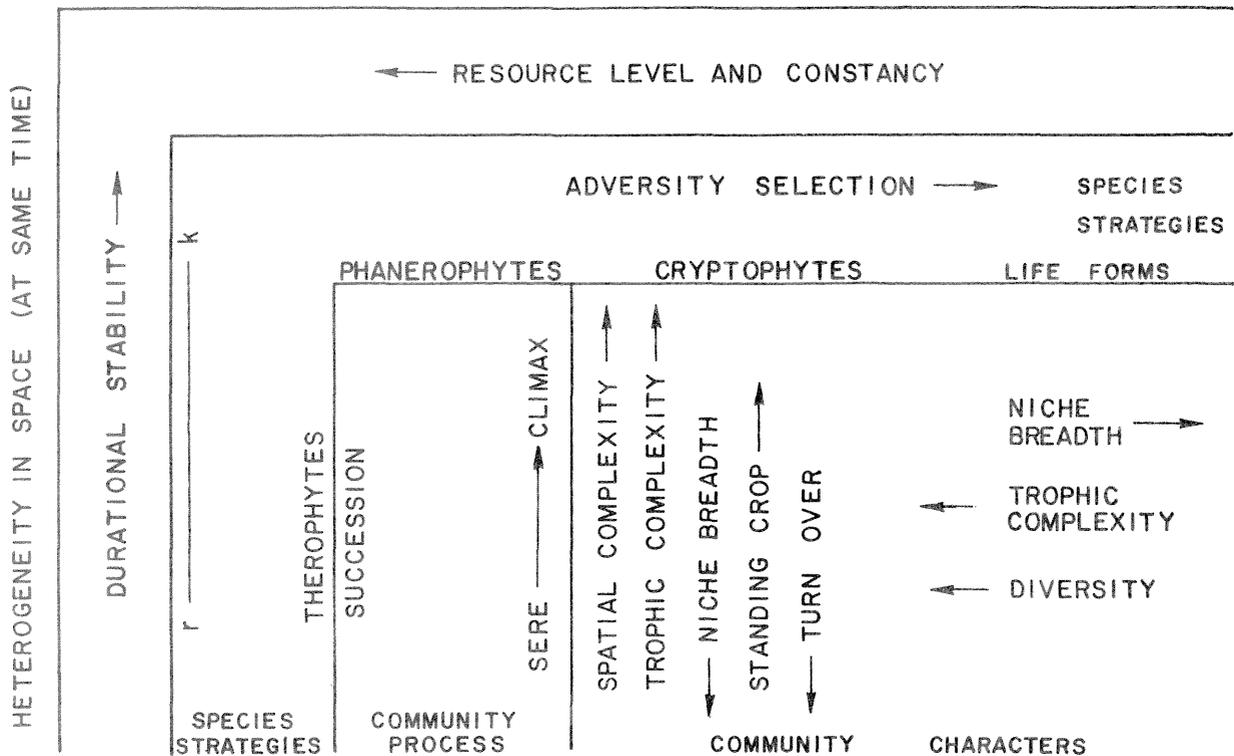HETEROGENEITY IN TIME (OF SAME SPACE)   +   UNFAVOURABLENESS

Figure 1.--Ecological strategies and the habitat templet (after Southwood 1977).

the problem of more than one life history strategy in a species. The influence of environmental certainty, trophic level, and resource availability in life history strategies have been discussed by Wilbur et al. (1974), and they suggest that additional ecological dimensions, such as environmental predictability and the relative trophic position of species may be important in the evolution of life histories. Nichols et al. (1976) agree that attempts to explain life histories as outcomes of single selective pressures have actually obscured the evolution of life history strategies, and they add that numerous organisms inhabiting variable environments exhibit temporally dynamic reproductive strategies (see also Giesel 1976). Ricklefs (1977) in a discussion of the evolution of reproductive strategies in birds suggests that the diversity in life histories must be sought primarily in environmental factors that directly influence fecundity, prereproductive survivorship, and adult mortality and in density-dependent or fortuitous relationships among those aspects of the environment.

Pianka (1970, 1974a:90) has tabulated several characteristics correlated with r- and K-selection (Table 1). Stearns (1976,

1977) has carefully examined the ideas and correlates of r- and K-strategists in an overview of life history tactics, and questions the validity of the underlying assumptions and theoretical predictions that have flourished in the literature. According to Stearns (1976), the key life history traits are brood size, size of young, the age distribution of reproductive effort, the interaction of reproductive effort with adult mortality, and the variation in these traits among an individual's progeny. The general theoretical problem is to predict which combinations of traits will evolve in organisms living in specific circumstances. Leon (1976) has addressed this problem in part by using optimal control theory.

Some bird species resemble r-strategists (see MacArthur and Wilson 1967) in that they have high reproductive potential (longer breeding seasons and raise more broods per year than do other species), extraordinarily catholic and unspecialized habitat preferences, high dispersal ability, and are competitively excluded from species-rich islands by K-selected species (Diamond 1975). These former species are called supertramps, and Diamond found that faunas dominated by supertramps maintain population densities up to nine times higher than those of K-selected faunas of the same number of species.

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Table 1.—Some of the Correlates of r and K Selection (After Pianka 1970, 1974:90).

	r Selection	K Selection
Climate	Variable and/or unpredictable; uncertain	Fairly constant and/or predictable; more certain
Mortality	Often catastrophic, nondirected, density independent	More directed, density dependent
Survivorship	Often Type III	Usually Types I and II
Population size	Variable in time, nonequilibrium; usually well below carrying capacity of environment; unsaturated communities or portions thereof; ecologic vacuums; recolonization each year	Fairly constant in time, equilibrium; at or near carrying capacity of the environment; saturated communities; no recolonization necessary
Intra- and interspecific competition	Variable, often lax	Usually keen
Selection favors	1 Rapid development 2 High maximal rate of increase, r_{max} 3 Early reproduction 4 Small body size 5 Single reproduction	1 Slower development 2 Greater competitive ability 3 Delayed reproduction 4 Larger body size 5 Repeated reproductions
Length of life	Short, usually less than 1 year	Longer, usually more than 1 year
Leads to	Productivity	Efficiency

It should be emphasized that although some bird species may be thought of as r-strategists, birds as a whole, compared with many other groups of organisms (e.g., insects), are more K-strategists on the r-K continuum. Southwood et al. (1974) have made brief reference to birds as r- and K-strategists and have concluded that while many vertebrate species may have arisen as a result of K-selection (in comparatively stable geological periods), many groups within these taxa have had their population parameters modified to conform to the habitats they occupy. Really successful K-strategists become precisely adapted to a very permanent (in generation terms) habitat type, they become larger in size, and, because of their extreme K-type population parameters, they lose their plasticity for selection. Another clear and straightforward discussion of optimal life history strategies with some reference to birds can be found in Southwood (1976). Brewer and Swander (1977) have examined life history traits as they influence the intrinsic rate of natural increase in forest, grassland, and marsh inhabiting birds. They conclude that forests can probably be thought of as K-selecting environments for birds, while grasslands and marshes probably are not,

specifically "because vegetational fluctuations make particular areas unpredictably uncrowded or overcrowded."

SUCCESSION

The appearance of species population densities along the time axis during succession is fundamentally similar to that found along spatial gradients (see fig. 1), but the rate of change slows as the community matures (Whittaker 1975). The properties of succession have been thoroughly reviewed by Margalef (1968), Odum (1969), Horn (1974, 1975, 1976), and Whittaker (1975). Succession is being viewed currently in the context of adaptations of individual species independent of any transcendent properties of the whole community (Drury and Nisbet 1971, 1973; Connell 1972; Horn 1974), and the replacement process is increasingly being represented by Markovian models (Horn 1976). The mechanisms of succession in natural communities and their role in community stability and organization have been reviewed recently by Connell and Slatyer (1977). They have suggested that the sequence of species observed after a relatively large space is opened up is a consequence of the following mechanisms. Species with broad dispersal powers

and rapid growth to maturity usually arrive first and occupy empty space. These species cannot invade and grow in the presence of adults ·of their own or other species. Several alternative mechanisms may then determine which species replace these early occupants. Connell and Slatyer (1977) have proposed three models of such mechanisms. The first they call the "facilitation" model that suggests that the entry and growth of the later species is dependent upon the earlier species "preparing the ground," and only after this can later species colonize. The second they have referred to as a "tolerance" model which suggests that a predictable sequence is produced by the existence of species that have evolved different strategies for exploiting resources. Later species will be those able to tolerate lower levels of resources than earlier ones. The third model they have called the "inhibition" model which suggests that all species resist invasions of competitors. The first occupants preempt the space and will continue to exclude or inhibit later colonists until the former die or are damaged, thus releasing resources that permit later colonists to reach maturity. The first and third models have the greatest supportive evidence, while the second model has little supportive data.

Kendeigh (1945) has long considered the general pattern of avian succession to be a manifestation of the habitat preferences and ecological requirements of the bird species. The replacement sequencing and habitat requirements of bird species during succession in a number of different communities have been examined (Adams 1908; Lack 1933; Grange 1948; Odum 1950; Beckwith 1954; Johnston and Odum 1956; Martin 1960; Mitchell 1961; Haapanen 1965, 1966; Karr 1971; Glowacinski 1972; Shugart and James 1973; Kricher 1973; Meslow and Wight 1975; Soots and Parnell 1975; Winternitz 1976), and all show that there is a high correlation between bird species and vegetation stage (fig. 2). Bond (1957) and Shugart and James (1973) have analyzed the correlation between bird and plant similarity coefficients between successional stages in communities and found that the correlations were both strong and significant.

The progressive changes in the composition and relative abundance of various bird species with the cropping of the forest on a 40-year cycle in Burgundy, France, has been examined by Ferry (1960). He found that the birds could be placed in four groups according to their responses to the changing environment. The first group of birds settle in the low herbaceous or bushy layer with open spaces above it, increase in density, and then disappear quickly. The second group consists of species that arrive fairly

quickly after the felling, increase in density, and then slowly decrease without disappearing completely (provided the forest is not permitted to return to climax). The third group includes those birds that settle at a particular, more or less early, stage, increase rapidly at first, and then more slowly as the populations build up to their limit. The fourth group contains those birds whose populations passed through a maximum during the early stage, diminish or disappear when the undergrowth becomes too dense, and become abundant once again in the mature plots. Similar findings have been reported from studies undertaken in different environments, notably in pine forests in Britain (Lack 1933), spruce forests in Finland (Haapanen 1965, 1966), and in several different communities in America (Monson 1941, Hagar 1960, Kilgore 1971, Curtis and Ripley 1975, Webb et al. 1977).

COMMUNITY CHARACTERS

According to Southwood's (1977) schema (fig. 1), certain community characters (spatial complexity, trophic complexity, niche breadth, standing crop, and turnover) change during succession while some community characters (niche breadth, trophic complexity, and diversity) also vary in terms of resource level and constancy and in terms of saturation or interaction selection, exploitation selection, and adversity selection (see Whittaker 1975). It should be stressed that the aforementioned community characteristics are highly correlated and interactive and, consequently, it is almost impossible to discuss a given community character without making reference to another characteristic with which it is highly correlated (e.g., species diversity and trophic complexity). In the following sections I will examine the community characteristics given by Southwood (1977) with particular emphasis on birds.

Spatial Complexity

Through successional stages, the spatial complexity of a location increases and the variety of niches also increases. MacArthur and Levins (1967) have suggested that increasing the dimensionality of resources allows more species to inhabit a community, and MacArthur (1971) has emphasized that any habitat containing many kinds of patches will contain bird species appropriate to these patches.

A number of studies have attempted to examine the relation between increasing spatial complexity of vegetation in a community and avian community organization (Cody 1974; Tomoff 1974; Wiens 1974, 1976; Willson 1974; Balda 1975; Roth 1976; Pearson 1977). There is agreement that more than one measure of complexity is needed. For example, vertical measures such as foliage
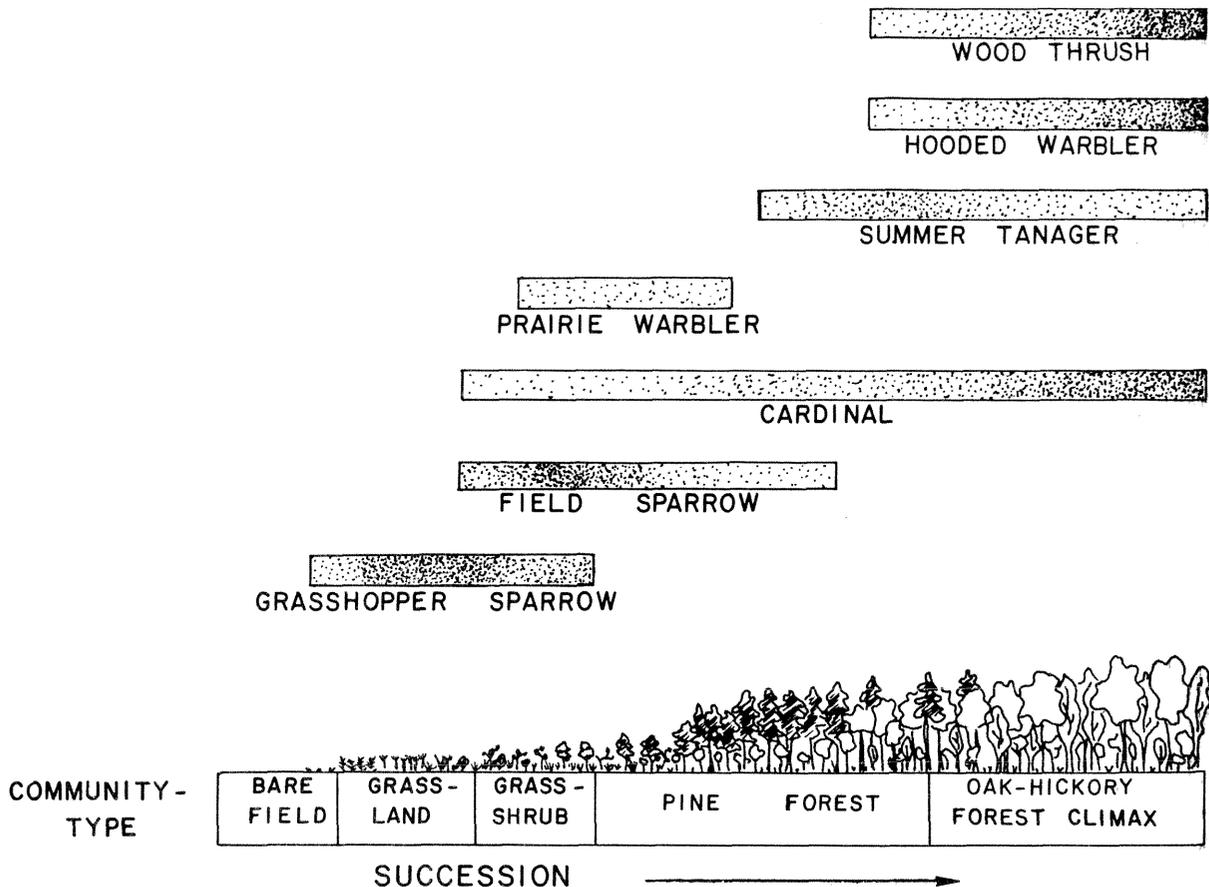
Figure 2.--The relationship between selected bird species and certain stages in old-field community succession. The differential stippling in the occurrence bars for each species indicates relative abundance (based on Johnston and Odum 1956).

height diversity (MacArthur and MacArthur 1961) and percent vegetation cover (Karr 1968, Karr and Roth 1971) do not measure horizontal patchiness of grain of the habitat (MacArthur 1968, Levins 1968). Wiens (1974) has developed a measure of heterogeneity for grasslands using the coefficient of variation, and Roth (1976) has done the same for four bird communities in the brush-grasslands of south Texas. Spatial complexity or habitat heterogeneity must be expressed in vertical and horizontal spaces, and in bird studies vegetational complexity has been measured in terms of (1) relative plant species richness, (2) horizontal foliage heterogeneity, and (3) vertical foliage profile (see Cody 1974, Tomoff 1974, Roth 1976, Pearson 1977).

Multivariate statistical analyses have been undertaken to determine the influence of a number of habitat variables on the distributions and microhabitats of entire avian communities (James 1971, Shugart and Patten 1972, Anderson and Shugart 1974, Shugart et al. 1975), and these studies also indicate that single measures of habitat complexity as predictors of bird species diversity may not be universally applicable. Shugart et al. (1975) have suggested that multivariate analysis can be a powerful tool in identifying the important habitat variables for each species in a community.

MacArthur et al. (1962) concluded that patchiness resulting from addition of layers was more important than the increased opportunity for vertical layering of birds. Karr and Roth (1971) found a sigmoid relationship which indicated that the sharpest increase in avian diversity occurs with the addition of the shrub and early tree layers and that added vegetation beyond that point produced diminishing returns. Willson (1974) also showed that the greatest addition of guilds (see Root 1967) takes place as trees appear. Roth (1976) found that while some new bird species can be absorbed in the additional patches in the transition from grassland to shrub-grassland, others may be vertically

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segregated because of the additional vertical habitat space. He further suggested that an increase in stratal specialists and, consequently, horizontal overlap (see Cody 1974) occurs in the transition from shrubland to forest. Thus, according to Roth, it would appear that increased patchiness helps explain why shrublands have more species than grasslands, and by the same token, decreased patchiness may explain why forests have fewer bird species than some shrublands despite their having more vegetation layers or volume.

Trophic Complexity

Trophic complexity is a function of several factors including among others: (1) the number of trophic levels, (2) the number of species at each level, (3) the abundance of each species, and (4) the foraging strategies of each species. The complexity results from the interactions of the component species of the community, and these interactions can be characterized as being mainly predator-prey (e.g., the diversity of prey eaten) and competitive (e.g., the degree of competition with other species that is tolerated). Menge and Sutherland (1976) have examined predation and competition in relation to trophic complexity and have suggested that competition regulates the number of species in a guild only when the members of that guild actually compete, i.e., when they are near or at carrying capacity. They believe this is usually true at relatively higher trophic levels because of the absence of other controlling factors, e.g., predation. Conversely, they suggested that predation characteristically regulates the number of species present in guilds at relatively lower trophic levels. When they extended this hypothesis to between-community and between-habitat comparisons, they predicted that in communities with few trophic levels, competition will be relatively more important than predation as an overall organizing factor. As the number of trophic levels and the number of species per level increase, predation will become relatively more important as an organizing factor. Menge and Sutherland (1976) further suggested that trophic complexity is related to temporal heterogeneity in that in areas of greater temporal heterogeneity (i.e., a less stable, less predictable, and more stressful environment) there is less trophic complexity with increased competitive exclusion. With regard to the relationship between complexity and stability, May (1976) believes that a predictable (stable) environment may permit a relatively complex and delicate balanced community to exist, while an unpredictable (unstable) environment is more likely to demand a structurally simple, robust community. May (1976) pointed out that as a mathematical

generality increasing complexity makes for dynamical fragility rather than robustness (but see McNaughton 1977).

According to Southwood's (1977) schema (fig. 1), trophic complexity decreases with increased adversity (sensu Whittaker 1975), and this decrease is associated more with an increase in niche width than a decrease in spatial complexity, although the latter does occur. In contrast, on the durational stability axis of Southwood's schema the relative importance of niche breadth and spatial complexity for trophic complexity is reversed.

A new measure of distance from the food source to any member of a food web has been introduced by Kercher and Shugart (1975). The measure is referred to as effective trophic position and is defined as a function of energy ingested per unit time by a population and the production of the autotrophs necessary to maintain that population. Trophic position thus defined is a generalization of the trophic-level concept capable of describing complicated food webs and based on the concept of ecological efficiency. Pimm and Lawton (1977) have recently suggested that the number of trophic levels in a community may be constrained by population dynamics and not by ecological energetics. Cohen (1977) has presented a new technique for using food webs to gain information about the minimum number of dimensions of a niche space necessary to represent, in a specific sense, the overlaps among observed trophic niche, and he concluded that within habitats of limited physical and temporal heterogeneity, the overlaps among niches along their trophic (feeding) dimensions can be represented in a one-dimensional space.

Considerable work has been done on predation and competition in birds in relation to community trophic structure. Some species differ both in food and habitat rather than either separately, and when a group of species exploits the same class of resources in a similar way in a community, the assemblage is called a guild (Root 1967). The spatial and temporal separation of some bird species has been correlated to food specialization and division of food resources (Edington and Edington 1972), and Schoener (1974) has discussed the underlying ways that similar species utilize different resources in their environment. With regard to birds, in considering the important particular dimensions in resource partitioning, habitat dimensions are more important than food-type dimensions, which are in turn more important than temporal dimensions, and as the number of species considered increases, so does the number of important dimensions in resource division.

In a thorough review of prey characteristics and the range of resources used by avian predators, Hespenheide (1975) concluded that bird species can be more closely packed in a community with

respect to food than to foraging behavior, implying that it is easier to adjust behavior (e.g., foraging zone or method) to avoid competition than to change food habits. Consequently, as species are added to the community diets will remain as wide as possible, but foraging zones should contract, resulting in habitat specialists but food generalists. Morse (1971) has provided a detailed review of how and where birds forage for food, and Schoener (1971) has examined theoretically the feeding strategies of birds and other animals with emphasis on the energetic costs of different foraging methods.

Currently, the established role of competition in structuring bird communities (Cody 1974) is being questioned (Connell 1975, Wiens 1977) because of the lack of experimental evidence in support of the idea. Connell (1975) has attempted to review the field evidence (of an experimental nature) in support of the existence of interspecific competition in birds and could find only one study (Davis 1973) indicating that one species excluded another from a particular habitat. However, this type of competitive exclusion has been proposed frequently to "explain" the within- or between-habitat or geographical segregations of certain bird species that show minimal or no overlap in their distributions (e.g., Terborgh and Weske 1975).

Niche Breadth

The concept of niche is closely integrated with spatial and trophic complexity, and it is often difficult to discuss one without making reference to the others. Before discussing the niche concept, a distinction among three aspects of the relationship of a species to environment should be reviewed (see Whittaker et al. 1973). The area of a species is the geographical range, while the habitat of a species is composed of the physical and chemical environment as well as other factors (e.g., elevation, topographic position), or of a kind of community. The niche of a species is the species' position in a community in relation to other species and is defined in terms of space, time, and functional relationships. The current theory of niche, as proposed by Levins (1968) and MacArthur (1968) and recently summarized and further developed by Vandermeer (1972) is based on the original definition of Hutchinson (1957). More recent general discussions of niche can be found in Colwell and Fuentes (1975), Pianka (1976), Whittaker and Levin (1976), and Kroes (1977).

Niche breadth, width, and size are frequently used as synonyms in the literature, and all can be thought of as the sum total of the variety of different resources exploited

by a species (Pianka 1976). In the absence of any competitors or predators, the entire set of resources utilized by the organism is referred to as the fundamental, pre-interactive, precompetitive, or virtual niche (see Vandermeer 1972). Rarely if ever in nature does a species exploit its fundamental niche, but rather its activities are curtailed or modified by other species (its competitors and predators) in the community, resulting in the species' realized, post-interactive, or post-competitive niche (Vandermeer 1972). Consideration of niche breadth necessitates consideration of foraging strategies with regard to specialization and generalization (see Orians 1971, Schoener 1971, Covich 1976, Ellis et al. 1976, Norberg 1977, Pyke et al. 1977, Sih 1977). Measures of niche breadth have been provided by Simpson (1949), Horn (1966), MacArthur and Levins (1967), Colwell and Futuyma (1971), Pielou (1972), Roughgarden (1972), Vandermeer (1972), Pianka (1975), May (1975a), and Slatkin and Lande (1976). In general niche breadth increases as resource availability decreases (Schoener 1971, MacArthur 1972).

Two fundamental components of niche breadth are the "between-phenotype" and the "within-phenotype" components (Roughgarden 1972, 1974). When individuals have little or no overlap in resources used (specialists), the niche breadth of the population has a high between-phenotype component, and in contrast, when individuals exploit the entire range of resources (generalists), the niche breadth of the population has a high within-phenotype component. The subject of niche overlap is yet another central aspect of niche theory (May and MacArthur 1972, Sabbath and Jones 1973, Pianka 1974b, May 1974, McMurtrie 1976, Harner and Whitmore 1977), and as Pianka (1976) has pointed out, this subject has generated a number of concepts (e.g., competitive exclusion, character displacement, limiting similarity, species packing, maximal tolerable niche overlap, and diffuse competition). It should be mentioned, however, that equating niche overlap with competition may be on occasion a questionable practice and is often misleading (Colwell and Futuyma 1971, Connell 1975, Pianka 1976, Wiens 1977). Competitive interactions in communities and their bases have been thoroughly discussed recently by Connell (1975), Pianka (1976), Levine (1976), deJong (1976), and Wiens (1977).

There has been considerable emphasis on niche theory in the work on avian communities. Cody (1968, 1974) has carefully examined niche theory in his work on the role of competition in the structuring of bird communities, and he has given detailed attention to niche breadth and overlap in his treatment. Niche overlap has also been studied in feeding assemblages of birds in New Guinea (Terborgh and Diamond 1970), in the avifaunas of Australian islands (Abbott 1975), in passerine birds in the

British West Indies (Ricklefs and Cox 1977), and in passerines in Swedish coniferous woodlands (Ulfstrand 1977). Alerstam et al. (1974) have studied the niche differentiation during winter in woodland birds in southern Sweden and on the nearby island of Gotland.

Several studies have shown that bird species broaden their niches on islands by changing their vertical foraging distributions, but seldom changing their foraging behavior (Crowell 1962, Diamond 1970, Yeaton and Cody 1974, Diamond and Marshall 1977). The origin of differences in community structure, such as those between different islands of the same archipelago, between different localities on the same island, between different adjacent habitats, and between different biogeographical regions have been reviewed by Diamond (1975). His hypothesis is that through diffuse competition, the component species of a community are selected and coadjusted in their niches and abundances so as to fit with each other and to resist invaders. The relationship between niche breadth and the amount of morphological variation within and between species has been examined by a number of investigators (Grant 1968, 1971; Willson 1969; McNaughton and Wolf 1970; Keast 1972; Rothstein 1973; Hespenheide 1975; Karr and James 1975; Willson et al. 1975), and although the results suggest that competitive displacement may be a particularly important determinant of avian community structure, such comparisons may provide results that are misleading (Wilson 1975).

Hespenheide (1975) has examined resource characteristics and consumer niche width in birds and has concluded that coexistence depends on maintaining minimum differences between species and, for strategic reasons, space and behavior are more easily divided than food directly in competitive situations. The data for foliage-gleaning species and for birds in general support this conclusion.

Standing Crop and Turnover Rate

Both standing crop (biomass) and turnover rate (productivity divided by biomass) vary during succession and as a result of the adversity of the environment (see fig. 1). Standing crop and productivity increase throughout successional stages, providing for increased spatial complexity (Whittaker 1975), but productivity frequently, but not invariably, falls in terrestrial communities as the climax is reached (Margalef 1969) so that turnover rate invariably falls (Watt 1971). Holt and Woodwell (in Whittaker 1975: 175) have examined secondary succession in the oak-pine forests of Long Island, New

York, and have found in the first year of succession, net productivity is low and increases to a fairly stable level in the meadow stage. Through the shrub and young tree stage, net productivity increases more steeply in the young oak-pine forest, at 45 to 55 years, and this level stabilizes and persists in the mature forest. The growth of the forest can also be expressed by the biomass accumulation ratio (the ratio of biomass to annual net productivity), and these ratios increase from about 1.0 in the annual stage, to 2-4 in the meadow stage, to 4-7 in the shrub stage, to 10 in the 55-year forest and probably 25-35 in the mature forest (Holt and Woodwell in Whittaker 1975:175).

Connell and Orias (1964) have suggested that greater plant productivity during succession should support greater diversity, everything else being equal. Productivity of the community should be positively correlated with the closeness of species packing (MacArthur 1971). Although rigorous data are scarce, there is nonetheless some evidence in support of this idea. Bird censuses in small areas of 4-6 hectares of nearly uniform habitat show that the number of species generally increases with the productivity of the habitat. If one compares the mean net primary productivity per unit area (dry $g/m^2/yr$) of Whittaker (1975:226) with measurements of species diversity (Tramer 1969) in nine types of communities, a pattern emerges that suggests that the more productive forest communities have the higher number of species (Table 2). Cody (1974:127) has also shown that the number of bird species and species diversity are, in part, correlated with community productivity.

Glutz von Holtzheim (1962), working in Switzerland on bird communities, suggested that greater production in a forest habitat allows it to support denser populations. Karr (1975) has also suggested that differences in productivity may be important in determining the number of individuals (not the number of species) that can breed in an area (but see Cody 1974:127-128). Several studies have examined changes in bird standing crop during succession and in different communities. Karr (1971) found a general increase in bird standing crop and existence energy as the ecological age of abandoned strip mine areas in Illinois increased. Similar findings have been reported by Sturges et al. (1974) and Shugart et al. (1975). In these studies there is general agreement that bird biomass and bird density increase in older communities, but when bird biomass is plotted on bird density, the slopes of the lines are often different (see Wiens 1975:238). Shugart et al. (1975) found that the general patterns of bird standing crop in the successional communities studied by Shugart and James (1973) was the same as the pattern of bird density, indicating that the average size of breeding birds did not fluctuate

Table 2.--Net Primary Production (Annual Basis) of Several Communities and Bird Species and Diversity*

Community Type	H'	S	Net primary productivity per unit area $(g/m^2/yr)$†
Marshes	1.79±0.34	6.33±1.32	2000
Grasslands	1.93±0.24	5.74±1.00	600
Shrublands	3.14±0.16	14.08±2.31	700
Deserts	3.25±0.60	14.17±5.68	90
Coniferous forests	3.53±0.14	17.43±1.92	1300
Upland deciduous forests	3.82±0.08	20.94±1.34	1200
Mixed forests	3.92±0.14	21.87±2.76	1200
Floodplain deciduous forests	4.07±0.16	24.22±2.84	2000
Tropical woodlands	5.23±0.24	55.14±11.24	2200

*Productivity information after Whittaker and Likens in Lieth and Whittaker, 1975:224; bird information after Tramer, 1969.
†Units are dry grams of organic matter per meter square.

widely through the successional sequence. However, they did note that in ecotonal stages the size of birds tended to be larger on the average, and in the mature forests the mean size appeared to be somewhat smaller. Wiens (1975), in comparing different coniferous forest communities of North America, found trends in total biomass of birds similar to densities of birds, although the magnitude of fluctuation in biomass was more variable. In all coniferous forest types biomass increase occurs at different rates. The rate of increase is most rapid in northeastern coniferous forests and Sierra Nevada avifaunas and markedly less steep in northwestern, northern, and southeastern coniferous forests. This indicates that the increase in density in these latter regions is through the addition of relatively small-sized individuals to the avifauna, while comparable incremental increases in avian density in northeastern and Sierra Nevada forests involve the addition of individuals of larger mean size (Wiens 1975). Moreover, in northeastern coniferous forests, immature stands, supporting the same number of individuals as comparable mature forest stands, contain more avian biomass; hence the mean size of individual birds is greater in the immature stands. McNaughton and Wolf (1973:346-348) have done a similar analysis on the data of Johnston and Odum (1956), and the results are in agreement with the notion that during successional changes in the avifauna of a community, early stages support fewer species and individuals and less avian biomass than older stages, and the species tend on the average to be larger and ecologically more dominant. Consequently, during succession the birds that invade tend to be smaller on the average than the species they replace. Breeding bird density

and bird standing crop in coniferous forests and in grassland habitats when compared show some comparable results (Wiens 1975, Wiens and Dyer 1975).

While standing crop of breeding birds in coniferous forests average 2 to 3 times that in grasslands, energy flow is nearly 10 times as great in the coniferous forest. This probably reflects the greater degree of dominance of extremely small species (forms which have relatively high energy demands per unit of body weight) in comparison to the larger species common in grasslands (Wiens 1975). Faaborg (1977) has examined the occurrence of nonpasserines in terrestrial avian communities with an emphasis on metabolic rates, activity levels, and resource availability. He concluded that the metabolically more conservative nonpasserines can support larger populations on a given amount of rare resource and expend less energy looking for these rarer resources. The differential occurrence of such resources in the tropics and in temperate areas probably explains why more nonpasserines occur in the tropics than in temperate communities.

Wiens (1975) and Wiens and Nussbaum (1975) have reported that the avifaunas of coniferous forests in North America during the breeding season from 1 April to 7 October have an energy demand ranging from 10.7 $kcal/m^2/season$ in the dry, hot forests to 20.8 $kcal/m^2/season$ in moist, transitional forests. These figures generated by simulation models are in general agreement with the calculated energy demand of 11.3 $kcal/m^2/year$ by the avifauna of an oak-hornbeam forest in southern Poland (Weiner and Glowacinski 1975). In the latter study, the authors pointed out that approximately 50% of the annual energy demand occurs during the breeding season.

Salt (1957) proposed that the ratio of consuming biomass to standing crop biomass of a community (CB/SCB) may be a measure of efficiency in food utilization in avian communities, because communities dominated by large species that require less energy per gram of body weight exhibit a greater discrepancy between consuming and standing crop biomass. A number of authors have concluded that there is an increase in community energetic efficiency (measured by the CB/SCB ratio) as succession proceeds towards the climax (Salt 1957, Karr 1968, Kilgore 1971, Wiens 1975), but McNaughton and Wolf (1973: 348) have noted that avian production efficiencies decline as succession proceeds in abandoned agricultural fields in the southeastern United States. Ecological efficiencies relating a trophic level to the preceding level tend to increase up the pyramid of productivity, but net growth efficiencies usually decrease, because the percentage of food energy respired tends to rise along food chains. Consequently, net of production efficiencies need not increase up the pyramid; they may in fact decline (Whittaker 1975:217).

The ratio of net productivity to biomass (P/B) or turnover rate decreases from grasslands to forest communities. Thus the time it takes to replace the peak biomass completely at a given successional stage increases as succession progresses. How do bird communities respond to the different turnover rates of vegetation during succession? Shugart and Hett (1973) found that the bird species composition of a community changed more rapidly than the plant species composition although the pattern of change was the same between plants and birds. Glowacinski and Jarvinen (1975) examined the turnover rate during secondary succession in forest bird communities in oak-hornbeam forest in Poland and in Finnish coniferous of spruce and pine. They found that the shrub phase is characterized by rapid changes in the bird community and its rate of change, while the forest proper has a slowly changing avian community and the rate of turnover changes relatively slowly.

Species Diversity and Abundance

The simplest community attributes that can be measured are the number and relative abundances of species in an area. It is not practical to study all the species of a given community, so that most workers have concentrated on a portion of a community or taxocene (e.g., birds, lizards, trees, ants). The term "taxocene" (Hutchinson 1967) means all the members of any taxonomic group of a higher level than a species. The emphasis

on species composition and abundance in communities during the last half century has resulted in a great number of measurements of species diversity for various communities (Williams 1964). These quantitative indices show the relation between community structure not only in number of species but also in the relative number of individuals of each species. There are a number of different indices of species diversity, and each varies in what it shows (e.g., Williams 1964; Lloyd and Ghelardi 1964; Pielou 1966, 1975; Dickman 1968; Lloyd, Zar, and Karr 1968; Hurlbert 1971; Whittaker 1972; DeBenedictis 1973; Peet 1974; Hair 1978).

The Shannon-Wiener function and the Simpson index are two of the most commonly used measures of species diversity. Ideally the Shannon-Wiener measure should be used only on random samples drawn from a large community in which the total number of species is known. The Shannon-Wiener measure combines two components of diversity: (1) number of species and (2) equitability or evenness of allotment of individuals among the species. In Simpson's index, relatively little weight is given to the common species. Recently the utility of diversity indices has been questioned in ecological studies (Peet 1975). The measures of species abundance and diversity have been reviewed analytically by May (1975b), and May (1976:158) has recently argued for describing the community by its full distribution of species relative abundance, and not trying to condense information into a single diversity index which may mislead and may obscure valuable information on the few uncommon species in the community.

It is important to distinguish between species diversity measurements in a single natural community and in a large heterogeneous region. Whittaker (1960) has defined three categories of species diversity patterns: (1) alpha diversity--the diversity in a sample drawn from a single community, often referred to as within-habitat diversity; (2) beta diversity--the diversity that expresses the rate of species turnover between habitats, sometimes called between-habitat diversity; and (3) gamma diversity--the total diversity found in all the available habitats in a fairly large geographical area. Additional considerations of these categories can be found in Whittaker (1972), Allan (1975), Tramer (1974a), and Pielou (1975).

Diversity Gradients

One of the most conspicuous aspects of the geographical patterns of bird species distribution is the gradient in numbers of breeding bird species from the poles to the equator (Dobzhansky 1950, MacArthur 1972:199, Welty 1975:413). More bird species occur in

Figure 3 data (numbers of land bird species breeding in quadrants):

```
                26
50  64  49  26
58  68  80  69  48  18
    92  89  81  38  19  17        16
    95 111 105  88  49        31  38   43
    81 128 142 119 100  61  45  48  71  67  68
   118 154 142 136 142 129 125 124 123 122
   150 146 148 139 129 142 136 141 129
   159 136 147 157 119 121 116 133
   140 162 176 134 109 110 109 120
       140 186 143 122  93  91  93
       110 213 190 153          72
               270 289 196
           192 295 412  ca.300
                    ca.500  ca.500
                            ca.600
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Figure 3.--The numbers of land bird species breeding in quadrants of 500 km per side in different parts of North and Central America (after MacArthur 1969 and MacArthur and Wilson 1967).

Figure 4 data (numbers of land bird species wintering in quadrants):

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                 9
24  26  21  15
32  34  31  22  15   7
    46  28  21  13   8   7           7
    50  39  27  17  10          12  16  15
    98  77  46  37  32  26  20  26  36  34  34
   101  98  67  47  46  43  42  46  47  51
   111  98  77  58  53  65  66  75  80
   138 110 101  75  67  86  88  90
   146 170 135  96  96  96  92 103
   189 186 148 134 114 105 109
       161 280 253 311         112
           333 348 371     258
           259 380 486  ca.375
                    ca.575  ca.555
                            ca.660
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Figure 4.--The numbers of land bird species wintering in quadrants of 500 km per side in different parts of North and Central America (after Tramer 1974a).

tropical communities than in temperate and arctic communities, and this pattern is found in most other terrestrial taxa of large enough size (Klopfer and MacArthur 1960, 1961; MacArthur and MacArthur 1961; MacArthur et al. 1966; MacArthur 1969; Orians 1969; Karr 1971; Karr and Roth 1971; Schoener 1971). The numbers of breeding land bird species in different geographical sectors and communities of North America have been computed (MacArthur 1965, 1969, 1972; MacArthur and Wilson 1967; Cook 1969; Tramer 1969, 1974a; Peterson 1975), and as Tramer (1974a) shows, during the breeding season the alpha diversity for bird species does not change significantly from 45°N to 25°N, but from 25°N southward, alpha diversity increases as one moves toward the equator. Gamma diversity of breeding birds, on the other hand, differs in both eastern and western North America. In the East, gamma diversity decreases from 45°N southward to southern Florida and the northern coast of the Gulf of Mexico. In the West, gamma diversity increases all the way to the equator (fig. 3). As can be seen in figure 4, during the winter the numbers of land bird species in different communities and regions of North America have also been

examined (Bock and Lepthien 1974; Tramer 1974a, 1974b), and in winter both the alpha diversity and gamma diversity of bird species increase southward (Tramer 1974a).

Tropical mountain-top communities have fewer bird species than would be expected on the basis of geographical latitude (Orians 1969, Kikkawa and Williams 1971, Diamond 1973), and although these communities have mean annual temperatures and short heights of trees more typical of temperate zones, there is no winter. Even though fewer species occur in mountain communities at higher altitudes, Terborgh (1971) has pointed out that in Peru an altitudinal transect showed more forest bird species than the entire eastern United States.

Certain communities have a higher avian species diversity than others (e.g., Margalef 1963, 1968; Recher 1969; Tramer 1969; Karr and Roth 1971; Cody 1974; Rov 1975; Reese 1976), and bird species diversity usually increases during succession (e.g., Kricher 1973, Shugart and James 1973, Hamilton and Noble 1975). What are the factors responsible for higher species diversities in communities as one moves toward the equator, and why do certain communities have higher species diversity indices than others?
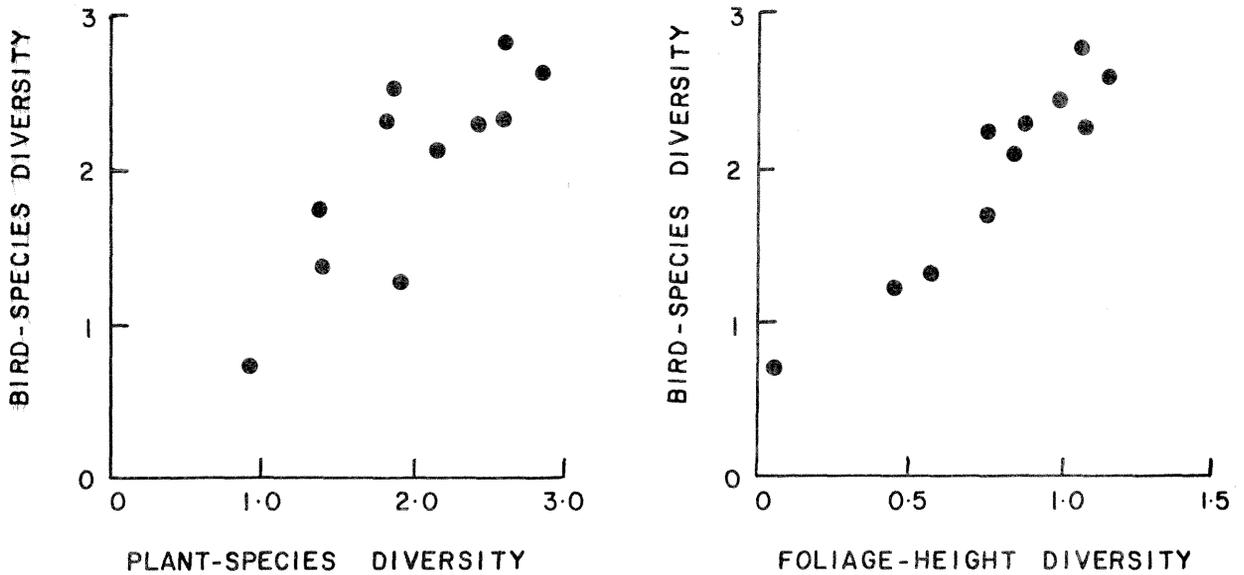
Figure 5.--Bird species diversity in deciduous forest plots of eastern United States in relation to (A) plant species diversity and (B) vegetative structure (after MacArthur and MacArthur 1961).

Determinants and Correlates of Diversity

In an effort to determine what factors account for species diversity in selected forest types, MacArthur and MacArthur (1961) found that from the layering of the vegetation alone they could predict the number of breeding bird species in temperate deciduous forests and that further knowledge of the number of plant species did not improve the understanding (fig. 5A and 5B). They concluded that height profile of foliage density in the layers 0-2 feet, 2-25 feet, and greater than 25 feet is important in determining bird species diversity, and they felt that these three layers correspond to different configurations of foliage--herbs, shrubs, and trees over 25 feet tall--in five acres of habitat (see MacArthur and Horn 1969). The height profile of foliage density is in fact a major component of the floristic community that allows birds to specialize on a particular part of the habitat (MacArthur 1964, Karr and Roth 1971, Cody 1975, Roth 1976).

That birds restrict their activities to different levels within a forest is well known. Even though birds are highly motile they are nonetheless characteristic inhabitants of a particular forest stratum, or even a particular level within a given stratum. Colquhoun and Morley (1943) in a paper on the relative stratal abundance of 12 species of birds in Bagley Wood in

England found that the majority of species utilized several strata with a particular stratum of abundance for each kind of bird. In an almost pure stand of Quercus robur, they identified five strata utilized by the birds: (1) upper canopy (above 35 feet), (2) tree (15 to 35 feet), (3) shrub (4 to 15 feet), (4) herb (3 inches to 4 feet), and (5) ground. Similarly, Kendeigh (1945) found breeding warblers generally stratified (or even substratified) in a sugar maple-beech-hemlock forest near Albany, New York, and concluded that diversification in niche requirements reduced interspecific competition and permitted a greater and more varied population to inhabit an area. Gibb (1954) studied coexistence in the Parids of Britain and demonstrated that different species fed in different strata when several occurred together in the same habitat. In structurally simpler habitats than forests (e.g., grasslands, fields, and marshes), the opportunities for within-habitat segregation are less, and there are fewer bird species per unit area (Cody 1968, Wiens 1969). Cody (1974:29) pointed out that in habitats taller than 3 feet vertical stratification is the single most important factor in the segregation of species' feeding activities.

Orians (1969) found that the number of bird species in Costa Rica was not correlated with the number of tree species but was closely associated with foliage height diversity. The same is true for the southeastern

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portion of Australia near Sydney (Recher 1969). In Puerto Rico, MacArthur et al. (1966) found vertical foraging ranges expanded, and species diversity was predictable when only two layers of vegetational height profiles were considered. Similarly, the vertical foraging range of birds was found to be expanded on species-poor islands in Panama Bay in comparison to mainland Panama (MacArthur et al. 1972). Karr (1971) likewise found that vertical foraging ranges in Illinois were more expanded in comparison to Panama, thus documenting the narrower vertical foraging ranges of tropical species. Pronounced vertical stratification has also been found in a dry forest in Peru, and moreover the vertical foraging ranges of many of the species shift as a function of time of day (Pearson 1971).

Although the number of species and their abundance can be predicted accurately on the basis of height profiles of foliage density, MacArthur (1964) failed to predict just what bird species would be present in the complex habitats on the slopes of the Chiricahua Mountains of southeastern Arizona. Additional findings do not support MacArthur's foliage profile hypothesis. Balda (1969) failed to find a significant correlation between bird species diversity and foliage profiles in ponderosa pine and oak-juniper forests in Arizona. Although juniper was the most abundant tree in the oak-juniper forests and had a good fit for bird use according to the height distribution of the foliage, juniper was sparsely used by the birds. Instead the birds used the two species of oak more heavily, and all parts of a tree were used by the several bird species. Total bird use of Douglas fir foliage by height class was not correlated because there was a large proportion of low foliage that was underused while the upper heights were overused. Consequently, the very few tall Douglas firs in the area were used greatly out of proportion to their availability. Marshall (1957) has earlier reported similar findings in his studies of bird utilization of pine-oak habitat in Arizona. In the latter two cases the birds were probably showing within-habitat segregation (e.g., (a) different parts of trees or bushes, (b) different species of plants, or (c) different sections of the habitat characterized by overall differences in vegetation structure) (Cody 1974:23).

Tomoff (1974) related bird species diversity to some measures of vegetative complexity (plant densities, foliage height diversity, and physiognomic coverage diversity) and found that the physiognomic coverage diversity (life forms divided into categories) was significantly correlated with bird species

diversity. Tomoff (1974) concluded that plant species diversity may be highly important to desert breeding birds because each plant species may have peculiar properties which are needed by the birds for breeding. Additional shortcomings of using only foliage height diversity to predict bird species diversity can be found in Balda (1975), Reese (1976), Roth (1976), and Pearson (1977).

Temporal Aspects

Most studies of bird species diversity in various communities have concentrated on breeding birds, and the seasonal aspects of avian diversity in the community have been largely ignored. Stewart et al. (1952) found that the composition of the avifauna changed throughout the year in Maryland with the greatest number of species occurring in the spring and the greatest number of individuals occurring in the fall. Kricher (1972) and Holmes and Sturges (1975), working in the New Jersey piedmont and in New Hampshire, respectively, noted that bird species diversity decreased from summer to winter as a result of fall migration. Dickson (1974) found that species diversity in a bottomland woods in Louisiana increased from summer to winter, indicating that there were more overwintering migrants in the area than breeding migrants. Cody (1974:154), working in the Santa Monica Mountains in southern California, and Reese (1976), working in the piedmont of South Carolina, found that bird species diversity increased from summer to winter in certain habitats but remained the same or decreased slightly in other habitats. These results based largely on alpha diversity measurements are in general agreement with the summer and winter gamma diversity measurements of Tramer (1974a). Clearly, considerably more work is needed on the seasonal dynamics of avian community ecology if we are to gain a better understanding of how avian communities are structured and organized.

EPILOGUE

In this presentation I have attempted to present an up-to-date overview of avian community ecology. My overview is fairly representative but not exhaustive. Ecology as a whole and avian ecology specifically is in the process of undergoing major revisions and reassessments (see Foin and Jain 1977). A few years ago complexity of the community was thought to impart stability to the community, but rather recently we have increasingly appreciated that stability (e.g., climatic stability) is a requisite for community complexity, and when stability is not present complexity cannot be achieved. Less complex communities cope better

with adverse and unpredictable environments. Goodman (1975) has recently critically reviewed the diversity-stability relationships in ecology and concluded that there is no simple relationship between the two. Competition has long been the cornerstone of niche theory, but lately some serious doubts have emerged regarding the role of competition in shaping diverse communities, and predation is being examined more closely. Likewise, many avian ecologists have been content with accepting foliage height diversity as the best predictor of bird species diversity, but several relatively recent studies have cautioned that foliage height diversity must be considered but one of many "dimensions" and factors dictating bird species diversity; bird behavior and climatic factors are receiving more attention. Avian communities show seasonally rhythmic changes, but there has been little appreciation for this fact as the preponderance of breeding season studies attests. We have much to learn of the energetic efficiencies of the avifauna in a community throughout the year and from year to year during succession. In depth experimental (manipulative) field studies of avian communities are needed if we are to make meaningful statements about man's influence on bird communities. We do have some knowledge of the structure and function of avian communities, but clearly much, much more remains to be done. Theory abounds and is very much in vogue, but carefully detailed empirical findings are needed most.

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Tuesday Afternoon, January 24

Effects of Management Practices on Nongame Birds

Moderator: Fred Kinard
            Westvaco Corporation

Effects of Management Practices on Nongame Bird Habitat in Longleaf-Slash Pine Forests

Gene W. Wood and Lawrence J. Niles[1]

Abstract.--Increase in numbers of habitat niches that de-
velop with increasing stand complexity is important to raising
the species richness and abundance of non-game birds in longleaf
and slash pine forests. Some silvicultural practices decrease
complexity while others increase it. Practices which lead to
eradication of the understory, destruction of dead trees and
generally promote monoculture appear to be deleterious to non-
game bird populations.

INTRODUCTION

The approach of this paper will be large-
ly a theoretical discussion of the response of
non-game bird populations to habitat changes
caused by silvicultural practices in longleaf
(Pinus palustris) and slash pine (P. elliottii)
forests. Non-game birds will be discussed
collectively with very little emphasis placed
on individual species. This is necessitated
by the dearth of published literature on non-
game bird response to silvicultural practices
in the southern pine forests.

LONGLEAF-SLASH PINE TYPE

Longleaf pine occurs naturally in por-
tions of 9 southeastern states in a climatic
zone characterized by long, hot summers and
mild winters. The main longleaf pine belt is
found on the Atlantic and Gulf Coastal Plain,
though it extends into the Piedmont and Appa-
lachian borders. Soils are characteristically
sandy in texture, low in organic matter, have
good to excessive drainage, and are low in
fertility. (USDA 1965:384-385)

Slash pine, in general, can be grown
wherever longleaf grows although its natural
range is considerably more restricted. The
natural range extends from southern South
Carolina to central Florida and southeastern
Louisiana although it has been planted as far
north as North Carolina and west to East

Texas. Soils are typically sandy and range in
drainage from well drained to poorly drained.
The wet soils of pond margins are most produc-
tive. (USDA 1965:458-459)

There are 18.3 million acres of land in
the longleaf-slash pine type. Five percent of
this land is in natural forest and five per-
cent in other public holdings. The forest in-
dustry owns 33 percent of the longleaf-slash
pine type with 57 percent in other private
holdings. (USDA 1973:304-305)

Within the geographical range of the long-
leaf-slash pine type there are 68 species of
birds that are year round residents, 40 of
which are associated with pine forest habitat.
There are 106 summer residents and 112 winter
residents of which 49 and 54 respectively are
associated with pine habitat. (Bent 1937,
1938, 1939, 1940, 1942, 1946, 1948, 1949,
1950, 1953, 1968; Robbins et al. 1966, Har-
rison 1975, Bull and Farrand 1977)

PRINCIPLES

The influence of silvicultural practices
on wildlife is based on the principles of the
relationships of plant community complexity
and productivity to habitat niche variety and
carrying capacity. The habitat niche is the
assimilation of environmental components nec-
essary for a species to maintain and sustain
life. The habitat is a more inclusive term
and refers to the general environment and
plant associations within which a species is
found. In this paper the habitat is the
longleaf-slash pine forest type. In prin-
ciple, habitat niche variety is directly re-
lated to habitat complexity and is the deter-

minant of the variety of animal species that can be accommodated. Simple plant communities, such as an even-aged monoculture, will not support as large a number of bird species as a more heterogenous community. The habitat niches simply are not there. In the forest, a tract of land with a wide variety of stand conditions can be depended upon to provide the habitat niches for a wide variety of bird species. Similarly, within a given forest stand vertical structure complexity will determine habitat niche availability with the most structurally complex supporting the widest array of bird species.

Carrying capacity is the number of individuals of a species that can be accommodated in a given habitat niche. In general, in natural communities, the size of the array of niches and their respective carrying capacities are expressions of site productivity potential. The potentially most productive sites in terms of dry matter productivity will usually support the most structurally complex and species rich communities. In addition to the wide variety of bird species that can be supported, relatively large numbers of individuals within these species will occur in these communities. This phenomenon in forest communities can be changed by silvicultural procedures. The implementation of procedures that channel nutrients, water, and energy into single plant species tend to greatly reduce natural complexity. This decreases the size of the array of niches and consequently species diversity, an expression of numbers of species and individuals within species, of non-game birds.

Data that support these principles with respect to non-game bird populations have been published by Saunders (1936), Kendeigh (1948), Odum (1950), Johnston and Odum (1956), Bond (1957), MacArthur and MacArthur (1961), MacArthur et al. (1962), Karr (1968), Davis and Savidge (1971), Shugart and James (1973), Kritcher (1973), and Roth (1976).

COMPLEXITY WITHIN AND AMONG STANDS

As previously stated a wide variety of habitat niches may be available in a forest that has a wide variety of stand conditions, i.e., successional stages and compositions of species. The complexity or heterogeneity in this area is referred to as beta-diversity. The forest manager's ability to create a forest mosaic that will support a species rich and diverse non-game bird population will depend on his ability to govern stand size, stand structure, and juxtaposition of stands.

The primary unit that the forester deals with is the stand, which is itself a plant community. The silvicultural treatments applied to the stand will determine its individual complexity or heterogeneity or alpha diversity. In addition, the natural changes in stand complexity concurrent with natural development are important to recognize in order to know what portions of the forest are providing the habitat niches and various levels of carrying capacity for given birds. For these reasons this paper will be confined to the influence of silvicultural treatments on stand complexity as it relates to raising and lowering the number of habitat niches.

REGENERATION CUTTING

The time of the final harvest of longleaf and slash pine stands is also the time of the beginning of the new stand. Three general methods of harvest may be used in these timber types and the method used will determine the nature of non-game bird habitat. The methods are seedtree, shelterwood, and clearcutting followed by planting. Each of these methods is preceded by prescribed burning for seedbed preparation. At this point there are two habitat parameters in which changes wrought by the silvicultural treatment will be reflected in bird response. These are the conditions of the understory and the existence of dead trees left standing.

Generally, seedtree and shelterwood cutting will lower the carrying capacity for overstory species but may raise it for understory birds. In these methods, prescribed burning will usually be carried out in the fall of good seed years and followed by logging. While much of the aerial portion of the understory may be killed by the fire most of the woody stems will remain standing. Enhancement of the non-game bird population may stem from several causes. First the destruction of the litter layer exposes quantities of seed that normally would have gone undetected by birds foraging in the winter habitat. Flocks of wintering sparrows, Robbins and Dark-eyed Juncos will frequently be seen taking advantage of this forage resource. In addition, where the woody understory is sparse, small mammals will be made more vulnerable to birds of prey. Sharp-shinned, Sparrow, Red-tailed, Coopers and Red-shouldered hawks may be seen hunting on recent burns. Second, the stand understory will make significant recovery in the first growing season following treatment. Many of the hardwood seedlings, shrubs and perennial herbs will resprout the following spring. Spring

nesting cover will in large part be missing, but foraging opportunities should be relatively abundant by mid-growing season.

Seedtree and shelterwood methods have minimum adverse impact on the bird population. The degree of impact will depend upon the amount of residual overstory left standing and the length of time before the residual is removed. Because of the heavier seed of longleaf, more residuals are required to insure adequate distribution of seedlings than is the case in slash. Walker (1962) recommended 10 to 12 seedtrees per acre to be left in a seedtree cut for longleaf or alternately 40 trees per acre in a modified shelterwood with residuals being removed in about two years. Croker and Boyer (1975) recommended 30 sq. ft. of basal area be left of seedbearers in a longleaf shelterwood. In this interim period from time of the regeneration cut to the time of the removal of the residuals the habitat is generally productive following either method but mostly for the shelterwood. Bennett (1965) recommended 4 to 6 seedtrees per acre in seedtree cuts and a basal area of 20 to 30 square feet in a shelterwood for slash pine with residuals being removed about one year after regeneration establishment. The existence of a broken overstory and a developing understory of seedlings, shrubs, and herbs is a complex habitat and one which has considerable niche diversity. Carrying capacity for overstory bird species will be governed by the heaviness of the cut while carrying capacity for understory bird species will be regulated by the vegetation response which in turn will be regulated by nutrient and moisture availability. Pine Warblers will be abundant in these stands in all seasons of the year. Once the understory develops Yellowthroats will also be common. Spring and summer birds may include Summer Tanager, Great-crested Flycatcher, Prairie Warbler, and Blue Grosbeak.

Clearcutting followed by intensive site preparation and planting has the most dramatic impact of the harvest and regeneration techniques on forest bird habitat. It is a technique employed in slash pine where the stand will be managed on a short rotation usually not exceeding 35 years. It may be employed in longleaf stands on very productive sites in the heart of the longleaf range along the Gulf Coast from Louisiana to western Florida.

This procedure essentially eliminates bird habitat for a short period of time. The overstory is completely removed in the harvest and the remaining vegetation destroyed during site preparation. Chopping, disking, burning, and bulldozing slashings, stumps and roots into windrows leaves essentially a bare soil surface with little forage and no protective cover. The community is in its simplest structure and niche diversity and space are at a minimum. The windrows created ameliorate the situation to some extent. They will contain some cover for shelter and escape. In addition, since the soil in the windrows is almost entirely top soil and contains large quantities of seed, dense vegetation will develop in the first growing season after treatment and offer both foraging and escape cover.

Clearcutting with natural regeneration has a much less destructive effect. In this case prescribed fire is used to prepare the seedbed before harvesting. After seedfall, the stand is harvested and seed germination occurs shortly thereafter. In this treatment there is drastic impact on birds that include the overstory as part of their niche but understory species may be enhanced.

STAND DEVELOPMENT

Johnson et al. (1974) recognized 5 stages of development of young southern pine stands that might be reflected in non-game bird population response. These were: (1) the devegetated area produced by site preparation, (2) seedling stage, (3) sapling or brush stage, (4) crown closure to an age of about 15 years, and (5) 15 years to the end of the rotation. Length of time in each of these stages will of course be affected by site conditions, method of planting, species treatments such as fertilization, precommercial thinning, and prescribed burning.

As previously pointed out, the site preparation stage has minimum capacity to support bird populations, but in the seedling stage the habitat begins to recover. Stransky et al. (1976) reported that a loblolly pine regeneration area that had been chopped and burned was rich in species of seed producing grasses, composites, legumes, vines and shrubs at the end of the first growing season following treatment. This same type of response could be expected on slash pine regeneration sites where the soils are moderately well drained. Longleaf regeneration sites are typically drier and the vegetation response will usually be less rapid.

The nature of the habitat in the seedling stage will be determined to some extent by the method of regeneration. In addition the stocking rates will influence the length of time until crown closure and the severity of competition with herbs, shrubs, vines and hardwood seedlings which add to habitat complexity. Under favorable conditions dense stands of regeneration can be established by clearcutting, seedtree, shelterwood and direct seeding methods. The removal of overstory residuals in the seedtree and shelterwood method will thin these stands to some extent by mechanical damage incurred during logging and provide growing space for plants other than pines. In these stands being naturally regenerated usually only prescribed burning will have been done for site preparation and the mix of herbs, shrubs and hardwood seedlings with the pine seedlings will create a substantially complex habitat. In direct seeding, however, the site will usually have been devegetated and the seedbed prepared by drastic disturbance. In this situation, particularly where seedling establishment is highly successful, the habitat will rapidly approach the minimum complexity of a monoculture.

Natural regeneration and direct seeding are more common in longleaf pine than in slash. Slash pine is most frequently regenerated by planting. Again the rate of seedling stocking will be important particularly for determining the character of the sapling or brush stage. The U. S. Forest Service Wildlife Habitat Management Handbook for the Southern Region (USDA 1971) recommends planting on a 10 ft. x 10 ft. or 10 ft. x 12 ft. spacing to encourage understory development. Hawley (1965) presented data showing that basal area in slash pine planted on a 6 ft. x 6 ft. spacing at age 9 years exceeded the 10 ft. x 10 ft. spacing by a factor of 1.6. This would be quite an expensive trade-off in timber value for bird habitat. Possibly more reasonable initial spacing might be 6 ft. x 8 ft. or 5 ft. x 10 ft. where Hawley (op. cit.) reported basal areas to be 93 percent and 83 percent respectively of the 6 ft. x 6 ft. spacing and still provide space for understory development.

The early seedling stage in both longleaf and slash pine may provide important habitat for grassland users especially on site prepared areas. Within the range of these timber types, summer use will probably be minimal. Summer temperatures on these areas are extremely high and the vegetative cover that can serve as shelter is largely missing. Some migrants and winter flocks of sparrows and juncos will use these sites heavily, however.

The length of time that the stand will be in the seedling stage will differ greatly between longleaf and slash. Slash pine may be in the sapling stage in 3 to 4 years and the stand may close by 5 to 6 years of age. Longleaf on the other hand may remain in the seedling stage up to 10 years depending upon the severity of brown spot needle blight. During this time the stand may be repeatedly prescribed burned on a 3-year schedule, the impact of which will be to maintain the stand in an "old field" type of succession. Grassland and shrub vegetation users will be accommodated in this situation.

Fire cannot be used in the seedling or sapling stage of slash pine development until the trees are 10 to 15 feet high (Cooper 1965). Neither can it be used in longleaf pine after leader growth begins until the stems are at least 10 feet high. The absence of fire in the habitat hastens the change from a primarily herbaceous community to a primarily woody plant system which largely eliminates niche space for grassland users. During the sapling stage however when the shrub and hardwood seedling component of the habitat is building and prior to crown closure by the pines, the community is quite complex and will provide for a large population of non-game birds. In short rotation systems, the bird niche diversity and niche space is at the highest point that will occur in the life of the stand in intensive management situations. The duration of this high carrying capacity situation is probably no more than 3 years in slash pine on moist sites where understory development is rapid although it is offset by rapid crown closure. In longleaf stands it may last for 6 to 8 years or more due to the growth habit of longleaf where branching is not heavy and although the saplings are putting on considerable height growth there remains a great deal of growing space for shrubs and hardwoods. The best longleaf sites will support a considerably complex habitat in this stage but on drier areas shrub and hardwood growth will be slow and herbaceous plants will make up a considerable portion of the vegetation.

Closing of the stand is accompanied by a drastic decrease in bird niche diversity and carrying capacity. The plant community approaches the pure monoculture where habitat complexity is minimum. During this stage most of the bird activity will occur along the edges of the stand. Brown Thrashers, thrushes and Towhees will frequent these stands but the non-game bird species diversity will be considerably lower than in the previous stage. The change will usually be more dramatic in slash pine than in longleaf.

From stand closure to age 15 to 20 years the stand remains relatively simple. Slash pine being managed on a short rotation will be dense with little to no understory. Longleaf pine will be somewhat more complex with degree of complexity depending upon frequency of prescribed fire.

At 15 to 20 years the amount of light reaching the forest floor should increase as some expression of dominance creates irregularities in the canopy. Light penetration enhances understory development although the new population of plants may be sparse and unthrifty. At the very best there is some additional complexity to add small but new niches. The newest and expanding niche at this stage however is the availability of tree trunks for bole feeders such as the Downy, Hairy, and Red-cockaded Woodpeckers, and Red-breasted, White-breasted, and Brown-Headed Nuthatches. In addition, Mourning doves will nest in stands in this stage of development.

From 15 to 20 years of age until commercial thinning or the end of rotation in short rotation stands, the complexity of the bird niche diversity and carrying capacity increase slowly. At about age 35 in short rotation management the stand will be harvested and regenerated. In long rotation stands, thinnings and natural mortality will begin to open up the stand enough to allow understory development and increase complexity. As the understory develops, niche diversity and carrying capacity will increase to around 50 to 60 years of age depending upon site conditions and frequency of prescribed fire.

Walker (1962) indicated that final harvest of longleaf may occur at age 70 in long rotation but may go to 120 years. The most significant new feature in old growth stands is the presence of large dead trees resulting largely from lightning strikes and insect attack. These are extremely important habitat features to the non-game bird population. Size of the carrying capacity is dependent on the density of dead trees. There are 17 cavity nesters that use dead trees in the longleaf-slash pine type. These species are most abundant in old growth stands and least abundant in young stands devoid of standing dead trees.

INTERMEDIATE TREATMENTS

Fertilization

Fertilization is a treatment used more in slash pine than in longleaf and primarily in young stands under intensive management. Phosphorus and a combination of phosphorus and nitrogen are the most used elements. They have been applied at two stages, the seedling stage and again at about age 25 to 30. Fertilization has two effects in the seedling stage. First, and most importantly when N is used, the herbaceous plant growth is stimulated. This adds complexity to the habitat but more importantly it probably adds to bird carrying capacity. Second the fertilization effect reduces the amount of time in the seedling stage and shortens the length of time until crown closure. The effect is to reduce the period of time in which a short rotation stand is at its highest carrying capacity for birds but probably raises the carrying capacity during this time.

If fertilization is done again when the stand is 25 to 30 years old, it is carried out in combination with thinning. The most important effect on birds will be on understory development. The interaction of increased nutrients and light should greatly enhance growth of tolerant shrubs and hardwoods and improve the quality of the habitat.

Prescribed Fire

Management of longleaf and slash pine is at least impractical and probably impossible without prescribed fire. In both species the need for control of hazardous fuel build-up, control of understory development, and seedbed preparation exists. As previously pointed out, periodic fire in longleaf pine in the grass stage is necessary for brown-spot needle blight control before leader growth can begin. Burning on about a 3-year schedule during this period suppresses shrub and hardwood development and enhances herbaceous growth. Grassland species benefit but where shrubs are allowed to encroach, niches are added for the shrubland species.

Fire must be kept out of seedling stage slash pine and the small sapling stage of both slash and longleaf. After this period, fire must be used for hazardous fuel and hardwood control. It has three impacts on the bird habitat: (1) control of the understory keeps niche diversity low, (2) reduction of the litter (rough) exposes seeds that would not otherwise be available for forage, and (3) destruction of dead trees which eliminates niches for dead tree feeders and cavity nesters.

There are 3 considerations in prescribing fire that will determine the nature of the impact. First, the season of burning is an important criterion determining impact on the understory as well as direct impact on the

birds. Burning during the spring and summer months may destroy nests of ground nesting birds as well as those of birds nesting in low understory. Spring and summer fires are more effective in killing understory than fall and winter burns. To minimize adverse impact the objective should be to control understory development rather than eradicate it.

Second, frequency of fire is the most important criterion determining structure of the stand understory. Fire is recommended in southern pine management on a 3 to 5 year schedule. Burning more often than every 3 years tends toward eradication of shrubs and hardwoods and greatly lowers bird niche diversity. As previously pointed out, understory control is tolerable in non-game bird habitat but eradication has a serious adverse effect. Where the fuel build-up can be tolerated, burning on a 5-year schedule is preferable to a 3-year schedule.

And third, the type of fire used has bearing on the nature of the effect. Back fires (burning against the wind) move slower, remain at the base of the hardwood stems longer, and are likely to produce more hardwood control than other types. Even though the kill may be greater, the back fire does not blacken, defoliate, and "de-branch" the shrubs and hardwoods and thereby have the immediate dramatic impact of headfires (burning with the wind) or flank fires (burning parallel to the wind). Headfires and flank fires are used primarily for fuel control and can only be used when the crown of the pines are far above the ground. Backfires, however, can be used in young stands.

In the case of the Red-cockaded Woodpecker, much has been made of the need for frequent fires to maintain open stands for foraging by the bird. Based on 24,300 observations on 6 separate clans and taken over the period of one year, we have found that the bird uses longleaf and loblolly stands with well developed understories at least with the relative frequency of stands with no understory. To maintain simple structured stands for the Red-cockaded is, in our opinion, not necessary and is to the detriment of a more species rich non-game bird population.

The numbers of standing dead trees in the forest is affected by the frequency and intensity of fire. These trees are important as a foraging medium for woodpeckers and to provide nest space availability for cavity nesters. Frequent fires will destroy dead pines long before they would fall from

natural decay. In addition charring of the bole surface and burning out cavities tends to detract from their usability.

Thinnings

Precommercial thinnings in slash pine have been recommended by Jones (1974) and Langdon and Bennett (1976). It is recommended that precommercial thinning be carried out at least by age 5 and be done whenever stand density exceeds 1000 stems per acre. Numbers of residuals would depend upon product goals. Jones (op. cit.) recommended mechanized thinning by cutting swaths 8 to 10 feet wide and leaving strips 4 to 8 feet wide. Such a disturbance to the stand would of course add to its complexity in vegetation structure and species composition. It will change a stand in which the crowns have closed and carrying capacity dropped to a minimum to habitat favorable to a large variety of non-game bird species.

Commercial thinnings that may be used in slash and longleaf pine are of four general types: (1) low, (2) crown, (3) selection, and (4) mechanical. Smith (1962:92) gave generalized curves describing the distribution of DBH classes that would be removed in each of these procedures (fig. 1). By assuming that crown sizes are roughly correlated with DBH one can get some idea of the relative amounts of understory response.

The low thinning where trees with crowns in suppressed or intermediate classes are removed may change the light regime at the forest floor to some extent but not very much. Understory vegetation may be slightly stimulated but not enough to significantly change niche diversity although carrying capacity may be improved to some extent.

The crown thinning may remove trees in all crown classes but it will concentrate on dominants and codominants. This will have a major impact on the understory. Niche diversity and carrying capacity will be enlarged. Crown thinning will more often be carried out in natural stands than planted stands and is usually the first thinning to be applied.

Selection thinning may be done at any time but concentrates on the removal of dominants. Again, since the larger crowns are being removed, a considerable response can be expected in the understory giving added complexity to the stand.

Mechanical thinning is mostly applied to plantations where rows of trees can be removed without regard to the quality or potential or
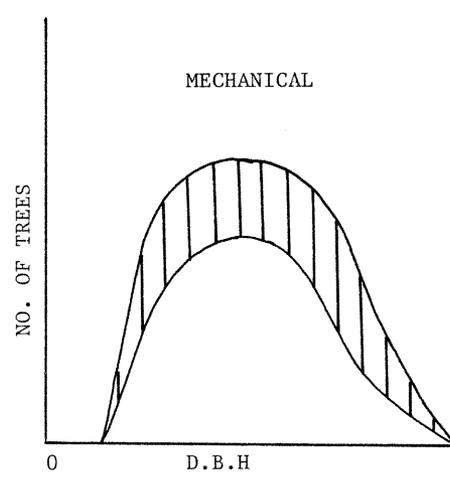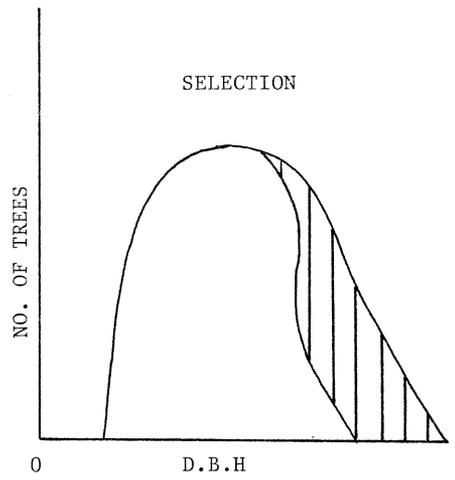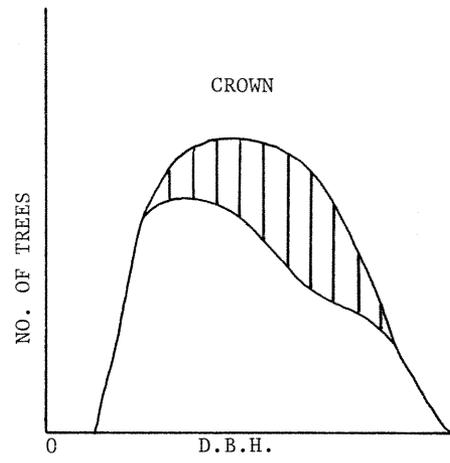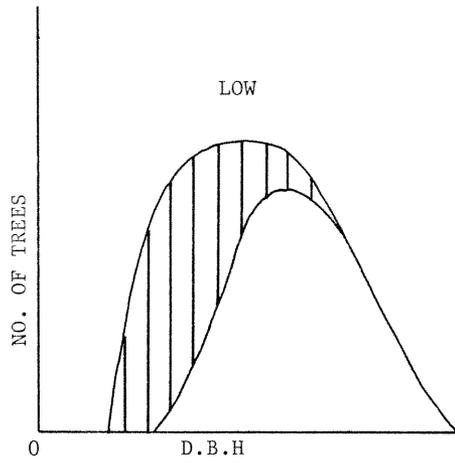
Figure 1.--Distribution of diameter classes that would be removed by
4 methods of thinning (after Smith 1962:92).

residual stems. It is usually a pulpwood cut made at a time in the life of the stand when a light understory is just beginning to develop. The treatment raises the stand from relatively nonproductive conditions in terms of potential to accommodate birds to one which may be very productive.

Sanitation and Salvage Cutting

The last silvicultural treatment to be discussed is sanitation and salvage cutting. These are the least intensive procedures and yet have one of the most important impacts on non-game bird populations. Lightning and insect attack are the primary causes for slash and longleaf pine mortality. Cavity nesting species, of which there are 17 in the longleaf-slash pine type (Table 1), are almost totally dependent on this mortality for nexting opportunities. Where salvage operations remove wounded trees before they decay to a state usable by birds, the cavity nesters are largely missing in the non-game bird population.

Table 1.--Cavity nesting species that use dead trees in the longleaf-slash pine type.

American Kestral	Yellow-bellied
Screech Owl	Flycatcher
Barred Owl	Carolina Chickadee
Yellow-shafted Flicker	Tufted Titmouse
Pileated Woodpecker	White-breasted
Red-bellied Woodpecker	Nuthatch
Hairy Woodpecker	Red-breasted Nuthatch
Downy Woodpecker	Brown-headed Nuthatch
Eastern Bluebird	Carolina Wren
Great-crested	
Flycatcher	

Dead pine trees may stand for 5 to 15 years and be heavily used for 80 to 90 percent of this time. A dead tree stocking of one stem per acre would be highly desirable. In addition planning for a population of dead trees should be made such that salvage operations do not prevent replacements made necessary by losses to prescribed fire and decay.

SUMMARY

The silvicultural practices in the long-leaf-slash pine type that tend to decrease stand complexity by eradicating understory, destroying dead trees, and generally promoting a pine monoculture with a bare forest floor are deleterious to non-game bird populations. This is done by destroying

and/or precluding niche development. Long rotation management provides for longer periods of time when the stand may accommodate large bird populations than does short rotation management. Cutting methods for natural regeneration and thinning practices enhance stand complexity and provide for a wide variety of birds. Precommercial thinning creates highly productive habitat in what was previously a simple monoculture. Prescribed burning is a necessary practice in longleaf-slash pine management, but when carried out with the objective of eradicating understory rather than controlling it, the practice has a highly detrimental effect on non-game bird habitat. Furthermore the loss of dead standing trees during prescribed burning can have a dramatic impact on the cavity nesters. Cavity nesters should be managed for by tempering intensity of sanitation and salvage cutting.

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Bird Communities Associated With Succession and Management of Loblolly-Shortleaf Pine Forests

Joseph M. Meyers and A. Sydney Johnson[1]

Abstract.--Published data from 17 winter and 32 summer bird censuses were used to determine changes in bird species composition, richness, and density in relation to plant succession and forest management in loblolly-shortleaf pine forests. Recommendations for habitat management are offered.

INTRODUCTION

Birds are a major faunal component of our forests. They are becoming a more valued recreational resource as man modifies and eliminates forests (Payne and DeGraaf 1973). Birds are useful as indicators of hazardous environmental conditions; the cases of DDT and PCB's provide good examples of how bird populations can forewarn us of potential hazards of pollutants. Bird populations, because of their great mobility, are important seed dispersers and vectors of diseases (Shugart et al. 1975). However, there are few data relating to the ecological roles of birds in forest ecosystems. Research on this subject has been emphasized for less than two decades and has established only a basic understanding of forest avifauna.

Likewise, forest management for birds other than a few game species has received serious consideration only recently. In the past wildlife management was synonymous with game management. "Nongame" management--management of wildlife other than game and commercially important species--is largely a product of increased environmental awareness in the 1970's. But, the term "nongame" is a vague one that does not describe animals; it only tells us what they are not. Wildlife management should not be approached on game and nongame terms but on a holistic basis with consideration for entire plant and animal communities. The purpose of this paper is to describe the possible bird communities that are associated with successional stages of loblolly-shortleaf pine (Pinus

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taeda-P. echinata) forests and how they can be managed in ways compatible with sound management of other forest resources.

THE LOBLOLLY-SHORTLEAF PINE PLANT COMMUNITY

The loblolly-shortleaf pine forest type, a major component of the southeastern forest (fig. 1), is widely distributed throughout the Southeast in both the Piedmont and Coastal Plain provinces, except in Florida and Tennessee. The loblolly-shortleaf type includes forests composed of 50 percent or more loblolly pine, shortleaf pine, and other southern pines, except longleaf (P. palustris) and slash (P. elliottii). Loblolly and shortleaf pines occur separately or in combination and are commonly associated with oak (Quercus spp.), hickory (Carya spp.), and sweetgum (Liquidambar styraciflua) (U. S. Forest Service 1969).

Loblolly-shortleaf forest is a subclimax or developmental stage in a successional sere leading to oak-hickory climax. Oak-hickory and other hardwoods formed the original cover of much of the region (Oosting 1942, Wahlenberg 1949). But, in the Coastal Plain large areas were forested with subclimax pines. Fire, and agriculture practiced by the Indians were important factors in arresting succession. Even in the Piedmont, extensive pine forests occurred on dry upland sites on gray soils derived from granite, gneiss, sandstone, or slate; hardwoods dominated sites on red clay loams (Pinchot and Ashe 1897, Harper 1943, Nelson 1957, Brender 1974).

Land Use History

Beginning late in the 18th Century, a wave of settlement moved southwestward from Virginia and North Carolina, and in little over a half century the entire region was settled by subsistence farmers and planters. Most of the loblolly-shortleaf type is in the old Cotton
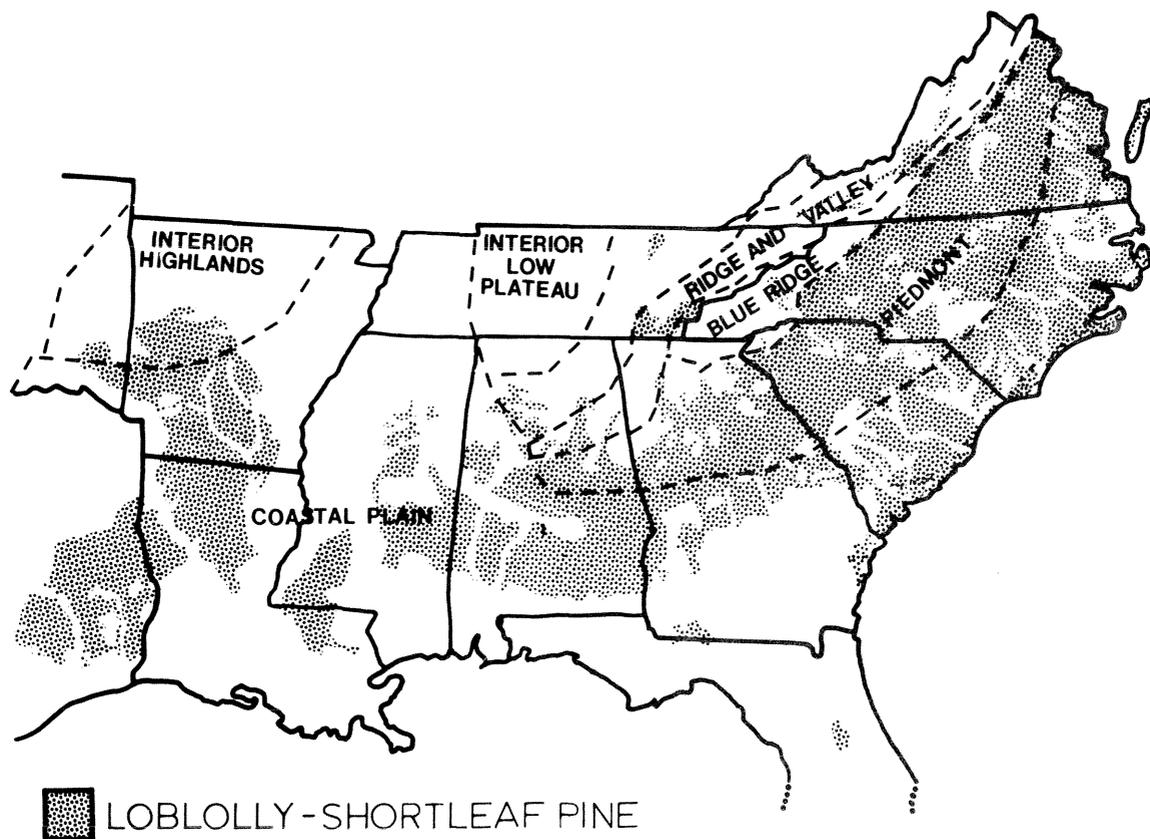
Figure 1.--Loblolly-shortleaf pine forest of the southeastern United States.
(U. S. Forest Service 1969).

Belt where intensive agriculture and the nature of the climate, soils and topography combined to produce severe soil erosion and loss of fertility. There were several periods of land abandonment, the most recent and most important coinciding with the economic depression and invasion by the cotton boll weevil (Anthonomus grandis) in the 1920's. Abandoned fields were invaded by loblolly pine and, on drier sites, shortleaf pine. Virtually all of the natural stands of loblolly-shortleaf remaining today developed on abandoned agricultural fields. Most stands established before 1945 have been heavily cut. Some have regenerated naturally; others have been planted and are under management for pulpwood.

Secondary Succession

Old Field Stage

On Piedmont uplands the first seral stage is a succession of herbs and grasses through the fifth year. Crabgrass (Digitaria sanguinalis) and horseweed (Erigeron canadense) dominate the first growing season following cultivation in the Piedmont, and young plant growth, less than 0.3 m, is present during the first bird breeding season. Taller growth up to 2 m develops by the end of the first year.

In the second year the dominant species are aster (Aster pilosus) and ragweed (Ambrosia artemisiifolia). Broomsedge (Andropogon spp.) attains dominance in the third year and persists until shaded out by pines, which begin to appear in the third year. Various shrubs (e.g. Rubus, Rhus, Prunus) and small deciduous trees also occur with the pines until canopy closure (Oosting 1942, Johnston and Odum 1956).

Elsewhere in the loblolly-shortleaf type, succession is less uniform and less predictable. This is especially true of the early stages where species composition of invading annuals and perennial grasses may vary with structure and fertility of soils, drainage, and previous land use. Soil fertility may also affect species composition and growth rates of trees.

Pine Forest Stage

By the 11th year pine dominates well seeded areas. Trees are 2.4-4.6 m tall with a broomsedge and shrub groundstory (Oosting 1942). Tree density is dependent on ample seed stocking, but differences in density diminish as stands age; dense pine thickets thin naturally on fertile sites and open-growth stands form closed canopies (Brender 1973).

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Canopy closure usually occurs between 10 and 20 years. Only small patches of ground-story plants exist in dense stands of this age class; there is essentially only one stratum of vegetation. More open, natural pine stands have hardwoods of tree size which slowly but steadily increase (Oosting 1942).

A shade tolerant hardwood understory appears in the later seral stages of the pine forest (fig. 2). The decline in pine density is accompanied by a steady increase in density of hardwoods. Natural pine stands 60 to 100 years old have a well developed hardwood understory and ground cover.
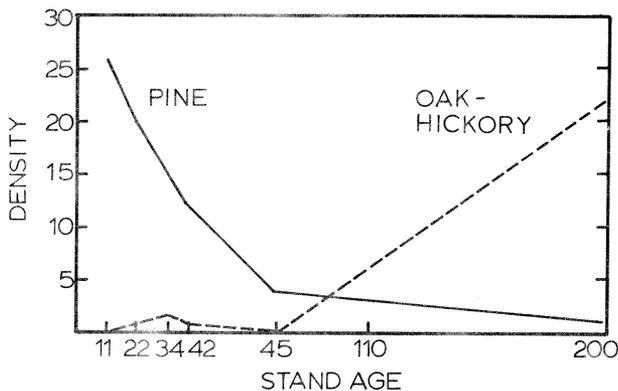
Figure 2.--Piedmont forest succession from loblolly-shortleaf pine to oak-hickory hardwoods. (redrawn from Oosting 1942).

Mixed Pine-Hardwood Stage

During the transition from pine to hardwood forest, habitat conditions are quite diverse. For this discussion we define mixed pine-hardwoods as stands with greater than 10 percent and less than 50 percent loblolly, shortleaf, and other southern pines, except slash and longleaf. Mixed stands usually occur in age classes between 80 and 120 years (fig. 2); however, younger stands can have a substantial amount of hardwoods depending on site conditions. Brender (1973) states that on poor sites, red heart disease (caused by Fomes pini) becomes established earlier, and pine stands begin to break up at age 60. Also, when pines are cut, many stands revert to hardwoods (Wahlenberg 1949); in the absence of fire, root stock of hardwoods in the understory is released when pines are removed.

Mixed pine-hardwoods develop three

vertical strata of vegetation--groundstory (0-3 m), understory (3 to 10 m), and overstory (over 10 m). Hortizontal clumping (patchiness) is more prevalent in mixed stands. Lightning, red heart disease, and the southern pine beetle (Dendroctonus frontalis) cause small openings and thereby create uneven age classes. Snags (dead standing trees) become more abundant as the pine forest is replaced by mature oak-hickory forest.

AVIAN COMMUNITIES

We divided the avian community into the two major populations--winter populations and summer breeding populations. More data have been accumulated on breeding bird populations. Data collected in spring and summer are more reliable than those collected during winter or migratory seasons because of breeding season territoriality in most bird species. Large flocks of winter foragers or migrants complicate studies at other times of the year. Statistical differences in non-breeding bird studies are difficult to detect because of high variances or low sampling effort.

For this review we analyzed winter bird populations from 17 census locations throughout the Southeast (table 1). These censuses include from 1 to 10 years of data and range through the succession of loblolly-shortleaf pine to mature oak-hickory forests. We also analyzed summer breeding bird communities from 31 census locations with 1 to 16 years of data (table 2).

Temporal Patterns

In the eastern United States a large proportion of the bird species are migratory. Some species migrate to the Southeast, while other species cross the Gulf of Mexico and spend the winter months in the Neotropics. There also are resident or sedentary species, such as the Carolina Chickadee (Parus carolinensis) [2] and Tufted Titmouse (P. bicolor). With migration, bird communities change seasonally. During the spring and summer, breeding territories are established and individual breeding birds are relatively sedentary. However, in the winter months interspecific flocks are common in most habitats. For example Kinglets (Regulus spp.), a northern coniferous forest breeder, are abundant winter residents in the southeastern forest and usually are found in pine forests with large groups of chickadees and titmice.

[2] All common names are those standardized and listed with scientific names by the American Ornithologists' Union check-list committee (American Ornithologists' Union 1957, 1973, 1976).

Table 1.--Locations and habitat data for winter bird population censuses of loblolly-shortleaf pine communities.

Census No.	Location	Plot size	Stand type	Percent pine overstory	Stand age[1]	Years of data	Source[2]
1	Moulton, Ala.	20 ha	pine	70%	7 yrs. (60%)	1	AFN 24(3)
2	Livingston Par., La.	12	pine	88	6	1	Noble and Hamilton 1976
3	Livingston Par., La.	12	pine	100	20	1	Noble and Hamilton 1976
4	Proffil, Va.	18	pine	100	∿35	7	AFN 2-8(3)
5	El Dorado, Ark.	5	pine	57	∿35	2	AFN 15-16(3)
6	Pine Bluff, Ark.	22	mixed	30	30	1	AFN 10(3)
7	Livingston Par., La.	12	pine	100	45	1	AB 28(3)
8	El Dorado, Ark.[3]	9	pine	90	mature	5	AFN 7-12(3)
9	Natchitoches Par., La.	9	pine	50	mature	5	AB 25-28(3)
10	El Dorado, Ark.	9	mixed	25	mature (60%)	6	AFN 5-8,10-11(3)
11	North Wilksboro, N.C.[4]	16	mixed	?	mature	9	AFN 18-19,21,23-24; AB 25-26,29(3),30(6)
12	Savannah, Ga.	10	mixed	30	mature	10	AFN 18-24; AB 25-27(3)
13	Moulton, Ala.[5]	20	mixed	25	mature	1	AFN 24(3)
14	Raleigh, N.C.	5	oak-hickory	< 5	mature	1	AFN 24(3)
15	Raleigh, N.C.	4	oak-hickory	< 5	mature	1	AFN 24(3)
16	Livingston Par., La.	12	S mixed hdwd.	6	mature	1	Noble and Hamilton 1976
17	McLean, Va.	11	oak-hickory	0	mature	2	AB 25,28(3)

[1] Mature pine stands are >45 years old; mature mixed and oak-hickory stands are >75 years old.

[2] AFN = Audubon Field Notes, AB = American Birds; volume and number are listed with each citation - "Winter Bird Population Studies."

[3] 75% is under forest management, 25% of the area was logged for pine in 1949 (2 years before the date of census).

[4] White pine - shortleaf pine and oak community in the mountains.

[5] Large flocks of Common Grackles and blackbirds were excluded.

Table 2.--Locations and habitat data for breeding bird censuses of loblolly-shortleaf pine forest stands and other pine-hardwood stands.

Census No.	Location	Plot size	Stand type [1]	Percent pine overstory	Stand age [2]	Years of data	Source [3]
1	Livingston Par., La.	12 ha	pine	88%	6 yr.	1	NH 1976 [4]
2	Warner Robbins, Ga.	10	pine	70	∿7	1	AFN 6(6)
3	Raleigh, N.C.	13	pine	∿50	∿7	1	AFN 21(6)
3a	Raleigh, N.C.	13	pine	∿50	∿9	1	AFN 23(6)
4	Durham, N.C.	7	mixed	35	1-10	1	AFN 20(6)
5	Oakland, Md.	11	pine	100	10-20	1	AFN 3(6)
6	Durham, N.C.	8	pine	95	10-20	1	AFN 20(6)
7	Livingston Par., La.	12	pine	100	20	1	NH 1976 [4]
8	Romney, W.Va. [5]	4	pine	90	20	1	AFN 21(6)
9	Durham, N.C.	10	pine	100	20-30	1	AFN 20(6)
10	Snowhill, Md.	9	pine	97	25-30	1	AFN 2(6)
11	Pine Bluff, Ark.	62	mixed	30	<30	1	AFN 9(6)
12	Athens, Ga.	10	pine	100	∿35	1	AFN 1(6)
13	Athens, GA.	8	pine	95	33	1	AFN 17(6)
14	Warner Robbins, Ga.	8	mixed	<20	∿35	1	AFN 7(6)
15	Durham, N.C.	10	pine	95	30-40	1	AFN 20(6)
16	El Dorado, Ark.	4	pine	57	35	2	AFN 14-15(6)
17	Southport, N.C.	12	mixed	40	35-40	2	AB 27(6),31(1)
18	Savannah, Ga.	7	pine	95	40-45	3	AFN 19-21(6)
19	Chapel Hill, N.C.	35	pine	92	30-60	1	AFN 20(6)
20	Livingston Par., La.	12	pine	100	45-46	2	NH 1976 [4]; AB 28(6)
21	Durham, N.C.	10	pine	85	70-80	1	AFN 20(6)
22	El Dorado, Ark.	8	mixed	30	mature	1	AFN 11(6)
23	Savannah, Ga. [6]	10	mixed	32	mature	10	AFN 17,19-24(6); AB 25-27(6)
24	Romney, W.Va.	6	mixed	30	mature?	1	AFN 21(6)
25	Fairfield, Ala.	10	mixed	24	mature	2	AFN 3-4(6)
26	El Dorado, Ark. [7]	9	mixed	20	mature	5	AFN 11(6)
27	N. Wilksboro, N.C. [8]	16	mixed	?	mature	16	AFN 8-9,11,14-24(6); AB 25-26,29(6)
28	Chapel Hill, N.C.	9	beech-maple	9	mature	2	AB 27-28(6)
29	Livingston Par., La.	12	S. mixed hdwd.	6	mature	1	NH 1976 [4]
30	Durham, N.C.	11	oak-hickory	<5	mature	1	AFN 20(6)
31	Berkley Spr., W.Va.	6	oak-hickory	0	mature	1	AFN 11(6)
32	Athens, Ga.	9	oak-hickory	∿5	mature	1	AFN 1(6)

[1] Pine = loblolly-shortleaf pine; mixed = pine and hardwoods.

[2] Mature pine stands are >45 years old; mature, mixed, oak-hickory, and beech-maple stands are >75 years old.

[3] AFN = Audubon Field Notes, AB = American Birds; volume and number are listed with each citation; see Breeding Bird Census.

[4] Noble and Hamilton 1976.

[5] Edge effect accounted for 4 of 14 species and 220 individuals/km^2.

[6] Slash and longleaf pine are 28% of the overstory, while loblolly is 4%.

[7] Some recent logging was done on the plot.

[8] White pine-shortleaf pine and oak community in the mountains.

Temperature and Latitudinal Gradients

During the winter, the number of bird species (richness) is closely related to the number of frost-free days (Bock and Lepthien 1974, Tramer 1974a). The mild and fairly stable winter climate of the Southeast is apparently important to many bird species that do not tolerate harsh northern winters. Climate does not seem to affect species numbers in areas with more than 245 frost-free days. Because of this relationship, more bird species should be present in pine forests in Louisiana than in Virginia or North Carolina. Also, more species should be present in milder coastal areas than interior habitats. Tramer (1974b) states that temperate zone winter ranges appear to be regulated by the effects of climate on food supply.

In general breeding bird species richness is inversely related to latitude; however, breeding species richness is less in the southeastern than in the northeastern United States. Various explanations for this were presented by Tramer (1974b).

Winter Bird Community

Successional Trends

Quay (1947) completed a detailed study of winter bird populations in an upland plant sere near Raleigh, North Carolina. His study was conducted during one winter, and density estimates within seral stages may reflect favorable or unfavorable climate that year. However, his study does delineate changes in winter bird populations associated with plant communities in that specific region.

Data on winter bird populations from the 17 census locations (table 1) were analyzed for changes in species richness and density with changes in the plant community (figs. 3, 4). In most censuses (source AFN, AB--see table 1) it was not possible to calculate the Shannon Index for species diversity (MacArthur and MacArthur 1961) because data tabulation was in rounded whole numbers (means) and included symbols (+) for uncommon species.

Species richness in winter populations increased in the early seral stage from 7-15 species in old fields to 27-30 species in young open-canopy pine stands with patches of older trees or open wet areas. However, very few data were available for this seral stage, and the apparent trend could be due in part to temperature gradients. Quay's (1947) study showed a slight decrease in species richness from bare ground to herb and broomsedge-pine habitats (fig. 3).

Census data for stands after canopy closure indicate a decrease in species richness,

which is not reversed until age 35 (fig. 3). Dickson and Segelquist (1978) found stands of dense pine saplings (age 15) practically devoid of birds; younger and older stands had substantially more species and higher densities. Bird densities (fig. 4) also follow the same trend in the few censuses available for these seral stages. In Louisiana winter bird densities decreased 50 percent (fig. 4, table 1) from a 7-year-old pine stand to a closed canopy stand (age 20); however, a 45-year-old pine stand showed an additional decrease in density from the 20-year-old stand (Noble and Hamilton 1976). These data contradict studies by Quay (1947) and Dickson and Segelquist (1978). Apparently reduced winter bird species and density in the 45-year-old stand was the result of annual burning, which eliminates the lower vegetative stratum (Noble and Hamilton 1976).

From mature pine to mixed pine-hardwood seral stages there is considerably higher density and species richness with the increase in percent hardwoods (figs. 3, 4). Decreases in density and species richness in mature stages of forest succession are apparent in colder, more northerly environments, e.g. North Carolina and Virginia (figs. 3, 4). This difference possibly results from greater availability of food in the southern latitudes (Tramer 1974b).

Species Composition

Fringillids (sparrows, towhees, goldfinches, etc.) are the major group of winter birds in young seral stages. Savannah Sparrow (Passerculus sandwichensis), Field Sparrow (Spizella pusilla), Dark-eyed Junco (Junco hyemalis), and Song Sparrow (Melospiza melodia) are common fringillids in old fields during the winter (Quay 1947, Odum and Hight 1957). Other common species in early stage old fields (0-5 years old) are Eastern Meadowlark (Sturnella magna), Bobwhite (Colinus virginianus), Killdeer (Charadrius vociferus), and Mourning Dove (Zenaida macroura). As shrubs, vines, and small pines become available for cover and foraging, White-throated Sparrow (Zonotrichia albicollis), Cardinal (Cardinalis cardinalis), Rufous-sided Towhee (Pipilo erythrophthalmus), and wrens become abundant.

The pine or mixed pine-hardwood forest is used by a variety of bird groups and foraging guilds. Woodpeckers are common through the winter in forest stands of all ages but are most abundant in mature stands. Golden-crowned and Ruby-crowned Kinglets (Regulus satrapa and R. calendula) are common to abundant in pine and mixed pine-hardwoods. These species breed in northern coniferous forests and winter in southern pine forests. They are commonly found in flocks with permanent residents, such as Carolina Chickadees, Tufted Titmice, and Downy
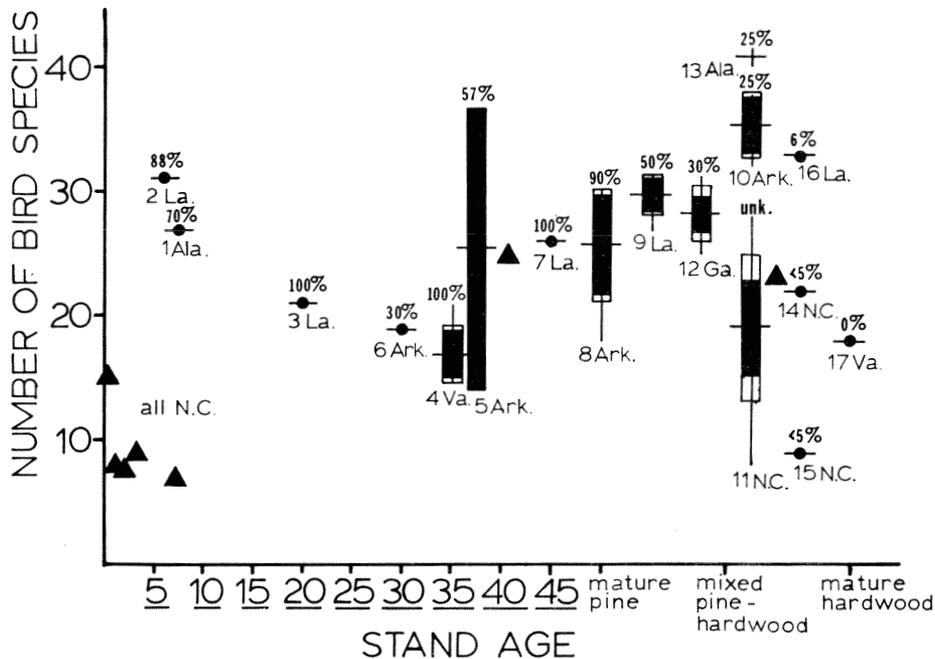
Figure 3.--The relationship of winter bird species richness with succession of loblolly-shortleaf pine forests. Vertical line represents the range, horizontal line the mean, hollow rectangle one standard deviation on either side of mean, and solid rectangle 95% confidence interval on either side of mean. Percent pine is given above each symbol and census location and number below each figure. Solid triangles refer to Quay 1947.
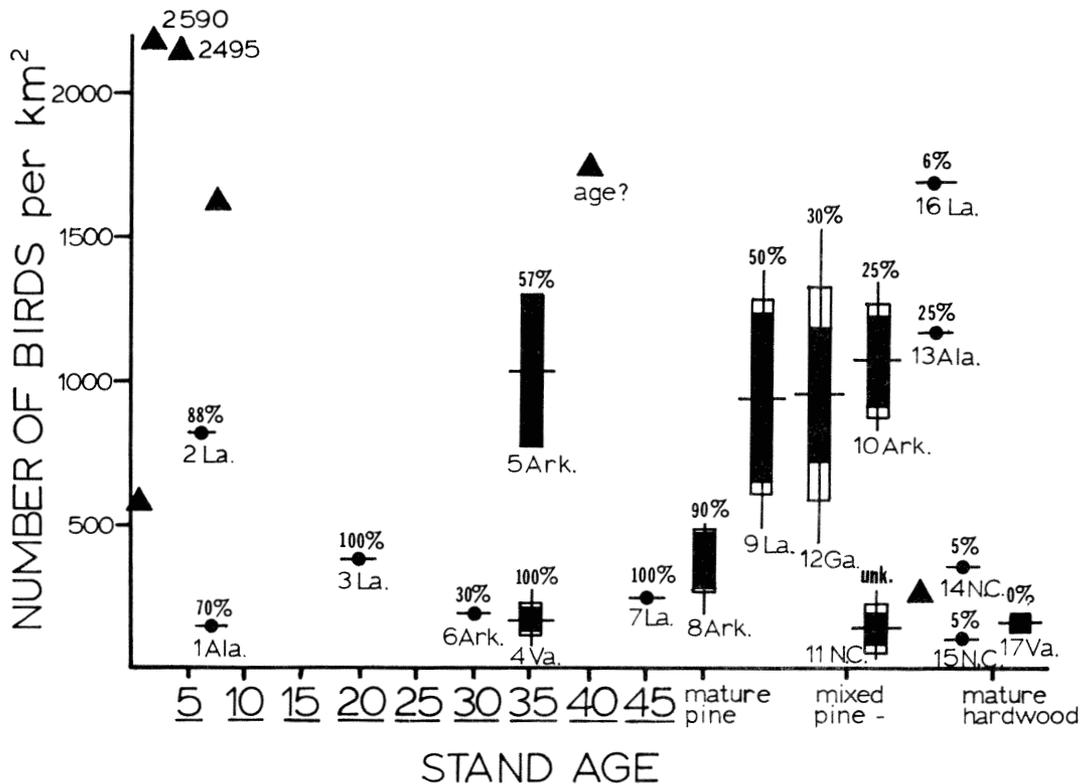

Figure 4.--The relationship of winter bird density with succession of loblolly-shortleaf pine forests. See figure 3 for interpretation of symbols.

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Woodpeckers (Picoides pubescens). In most
cases pine forests in the Piedmont loblolly-
shortleaf type have higher populations in
winter than deciduous forests because of the
addition of kinglets to the permanent resi-
dent populations (Johnston and Odum 1956).
Pine warblers (Dendroica pinus), permanent
residents, are common in pine stands of all
age classes. Another parulid, the Yellow-
rumped Warbler (D. coronata), is abundant in
some years in young seral stages, and is also
commonly found in flocks of permanent resi-
dents in older forest stands.

Summer Breeding Bird Community

Successional Trends

Breeding bird habitat in the Southeast
is grouped into four broad stages; (1) grass-
lands, (2) shrubland, (3) pine forest, and (4)
hardwood forest (Johnston and Odum 1956).
Most of our discussion will be concerned with
the first three stages and the transition
i.e. mixed pine-hardwoods) from pine to oak-
hickory.

Grasslands are predominant in the
southern Piedmont and the Coastal Plain during
the first 3 years of natural succession. Bird
populations and species richness are low
during this stage (figs. 5, 6). Only two or
three species breed in this habitat in the
Southeast. However, in the shrub and young
pine stage a rapid increase in breeding
density and species takes place. Shrubs add
patches and an additional vegetative stratum
for nesting. This increase is short-lived as
pine canopy closure at 10-20 years eliminates
the ground cover and understory vegetation.
Densities decrease from 600 territorial males
per km^2 to 200-300 per km^2. Breeding bird
species also decrease about 50 percent. These
reduced populations are common in pine stands
from age 15 to 30 years.

Pine tree density decreases rapidly from
age 11 to age 34 (fig. 2). This natural thin-
ning allows greater light penetration to the
ground and development of understory vege-
tation. At stand age 35 densities and species
of breeding birds again rapidly increase to
values similar to those of the shrubland stage.
Bird species richness is higher from stand age
40 to 80 than in any younger age class
(fig. 5). Again richness and density in the
annually burned stand (census 20) was consider-
ably lower (60-70 percent less) than for
unburned or irregularly burned plots (figs. 5,
6).

Mixed loblolly-shortleaf pine-hardwood
forests are important breeding habitat for
many species. Density and species richness in
these stands are similar to mature hardwood
forests. The average density of breeding pairs

(territorial males) in mixed pine-hardwood is
550 per km^2. Approximately 20 breeding species
(mapped territories, not visitors) are found in
mesic pine-hardwood forest. Bottomland pine-
hardwood forests (census 22; figs. 5, 6) are
higher in total density and species richness
than drier sites. Within the loblolly-short-
leaf pine type the mixed pine-hardwoods and
mature pine stands have the highest density
and species diversity.

Relationships in Breeding Bird Populations

Density and species richness are highly
correlated in breeding bird communities. Note
that the graphs of species richness (fig. 5)
and breeding bird densities (fig. 6) are very
similar. Increase in population density is
caused primarily by the addition of new species
(Tramer 1968). Territoriality would limit
increase in density of bird species already
present. Species diversity in breeding bird
populations also is highly correlated with
number of species.

Foliage height diversity, an indirect
measurement of the amount of leaf surface area
present in the horizontal strata of the forest,
is positively correlated with bird species
diversity (MacArthur and MacArthur 1961). Roth
(1976) shows that spatial heterogeneity or
patchiness is also significantly correlated
with bird species diversity. Both of these
vegetative measurements are useful to bird
managers as indicators of bird diversity. But
diversity should not be the sole objective in
bird habitat management. Densities and species
composition and distribution should also be
considered.

Species Composition

Figure 7 presents breeding bird species
composition and densities with succession in
loblolly-shortleaf pine stands. This list is
not complete, but it contains the major
breeding birds of concern to managers. Rare
and endangered species will be discussed in a
later section. Birds with large territories,
such as raptors, are not well represented in
breeding bird censuses because census tech-
niques for breeding raptors are not compatible
with passerine census techniques.

Three common breeding species of the
grassland stage in the Southeast are Bobwhite,
Eastern Meadowlark, and Grasshopper Sparrow
(Ammodramus savannarum). Fall and winter
Bobwhite populations are highest in 2-year-old
fields in pine plantations (Brunswig and
Johnson 1972). In unmanaged natural succession
Bobwhite breeding populations presumably would
be higher in 3- to 5-year-old fields than in
managed pine stands of the same age, as manage-
ment speeds up succession and shortens the
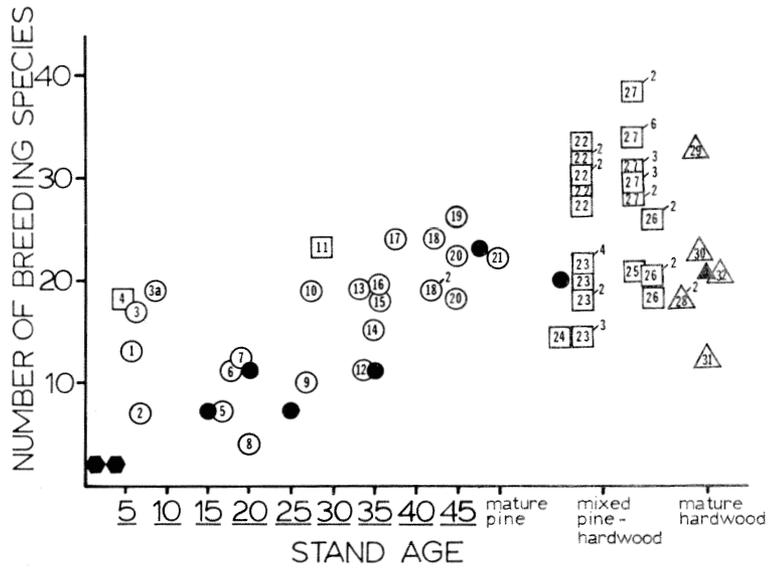duration of optimum breeding habitat. The

Figure 5.--The relationship of breeding bird species richness with succession of loblolly-shortleaf pine forests. Hexagon = grassland, circles = 50 to 100% pines, squares = 10 to 49% pine, triangles = < 10% pines. Numbers on symbols refer to censuses in table 2. Numbers outside the symbols refer to duplicate points. Solid symbols refer to Johnston and Odum 1956.
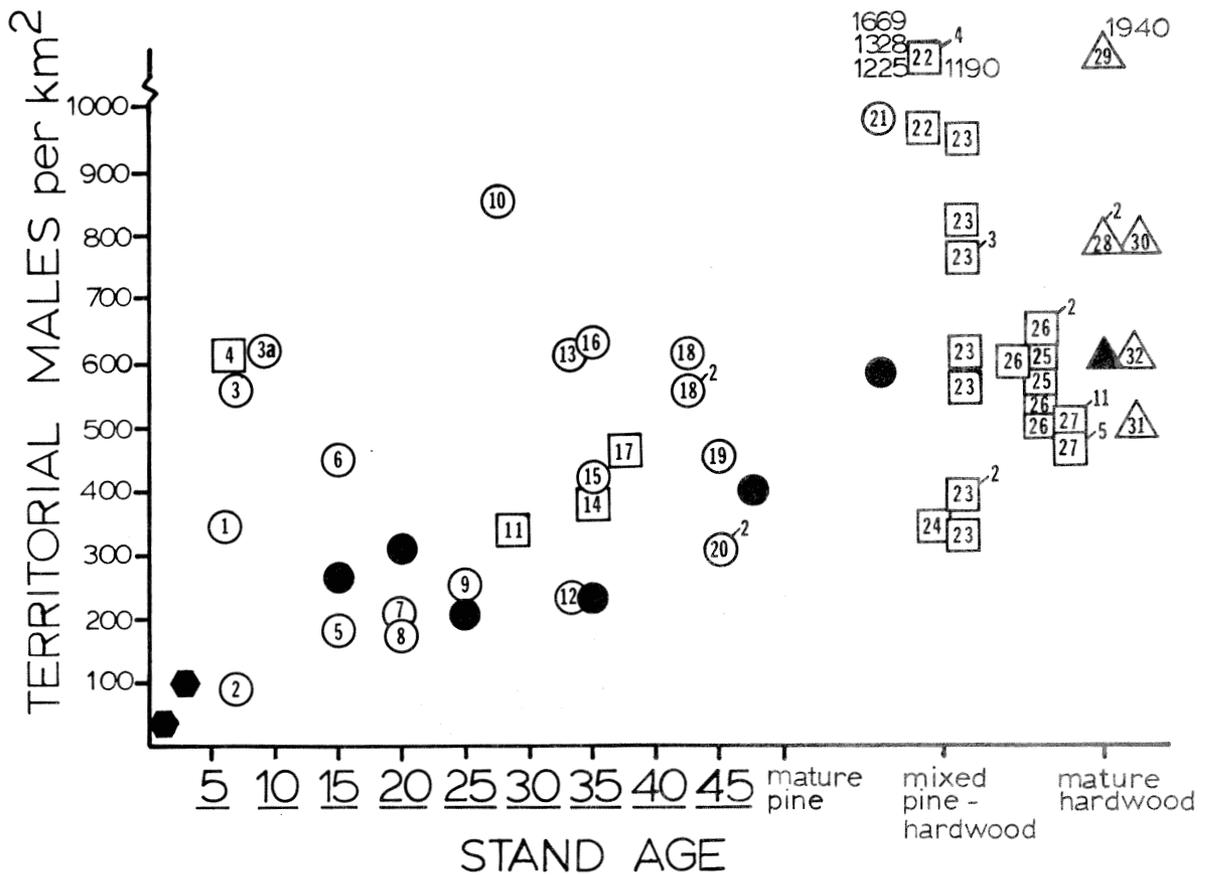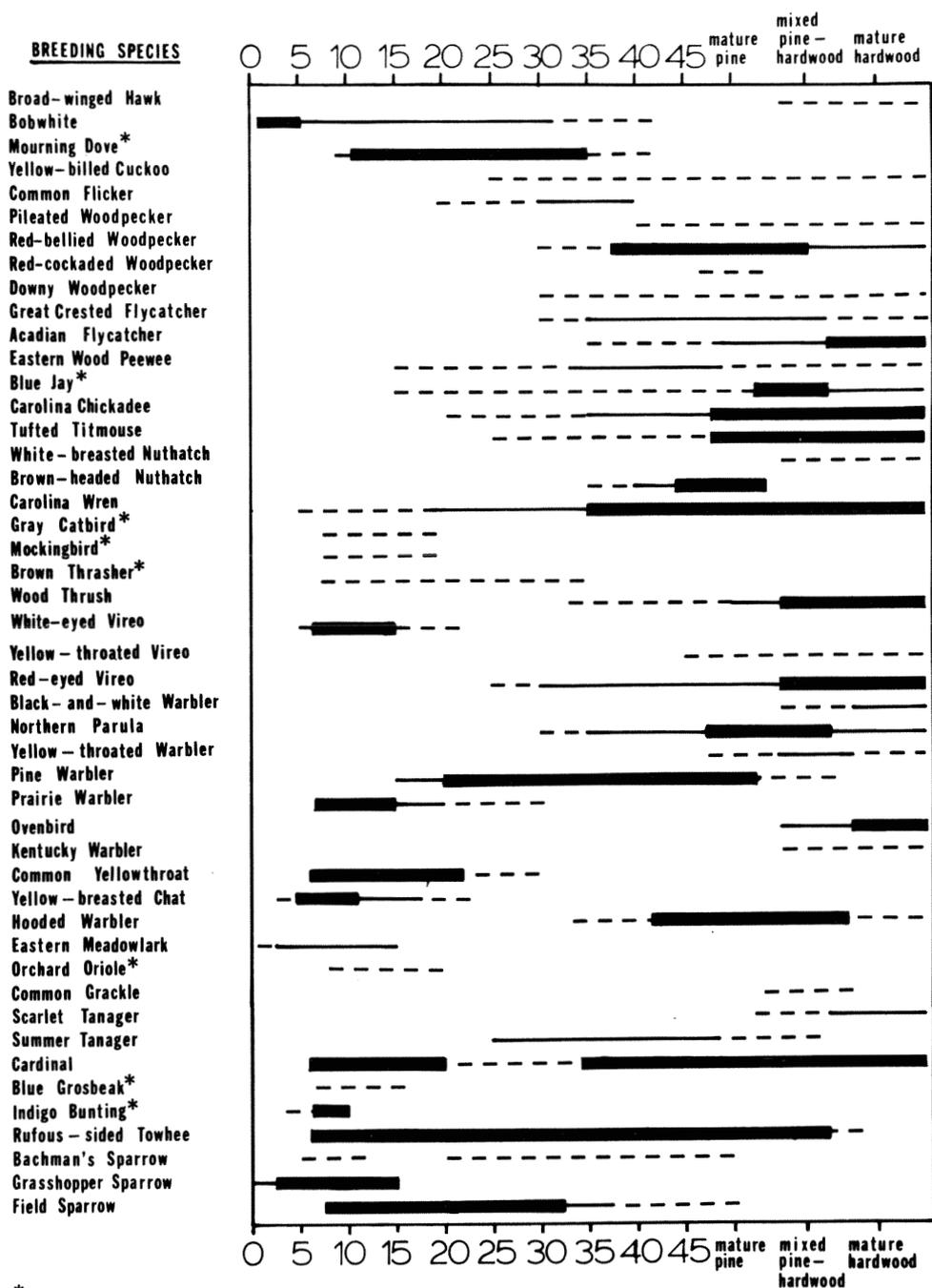

Figure 6.--The relationship of breeding bird density with succession of loblolly-shortleaf pine forests. See figure 5 for interpretation of symbols.

STAND AGE

Figure 7.--The approximate density of selected breeding birds in the seral stages of loblolly-shortleaf pine and oak-hickory forests. Dashed line = < 5 pairs per 40 ha, solid line = > 5 < 10 pairs per 40 ha, and solid bar = > 10 pairs per 40 ha. Data from table 2 and Johnston and Odum 1956.

Grasshopper Sparrow and Meadowlark are true grassland species and the only breeding species found in large uniform fields without shrubs or trees (Johnston and Odum 1956). Two other uncommon species not presented in figure 7 are Killdeer and Horned Lark (Eremophila alpestris). Both of these birds feed and nest on essentially bare ground and are pioneer species in the successional series. Horned Larks have been extending their breeding range eastward from the prairies (Johnston and Odum 1956).

The shrubland habitat (age 5-15) is important to "edge species," which require two or more plant communities usually of widely separated ages (Johnston and Odum 1956). These species are common in shrubland and usually also common at forest-shrub boundaries in older stands (fig. 7). A few other species are most abundant only in the shrubland stage and rapidly decrease in forest stands. Prairie Warbler (Dendroica discolor), Yellow-breasted Chat (Icteria virens), Indigo Bunting (Passerina cyanea), White-eyed Vireo (Vireo griseus), Common Yellowthroat (Geothlypis trichas), and Field Sparrow are common breeding species only in shrubland. Mourning Doves, an edge species, become fairly abundant in the latter part of the shrub stage. Edge and shrubland species are a major component of bird communities. Possibly more than 30 to 40 percent of common breeding birds in the Georgia Piedmont belong to this category (Johnston and Odum 1956). These species are also some of the most widely recognized birds found in low density residential areas.

By age 20 most pine stands have closed canopies with shrub and grass cover significantly reduced. However, in natural succession poorly seeded areas and eroded or wet areas often create a patchiness of habitats with clumps of pines interspersed with small openings of earlier seral stages. These openings increase the bird diversity and density in pine stands which otherwise would have low densities.

The Pine Warbler, Brown-headed Nuthatch (Sitta pusilla), and rare Red-cockaded Woodpecker (Picoides borealis) are the only breeding birds restricted to the southern pine forest (Johnston and Odum 1956). Pine Warblers are most abundant in pure stands of pines, and their density decreases significantly with the invasion of hardwood species (fig. 7). The uncommon Brown-headed Nuthatch, a cavity nester, is generally a breeding bird of mature pine stands. The Red-cockaded Woodpecker breeds in mature pine stands with infections of red heart disease and is generally more common in the Coastal Plain than Piedmont.

In southeastern pine forests bird populations are determined mainly by the understory (Johnston and Odum 1956). Grasses under mature pine forests create breeding habitat for Bobwhite and Bachman's Sparrow (Aimophila aestivalis). Thick patches of shrubs or well developed understory in mature pine forests are good breeding habitat for the Carolina Wren (Thryothorus ludovicianus), Great Crested Flycatcher (Myiarchus crinitus), Summer Tanager (Piranga rubra), Yellow-throated Vireo (Vireo flavifrons), Eastern Wood Peewee (Contopus virens), Hooded Warbler (Wilsonia citrina), Northern Parula (Parula americana), Cardinal, Rufous-sided Towhee, and many other less common species (fig. 7 and data from sources in table 2). Many of these species also occur in hardwood forests which usually have a well developed understory.

As pine forests mature, hardwood species replace pines and produce a mixed pine-hardwood stand (fig. 2). These mixed forest types have highly diverse bird populations. Woodpeckers and other cavity nesters, such as the Carolina Chickadee, Tufted Titmouse, Great Crested Flycatcher, and White-breasted Nuthatch (Sitta carolinensis), are fairly abundant at this stage. Some of these species also are found in younger pure pine stands with dead standing trees (Noble and Hamilton 1976). In addition, many predominantly hardwood forest birds, such as the Broad-winged Hawk (Buteo platypterus), Acadian Flycatcher (Empidonax virescens), Wood Thrush (Hylocichla mustelina), Red-eyed Vireo (Vireo olivaceus), Black-and-white Warbler (Mniotilta varia), Ovenbird (Seiurus aurocapillus), and Scarlet Tanager (Piranga olivacea), begin to breed commonly in mixed pine-hardwood stands (fig. 7).

Endangered Species

The only endangered species closely associated with upland loblolly-shortleaf pine is the Red-cockaded Woodpecker. Considerable research is being done on management of this species' habitat (Hooper et al. 1977, Baker 1977, Jackson 1977). The Red-cockaded Woodpecker breeds in open, mature pine stands. The nest trees are almost always infected with red heart disease.

This woodpecker usually occurs in clans of 2-10 birds, with only 1 pair breeding and the remaining birds acting as helpers. Cavities are almost always in mature, living pines and are readily identified by the glaze of white resin surrounding the entrance. The home range of a pair is 14 to 20 ha, and clans of 8 birds utilize up to 65 ha.

Management of this species is achieved by providing suitable nest and roost trees, which include loblolly, shortleaf, longleaf, slash, and pond pines (Pinus serotina) at least 80 years old. Stands for nest sites should have

an average density of 110-124 stems/ha with a basal area of 11 to 14 m^2/ha. Understory should be no more than 4.5 m tall and preferably less than 2 m. The exact stand size necessary for the preservation of the clan is not known, but is in the range of 14-65 ha (Chamberlain 1974).

TIMBER MANAGEMENT IN RELATION TO BIRD HABITAT

Management Trends

Forest management trends have accelerated within the last 20 years. Land ownership, management objectives, and multiple use management are the major areas of change. For instance, forest industrial land holdings in the Georgia Piedmont increased 26 percent from 1961 to 1969, and in 1973 20 percent of the Georgia Piedmont forest was managed by forest industries, mostly for production of pulpwood (Brender 1973). Management of loblolly-shortleaf pine types has become more intense and mechanized. Rotation lengths are shorter with intensive management.

Maintenance of forest stands in earlier successional stages by shorter rotations is eliminating mature pine and hardwood forests. One can readily recognize that compartmental control of a loblolly-shortleaf pine forest with no stands older than 35 years would eliminate many breeding bird species (fig. 7). Short rotation stands lack (1) suitable cavities for nests, (2) an understory nesting stratum, (3) high energy fruits and mast, and (4) deciduous foliage necessary for many songbirds (Johnson et al. 1975). More intensive management, with elimination of hardwoods by herbicides or burning and row planting of pines, further reduces breeding habitat for ephemeral bird species in the grass and shrub stages.

Multiple resource management is now the policy on most publicly owned forests, where a diversity of age classes are maintained. Timber, water, wildlife, and recreation are the major resources of these forests. However, deliberate nongame bird management has not been widely practiced. Much of what happens is incidental to timber and game management.

Only a few studies have been completed on bird populations and the effects of site treatments in the early stages of succession of pine plantations (see tables 1, 2). Obviously shorter rotation lengths in managed pine forests will produce more forest in early stages of succession. More research is needed on bird populations during the first 35 years of managed and unmanaged pine forests.

Succession is predictable only on a macroscopic level (Margalef 1968). Many sites of the same stage of succession will be phytologically different because of past land uses, soil fertility, soil moisture, or microclimate. Local site characteristics are important when overall management decisions are made for songbird habitat.

Harvest and Regeneration

Harvest methods can greatly affect bird communities. Southern pine forests generally are managed in even-aged stands, harvested by clear cutting, seed-tree, or shelterwood cutting. Much of the literature on the effects of even-aged timber management on bird populations concerns clearcutting. Clearcutting with intensive site preparation eliminates the overstory and reduces the site to mineral soil. When soil preparation and planting are done during the fall and winter, the spring vegetation is sparse and all forest breeding birds are eliminated. Killdeers would be the only bird breeding in this habitat (Johnston and Odum 1956, Perkins 1973). However, if the site is not intensively prepared and "whips," shrubs, and logging slash are present, the breeding bird populations are considerably higher, possibly higher than populations in uncut loblolly-shortleaf forest (Perkins 1973). This would be true also for non-breeding bird populations. Snags left in harvested areas are important to cavity-nesting birds such as bluebirds (Sialia sialis) (Conner and Adkisson 1974), woodpeckers, and other nesting birds; and they hardly affect timber production goals. Conner and Crawford (1974) found that one-year-old oak clearcuts with slash and debris were excellent foraging areas for Downy Woodpeckers and Hairy Woodpeckers (Picoides villosus); however, the source of insect prey was much less abundant in 5- and 12-year-old clearcuts. Perkins' (1973) data on bird species richness of mist blown-injected and bedded (with burned windrows) sites indicated that mist blown-injected sites have more than twice as many species during spring and summer as uncut forests. Many early successional bird species are common in these habitats, as the greater volume of vegetation in the lower strata significantly increases the number of species. Windrows often support plant communities quite different from the adjacent treatment area (Perkins 1973). Shrubs and hardwood saplings in windrows create an "edge effect," which usually increases breeding bird species diversity and density.

Clearcut size and shape, and juxtaposition of different age classes are important in bird management. Arner (1972) reported that the average size of clearcuts in southern forests was 92 ha (range 20-600 ha) on commercial land and 26 ha (Piedmont) to 36 ha (Coastal Plain) on public land. Clearcuts of 20 to 40 ha are

acceptable units for nongame bird management. This range coincides with clearcut sizes suggested for many game species. Clearcuts larger than 40 ha are less important to "edge" bird species, but, if rotations are long (60-80 years), these clearcuts could provide more habitat for forest interior species.

Long narrow clearcuts clearly benefit "edge" species. However, a more important harvest treatment is the undulating boundary (scalloped edge), which is the natural edge of mature systems (Margalef 1968). Meyers (unpublished data) has found significantly higher bird densities on scalloped forest edges of transmission line corridors. It is quite possible that clearcuts with undulating boundaries rather than straight boundaries are higher in bird density and diversity. Undulating boundaries have more edge and also create patchiness of habitat types. Further research on this phenomenon is needed before we make management recommendations. Johnston and Odum (1956) state that boundaries separating habitats of widely different age classes (e.g. grassland and forest) are most important to forest edge bird species. Clearcuts, by maximizing mature forest-grassland edge usually increase densities of edge bird species and bird species diversity. But, we caution against exclusive use of the "edge effect" as a management objective. Many of the edge species are common, whereas forest birds, particularly those of mature pine and hardwoods, are less common, and current forest management trends could further reduce their populations.

Narrow spacing of trees on intensely managed sites usually causes early crown closure, while wider spacing of planted pines results in a delay in crown closure. The delayed crown closure benefits early seral stage birds. Clumping from natural or aircraft seeding and seedling mortality from climatic or edaphic conditions both increase the variety of breeding birds. Regular spacing of trees possibly reduces bird species diversity (Roth 1976).

High breeding bird densities (1800 pairs/km^2) in an intensively managed plantation interplanted with Norway spruce (Picea abies) and European beech (Fagus sylvatica) were reported by Williamson (1970). The plantation was bounded by a fringe of mature beech and oak, field hedgerows, and grassland access roads and firebreaks. The fringe of mature trees was used to screen the new plantation from the public roads. Although southern pine management currently does not include interplanting of hardwoods, birds would most likely benefit greatly by this management.

The other methods of regenerating even-aged stands--shelterwood and seed-tree

harvests--do not produce the very low bird diversity and density during the first year after harvest. The presence of overstory trees during the early stages of succession encourages both forest and field or shrubland breeding birds. Also, natural mortality of residual trees associated with these methods (Brender 1973), provides bird habitat for nesting and foraging.

Selection harvesting of loblolly and short-leaf pine is controversial. It is useful for managing small holdings where the landowners expect a regular income at short intervals. Sawtimber and veneer stock are the principal products of uneven-age management (Brender 1973). Since selection harvesting is not a widely used method in the South, there have been no bird studies in uneven-aged loblolly-shortleaf pine. Research on all silvicultural systems as they relate to bird habitat in southern pine forests is scarce.

Intermediate Treatments

At mid-rotation (about 15 years) pine stands, especially on dry sites, are devoid of groundstory vegetation. If there is a pulp market available, stands should be thinned, especially on average to poor sites (Brender 1973). Thinning dense stands can significantly increase timber volume and provide improved bird habitat. Natural thinning encourages a patchier habitat than mechanical thinning and therefore may support more breeding bird species. However, if management of birds is of particular interest, mechanical methods that create non-uniform habitat are suitable, especially on poor to average sites that do not thin naturally.

Burning is commonly prescribed in the management of loblolly-shortleaf pine forests for timber and game. Prescribed burning at 3- to 4-year intervals is useful in hardwood control and can create a patchiness in the understory that may increase bird species and densities. A few species, such as Bachman's Sparrow, benefit from more frequent prescribed burning. However, a vast majority of the breeding birds nest between ground level and 3 m (Preston and Norris 1947); therefore without understory, significant numbers of breeding species are eliminated. Annual burning is not desirable for management of most songbirds, and for timber management generally is unnecessary. Noble and Hamilton (1976) concluded that burning at intervals of 3 to 4 years provided the same results for forest management as annual burning in a 46-year-old stand of loblolly pine. Research is needed on burning rotations greater than 4 years, spot-burning, and other techniques of prescribed burning for non-game bird management.

NATURAL AGENTS MODIFYING BIRD HABITAT

Two animals, the beaver (Castor canadensis) and the southern pine beetle, have a significant impact on forests by creating openings. Reese and Hair (1977) examined birds associated with beaver pond habitat in South Carolina and found highly diverse communities. Dead standing trees, wetland habitat, forest edge, and abundant shrub cover are prominent components of beaver ponds. All of these structures contribute to the increased species diversity in the pond area.

The southern pine beetle is one of the most damaging forest insects in the South (U. S. Forest Service 1969). Damage is within a well-defined area from the Piedmont in central Alabama to south-central Virginia with scattered areas reported on the Coastal Plain. The boundaries of the damage-prone area have changed little since the late 1800's (U. S. Forest Service 1969). Southern pine beetles are natural agents that set back succession. Dead standing trees in damaged areas are valuable woodpecker foraging areas and nest sites for cavity-nesting species. Small, scattered infested areas are important bird habitat; however, large areas are not as valuable to birds.

Lightning strikes, damaging tropical storms, glaze storms, and wild fires are significant agents modifying bird habitat in the loblolly-shortleaf pine type. Before the arrival of European man they were very important to bird species of earlier successional stages. Lightning-struck and wind-damaged trees are readily used by foraging woodpeckers and also are used as nest sites. Large wind-thrown areas create forest openings that are useful demonstration and management areas for the effects of natural habitat modifications on bird populations. Wildfires are of less importance today because of fire control technology. Large burned areas obviously benefit early seral stage birds, but the loss in lives, timber, and property would be great if these fires were not controlled. Man replaces the effects of wildfires by harvesting and other silvicultural practices.

LAND USE TRENDS AND BIRD HABITAT

Regional land use trends can significantly modify bird populations (Dambach and Good 1940, Warbach 1958). In the Southern Piedmont a trend of increased timberland and decreased farmland has been evident for the last 5 decades. Small farms are being displaced by large agribusinesses employing highly mechanized and more intensive practices with fertilization, irrigation, and large open fields without hedgerows. High operation costs have eliminated diverse habitat that is valuable to many wildlife species on farmland. More land is used in crop production on today's highly mechanized farms that depend heavily on outside energy sources (e.g. fertilizer, irrigation, pesticides).

Private lands in relatively small holdings make up a significant percentage of the land area but receive relatively little attention from wildlife biologists. These lands usually are not available for management by wildlife biologists; but, we should make information available to landowners interested in bird management and recommend that they consider management of the entire bird community and not individual species (except in the case of endangered species).

Rapid human population growth in the South is causing large increases in subdivisions and corresponding loss of forest bird habitat. Few studies have been completed on the effects of subdivisions on summer and winter bird communities. None have been done in the loblolly-shortleaf pine type. Commonly subdivisions are thought to provide only House Sparrow (Passer domesticus) and Starling (Sturnus vulgaris) habitat; however, with proper management and initial subdivision planning, these habitats should produce diverse bird communities with very high densities. Subdivisions may be an important factor in the breeding range extensions of many songbird species.

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Forest Bird Communities of the Bottomland Hardwoods

James G. Dickson

Abstract.--Bottomland hardwoods, which are dwindling in
area, support abundant breeding and winter birds. To help
birds associated with bottomland hardwoods, land managers
should: keep land in forests, maintain diversity of trees
species and stand ages, maintain some old stands, maximize
stand vertical foliage layers and habitat patchiness, and
take special measures for rare bird species.

In 1970 the oak-gum-cypress forest complex,
commonly called bottomland hardwoods, extended
over about 13 million ha throughout the South
(USDA 1975). This forest occurs mainly along
major rivers and tributaries that extend into
upland pine sites. Bottomland forests have
long been recognized for their abundance of
game animals, such as deer, turkey, and
squirrels (Stransky and Halls 1968), and are
also productive of nongame birds.

SITES AND FOREST TYPES

The two major areas in which bottomland
hardwoods are found are first bottoms and ter-
races (Putnam 1951). First bottoms were
formed by the present drainage system and are
subject to frequent flooding unless afforded
levee protection. Terraces were formed by
earlier drainage systems and are not flooded
except during superflood stages. Within both
first bottoms and terraces are ridges, flats,
sloughs, and swamps. New land or front is
found only in first bottoms.

There are eight primary bottomland hard-
wood forest types and several variations of
these (Putnam 1951). The sweetgum-water oak
type is usually found on terrace flats and on
first bottom flats and ridges. The white
oaks-red oaks-hardwoods type occurs mainly on
sandy loam soils of first bottom ridges and
on terrace ridges. The hackberry-elm-ash
type is found mainly on first bottom low
ridges and flats, in first bottom sloughs, on
terrace flats, and in terrace sloughs. The
overcup oak-bitter pecan type is situated on
low, poorly drained flats, sloughs, and in
the lowest backwater basins. The cottonwood

type is a pioneer type found mainly on front
land ridges and well-drained flats. The wil-
low type is also a pioneer type usually found
on front land sloughs and low flats. River-
front hardwoods (sweet pecan, sycamore, hack-
berry, American elm, green ash) occur on all
front lands except deep sloughs and swamps.
The cypress-tupelo gum type grows in very low,
poorly drained flats, deep sloughs, and swamps
in first bottoms and terraces, and in river
estuaries.

FACTORS AFFECTING STAND COMPOSITION

Natural Succession

Tolerant species gradually replace in-
tolerant species in the successional process.
Eastern cottonwood and black willow are the two
main pioneer species on recent alluvium. They
are intolerant of shade and will not succeed
themselves. Cottonwood grows on higher sites
having coarse-textured soils and is succeeded
by riverfront hardwoods (Johnson 1973), which
are usually replaced by the sweetgum-water oak
association (Putnam et al. 1960). Black wil-
low establishes itself on fine-textured soils
on lower sites and is normally succeeded by
the hackberry-elm-ash association (Johnson
1973). As the alluvium ages, these ridges and
flats are occupied by a variety of species.

A slow succession of plant communities
occurs as sloughs and swamps fill with sedi-
ment (Putnam et al. 1960). Normally black
willow first occupies the site, then is usually
followed by bald cypress and tupelo in swamps
and overcup oak and water hickory in small
sloughs.

Geological Changes

But differences in forest types mainly
result from such geological changes as soil
deposition, flooding, and changes in stream
courses (Hosner and Minckler 1963, Broadfoot

and Williston 1973), rather than from natural succession (Odum 1969). Floodwaters deposit coarse sands nearer channels and the fine clays away from channels. These deposits alter the sites and consequently the trees growing thereon. As silt builds up, streams and rivers change directions, thereby altering sites and stand composition.

Animals and Fire

The composition of bottomland hardwood stands has also been affected by insects, diseases, livestock and wildlife predation on seed and seedlings, and fire. For example, cattle can severely compact the soil and eliminate natural regeneration in overgrazed stands. Virtually all species of bottomland hardwoods are vulnerable to fires (Brown and Davis 1973), and past fires have consumed young vegetation in stands and provided entry for decay in older trees (Putnam 1951).

Forest Management Practices

Composition of most stands today reflects past decisions to cut the more valuable species and the more valuable individual trees (Putnam et al. 1960). For example, the tolerant boxelder persists in the understory of riverfront hardwoods and has dominated many sites after more valuable hardwoods were harvested (Johnson 1973).

Management goals, stand composition, and species-site relationships determine the choice of regeneration system. The single tree selection system that has been used and often misued for so long in the South (McKnight and Johnson 1966) has fallen into disfavor. This regeneration system opens stands gradually and favors commercially less desirable, shade-tolerant species (Johnson 1973). Most harvest/regeneration systems now being promoted favor the commercially valuable, intolerant species such as cottonwood, sycamore, and yellow poplar.

Clearcutting is being conducted in even-aged cottonwood and willow stands, and is also appropriate where advanced reproduction is present, where sprouts will provide adequate regeneration, or where an appropriate seed source and receptive site occur together.

Seed tree cuts, where 20 to 25 seed trees per ha are left, can be successful for light seeded species on exposed mineral soil. This technique has been used for cottonwoods (McKnight and Johnson 1966), but is sometimes impractical because good seed crops are difficult to obtain on mineral soil before the site is overcome by brush.

In the shelterwood system, trees are harvested and the stand gradually opened in a series of cuts. Advance reproduction is established before the final cut. The shelterwood system is appropriate for heavy seeded species such as oaks, but is not satisfactory for species with intolerant seedlings (McKnight and Johnson 1966).

Group selection is cutting in small patches (McKnight and Johnson 1966) and is appropriate where advance regeneration, sprouts, or a seed source will fill the vegetative void created by the harvest.

Many mixed hardwood stands are being converted to hardwood monocultures. Cottonwood is the primary species planted, followed by sycamore and sweetgum. Cottonwood thrives on well-drained sandy and silty loams which are common in the batture (area between the river and levee) of the lower Mississippi River (McKnight 1970). About 0.4 million ha are suitable for cottonwood plantations (Dutrow et al. 1970).

Land Use Changes

The conversion of hardwood stands to agricultural crops has had a severe impact on bottomland hardwoods, especially in the Mississippi Delta. In the early 1930's the Delta region of Arkansas, Mississippi, and Louisiana had nearly 4.8 million ha of hardwood forest (Sternitzke 1976). The last Forest Service surveys (1967 for Mississippi, 1969 for Arkansas, and 1974 for Louisiana) showed only 2.9 million ha remained in hardwoods. Most cleared land went into soybean production. From 1964 to 1974, eighty percent of cleared bottomland hardwoods in Louisiana went into soybeans, and most of the remainder was converted to improved pasture and cotton (Sternitzke 1976).

Hardwood land along most rivers throughout the South has also been lost to reservoirs. In East Texas, for example, Toledo Bend and Sam Rayburn reservoirs alone occupy over 100 thousand ha which once supported mostly bottomland hardwoods.

BIRD-HABITAT RELATIONSHIPS

Birds are associated with numerous habitat parameters, such as number of vertical foliage layers (MacArthur and MacArthur 1961), total foliage volume (Willson 1974), foliage density near the ground (Dickson and Segelquist unpubl. data), overstory hardwood/conifer mixture (Hooper et al. 1973), habitat patchiness (Roth 1976), successional stage of stand (Shugart and James 1973), and moisture gradient (Bond 1957, Smith 1977).

Bottomlands are normally moist for at least part of the year, although front ridges with sandy soils and flats with heavy clay soils often have little available moisture. The greater moisture on most bottomland sites

usually allows more understory vegetation and should increase bird density. But long-term flooding and standing water in swamps can reduce or virtually eliminate foliage layers near the ground. This condition reduces ground nesting birds such as the Kentucky Warbler and overwintering ground foragers such as the White-throated Sparrow (Dickson 1974), but may provide some protection from predators for colonial nesters such as herons, egrets, and Red-winged Blackbirds.

Bird Populations in Breeding Season

The moist bottomland hardwoods of the South support an abundance of breeding birds. When bird density and species diversity (calculated from the information theory, Shannon 1948) in a pine, a pine-hardwood, and a mature bottomland hardwood stand were compared in an East Texas study (Anderson 1975), the hardwood stand had a higher bird density (1050 per km^2) during spring, than the other two stands (835 per km^2--pine, 422 per km^2--pine/hardwood). Number of bird species and species diversity were similar in the bottomland hardwood and pine-hardwood stands, but substantially higher than that in the pine stand.

Similar results were evident from a comparison of breeding bird censuses in different habitats in the Louisiana-East Texas area (Table 1). Higher bird densities were recorded in mature bottomland hardwoods than in upland pine and pine-hardwood stands of different ages. Bird density in three bottomland hardwood stands ranged from 752 to 1480 territorial male birds per km^2, about 2 to 4 times that in the best upland stands. Bird species diversity in the bottomland hardwoods was higher than diversities in shorter pine and pine-hardwood stands, but about the same as that in mature upland pine and pine-hardwood stands of similar height. The bottomland hardwood stands would probably have had higher bird diversities but high stand densities (29-45 m^2/ha basal area) limited light penetration, understory vegetation, and habitat patchiness.

Some bird species are associated with stands of particular age and height classes. Bird species associatd with young stands (< 4 m tall) include the Yellow-breasted Chat, Common Yellowthroat, Indigo and Painted Buntings, and Red-headed Woodpeckers that nest in remnant snags.

A sample of species and estimated densities of breeding birds in mature bottomland hardwoods in the Louisiana-East Texas area is shown in Table 2. Although some birds such as the Cardinal and Carolina Wren are ubiquitous in habitat distribution, other species are more restricted to deciduous bottomland hardwood stands. Barred Owls and Red-

shouldered Hawks are two birds of prey commonly found in hardwood bottoms, but they are not normally detected in singing male bird censuses of small areas. Wood ducks, which feed on hardwood, mast commonly nest in tree cavities. Many colonial nesters, such as the Yellow-crowned Night Heron, nest and feed in swamps throughout the South. The Yellow-billed Cuckoo is widespread in the canopy of hardwood bottoms. The Acadian Flycatcher is associated with moist forests (Shugart and James 1973, Smith 1977) and is abundant in the Louisiana-East Texas hardwood bottoms. Prothonotary Warblers, Parula Warblers, and American Redstarts are all associated with floodplain forests in the Big Thicket area of East Texas (Bryan et al. 1975), and Prothonotary and Parula Warblers are common during breeding season in swamps (Table 2). The Prothonotary Warbler nests in cavities, which are abundant in trees killed by standing water. The Parula Warbler builds in nest in Spanishmoss, which is found in moist habitats (Lowery 1974: 505). The Swainson's Warbler, common in the Louisiana hardwood bottom, is primarily associated with river floodplains and moist woods of the Southern Appalachians (Meanley 1971).

Several rare (or extinct) species have been linked with southern bottomland hardwoods. Hooper and Hamel (1977) determined that nesting habitat of the extremely rare Bachman's Warbler had been bottomlands and headwater swamps that were inundated for short periods and subject to disturbances. The Ivory-billed Woodpecker, a bird of the once extensive mature bottomland hardwoods (Tanner 1942), is now probably extinct because of timber cutting.

Bird Populations in Winter

Mature bottomland hardwoods have dense bird populations during the critical winter period. In a bottomland hardwood stand in East Texas, the estimated winter bird population was 1168 per km^2, higher than numbers in a nearby pine stand (845 per km^2) and in an adjacent pine-hardwood stand (672 per km^2) (Anderson 1975). Number of species and species diversity varied little between stands. In a south central Louisiana mature hardwood bottom, estimated monthly winter populations varied between about 1400 and 2000 birds per km^2, about twice the breeding bird density (Dickson unpubl. data). Winter visitors, which inhabit more northerly habitats or other habitats during breeding season, dominated the bird community. White-throated Sparrow density approached 500 per km^2 and Common Grackles varied between approximately 100 and 1,000 per km^2 (Dickson 1974). Red-headed Woodpeckers, which select habitat with open understories during the breeding season, were common winter residents in the bottomland hardwoods. Yellow-bellied Sapsuckers, Blue Jays, Brown Thrashers, American Robins, Hermit

Table 1.--Comparison of breeding bird density, diversity, and number of species in different habitats in Louisiana and East Texas.[1]

Stand	Bird species diversity[2]	Number of species	Bird density (territorial males per km^2)
Pine			
Small sapling	2.32	12	313
Sapling	1.06	3	25
Pole	1.91	9	161
Pole (Cleaveland 1973)	2.21	11	205
Sawtimber	2.66	18	365
Sawtimber (Noble and Hamilton 1974)	2.69	18	300
Pine-hardwood			
Small sapling	2.27	14	359
Sapling	2.24	11	295
Pole	2.11	9	292
Sawtimber	2.63	17	358
Bottomland hardwoods			
Tupelo swamp (Ortego and Noble 1975)	2.69	23	1480
Oak-gum (Dickson 1973)	2.32	16	752
Oak-gum (Hightower et al. 1974)	2.40	22	864

[1]Data from U.S. Forest Service studies and Breeding Bird Censuses published in *American Birds*.

[2]Calculated from Shannon information formula (1948), $H' = -\Sigma p_i \ln p_i$, where p_i = the proportion of all birds in a stand of each species.

Thrushes, and Ruby-crowned Kinglets are other birds commonly found in bottomland hardwoods during winter.

Breeding and Winter Bird Populations in Hardwood Plantations

In some hardwood areas, primarily in the Mississippi Delta, uneven-aged stands are being converted to hardwood plantations, mainly cottonwood, sweetgum, and sycamore. These plantations and natural cottonwood and willow stands on new land are deficient in plant species mixture and foliage height diversity, unlike the natural uneven-aged stands of many tree species. Plantations can therefore be expected to have fewer birds and lower species diversity than natural stands. A recent investigation of wildlife populations in cottonwood plantations in Mississippi confirmed these expectations (Wesley et al. 1976). Birds were censused in a natural stand and in an unthinned plantation on Catfish Point and in a natural stand, an unthinned plantation, and a thinned plantation on Huntington Point. During winter there were 79 percent more birds in a natural stand than in an unthinned cottonwood plantation. During breeding season,

Table 2.--Territorial male birds per km^2 in three mature bottomland
hardwood stands in Louisiana and East Texas.[1]

Species	Tupelo swamp (La.)	Stand Oak-gum (La.)	Oak-gum (Tx.)
Wood Duck	20		
Yellow-crowned Night Heron	20		
Purple Gallinule	10		
Yellow-billed Cuckoo	20	86	60
Chimney Swift	40		
Pileated Woodpecker		12	4
Red-bellied Woodpecker	80	12	16
Ruby-throated Hummingbird			16
Downy Woodpecker	80		32
Great Crested Flycatcher	190	6	28
Eastern Kingbird	10		
Acadian Flycatcher	140	62	224
Eastern Wood Pewee			4
Blue Jay	30		
Carolina Chickadee	80		12
Tufted Titmouse	20	80	64
White-breasted Nuthatch			8
Carolina Wren	80	148	64
Wood Thrush		6	
Blue-gray Gnatcatcher			48
Starling	40		
White-eyed Vireo		136	4
Yellow-throated Vireo		31	12
Red-eyed Vireo	10	25	92
Black-and-White Warbler			4
Parula Warbler	110		
Yellow-throated Warbler			12
American Redstart			4
Swainson's Warbler		25	

Table 2.--Continued

Species	Tupelo swamp (La.)	Stand Oak-gum (La.)	Oak-gum (Tx.)
Prothonotary Warbler	200		64
Kentucky Warbler		12	
Hooded Warbler		12	
Red-winged Blackbird	90		
Common Grackle	70		
Summer Tanager	20		12
Northern Oriole	40		
Cardinal	80	93	80
Rufous-sided Towhee		6	

1/ Data from breeding bird censuses published in American Birds:
Tupelo swamp (La.) (Ortego and Noble 1974), Oak-gum (La.) (Dickson 1973),
Oak-gum (Tx.) (Hightower et al. 1974).

bird density and number of bird species were consistently lower in unthinned cottonwood plantations than in natural stands. On Huntington Point in the thinned plantation, the number of breeding bird species was similar to that in the natural stand, but bird density was lower. Cavity nesters such as the larger woodpeckers, the Great Crested Flycatcher, and the Prothonotary Warbler avoided the thinned and unthinned plantations, as did some birds, such as Hooded and Kentucky Warblers, that are associated with hardwood midstory (Dickson and Noble in press). Although the number of bird species was lower in the plantations than in the natural stands, the investigators thought that number of bird species in the entire area was probably increased because some species such as Red-winged Blackbirds, Yellowthroats, Yellow-breasted Chats, Norther and Orchard Orioles, Rufous-sided Towhees, and Warbling Vireos were commonly found in plantations but not in natural stands.

MANAGING BIRD HABITAT
IN THE BOTTOMLAND HARDWOODS

The main threat to birds that inhabit bottomland hardwoods is the conversion of forests to agricultural land and reservoirs. Thus, the first management priority should be to keep bottomlands in hardwoods. Birds such as Prothonotary and Parula Warblers, which have specific habitat requirements and are as-sociated with bottomland hardwoods will decrease in proportion to their dwindling habitat.

Land managers should maintain a diversity of tree species and age classes. Multiple objectives of bird and timber management can be met through harvesting by single tree selection, group selection, or small clearcuts (e.g., < 40 ha). Interspersion of forest stands with non-forested land such as crops should increase bird diversity.

Some natural mature stands (> 100 years old) should be maintained. Some birds of the bottomlands thrive in the canopy or shaded understory of mature stands. Decayed wood is abundant in natural mature stands but is being eliminated by intensive timber management. Many birds nest and feed in decayed wood. For nest building woodpeckers depend on trees infected with heart rots (Conner et al. 1976). Many other secondary cavity nesters use woodpecker excavations for nests (Balda 1975).

Although diversity of habitat should be used as a general guideline, some large mature stands (> 1000 ha) and corridors of mature trees between stands should be maintained. Such corridors should insure genetic variability by maintaining gene flow between bird populations that might otherwise become isolated.

To increase bird density and diversity, managers should manipulate stands by plantings, thinnings, harvests, etc., that maximize foliage layers beneath the canopy. A basal area of about 20 m^2 per ha over a portion of each stand should allow understory vegetation to develop, but be dense enough to curtail epicormic branching. Basal areas lower than 20 m^2 per ha can be maintained without profuse epicormic branching if thinnings and harvest cuts are conducted gradually.

The same management techniques discussed above plus stand size can be used to enhance habitat patchiness by producing dense clumps of vegetation interspersed with sparse or open areas.

Rare species, colonial nesters, and their respective habitats, deserve special efforts in research and habitat management.

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Wednesday Morning, January 25

EFFECTS OF MANAGEMENT PRACTICES
ON NONGAME BIRDS (continued)

Moderator: J. W. Hardy
Florida State Museum

Oak-Pine and Oak-Hickory Forest Bird Communities and Management Options

Keith E. Evans[1]

Abstract.--Successional trends, soil-site characteristics, and land use options in the oak-pine and oak-hickory forest types are discussed in relation to bird populations and bird-habitat associations. Management guidelines are provided. Management alternatives include attracting birds to recreational areas, identifying unique birding areas, managing for ecosystem integrity, and enhancing the habitat for cavity nesting bird species.

INTRODUCTION

The 125 million acre oak-hickory and the 34.5 million acre oak-pine forest types make up most of the inland forests of eastern United States and account for 30 percent of all commercial timberland in the United States (USDA Forest Service 1977). In addition, much of the loblolly-shortleaf pine forests would be replaced by oak-hickory species if successional trends were unchecked (USDA Forest Service 1973a).

These vast forests are extremely important to many birds. From 300 to 400 species use the area each year, and 150 to 200 of them nest in the eastern midcontinent region. I recognize that many of these species are not dependent directly on the oak-hickory and oak-pine forest types. Emphasis will be on those bird species that nest or winter in association with oak-hickory and oak-pine types. Migrating species, although important, seem more adaptable to habitat variations and are less affected by most forest management options. Management goals for migrants should be directed to those species with specific needs (Sprunt 1975).

Many agencies, including the Forest Service, have recently expended much effort to include nongame birds in their management plans. The main cooperative endeavors include: (1) Service-wide Timber-Wildlife Coordination Workshop (USDA Forest Service 1973b), (2) Timber-Wildlife Management Symposium (Slusher and Hinckley 1974), and (3) Symposium on the Management of Forest and Range Habitats for Nongame Birds (Smith 1975). These efforts along with regional workshops will set-the-stage for future management programs and identify high priority research needs.

PLANT COMMUNITIES

The area occupied by oak-hickory and oak-pine forest is highly diverse due to elevation gradients, north-south climatic gradients, topography, soil-site differences, aspect, successional stages, and land-use options. Somewhere between 3,000 and 5,000 plant species occur in the area. Most of the emphasis in this paper will be on vegetative shape or structure and the variations in structural attributes caused by succession, soil-site characteristics, and land use-options.

Natural Succession

Oak-Hickory Forests

Succession is a dynamic process with rapid changes occurring for approximately 40 years before a more or less stable oak-hickory forest community persists. The first year after a cultivated field is abandoned, a wide variety of annual grasses and forbs appear.

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Years 3 to 6 show a change from annual species to perennial grasses and forbs, and shrubs begin to invade. Years 6 to 15 are the "brush" years--shrub species dominate and there is an increase in post oak, shagbark hickory, and the clonal tree species. By year 15 many clonal species such as persimmon are decreasing. Between years 15 and 40, an increase occurs in the more climax species such as white and black oak (Drew 1942, Shelford 1963). The quality of the site determines the dominants in the older oak-hickory stands. The best sites will produce white, red, and black oak; the intermediate sites will produce white and post oak; and the poor sites will produce mostly post and blackjack oak.

Oak-Pine Forests

Succession for the oak-pine type is similar to the oak-hickory except that pine seedlings come in after site disturbances. The pine often persist for up to 100 years. In the piedmont area, abandoned cultivated areas will first be vegetated with annual forbs and horseweed and then be invaded with broomsedge. The broomsedge (as a dominant) will be replaced by pine after about 6 years. The oak-pine forests that develop often contain large amounts of yellow-poplar and blackgum after 15 to 40 years of succession. If logging, fire, and other disturbances are eliminated, the oak-hickory forest components will begin to dominate after 40 years (Oosting 1942, Johnston and Odum 1956).

Old field successional stages are different than succession after a clearcut. These differences are more obvious in the oak-pine type than in the oak-hickory type. Old fields proceed into nearly pure pine stands that persist for many years before the oak forest components appear. However, when an oak-pine forest is clearcut, the entire range of oak-pine forest components will be present throughout stand development. For the purposes of this paper, my comments will include forest situations where oak-pine components exist and exclude situations where the land-use option is to maintain and manage for pine.

Soil-Site Characteristics

Soil-site attributes play an important role in the structural development of a forest. The better sites tend to have more plant species and a more developed under-story. Soil type and fertility is an ecological force that influences the quantity and quality of food and cover. Thus soil characteristics must be considered as an integral part of a model that associates bird species with attributes of nesting, roosting, and feeding sites.

A relatively tight crown closure is common throughout the oak-hickory and oak-pine forests. Murphy and Crawford (1970) found that 85 percent of their oak-pine plots, and 91 percent of their oak and mixed hardwood plots had a crown closure exceeding 70 percent. Total vegetation production on these plots was generally less than 200 pounds of oven dry material per acre per year. Density of forest stands and crown closure probably influence understory development more than any other factors (Table 1).

Table 1.--Frequency of occurrence of forest understory plants in Missouri (Murphy and Crawford 1970). (In percent)

Plant	Oak-pine	Black-scarlet oak	White oak
Panic grass	26	19	26
Little bluestem and broomsedge	23	13	12
Sedge	14	18	22
Poverty oatgrass	9	8	11
Lespedeza	33	22	24
Tick trefoil	27	27	40
Aster	25	22	24
Pussytoes	17	12	21
Dittany	13	8	15
Goat's rue	13	--	--
Sunflower	9	9	--
Blueberry	42	28	32
Hickory	20	23	16
White oak	19	18	34
Sassafras	18	21	15
Black oak	15	18	15
Post oak	12	11	--
Shortleaf pine	11	--	--
Scarlet oak	10	8	--
Grape	10	12	13
Flowering dogwood	9	10	17
Woodbine	--	9	14
Hawkweed	--	--	8
Blackgum	--	--	10

Stand development after a regeneration cut in upland hardwoods is similar to old field natural succession except for a short herbaceous stage. The first 10 to 15 years after a regeneration cut are referred to as the "brush" stage when 25,000 woody stems per hectare is common. By year 20, 75 percent of these will die on areas with a site index of 55, 80 percent will die on areas with a site index of 65, and 85 percent will die on areas with a site index of 75. By age 80, natural death in unthinned stands will eliminate 90 percent of the woody stems that were present at age 20. By age 80, site index 55 areas will support approximately 600 trees per hectare (average of 23.4 cm d.b.h.), site index 65 will have 460 trees per hectare (average of 27.2 cm d.b.h.), and site index 75 will have 410 trees per hectare (average of 29.2 cm d.b.h.) (Gingrich 1971). These dead and dying trees provide important nesting sites and feeding resources for many birds throughout the rotation age of the forest (Hardin and Evans 1977).

Land Use Impacts

Timber, range, agriculture, and urban activities, along with many other land use options, have a significant impact on the structural characteristics and successional stages of forest areas (Table 2). Species composition changes as vegetation type and structure changes, but all birds are never eliminated. From the diverse habitat preferences of eastern deciduous bird species, and the large number of species selecting edge types, we can assume that these species evolved in an area of high diversity with considerable edge. The greatest potential detrimental impacts of modern silvicultural practices are probably the removal of cull and dead trees and the elimination of large tracts of old growth.

Table 2.--A digitized classification system for the vegetational conditions (structural communities) existing in the area of eastern United States occupied by oak-hickory and oak-pine forest types

100   Forest openings
   110   Cultivated, row crops
   120   Pasture
      121   Mowed
      122   Grazed
   130   Early successional stages or shallow soil
      131   Bare ground and rock outcrops
      132   Low herbaceous cover, mostly annual plants
      133   Herbaceous, mostly perennial grasses and forbs
      134   Herbaceous, mostly grasses and forbs with shrub invasion
      135   Clonal shrubs such as corralberry, persimmon, and eastern redcedar
      136   Small tree glade, with eastern redcedar, winged elm, sumac, persimmon, and mixed hardwoods less than 4 m tall
200   Urban areas
300   Forest and woodland
   310   Regeneration (less than 5 cm d.b.h.)
      311   Without site preparation
      312   With site preparation
   320   Seedling-sapling (5-10 cm d.b.h.)
      321   Natural regeneration
      322   Artificial regeneration
   330   Pole stand (10-25 cm d.b.h.)
      331   Natural thinning only
         331.1   Limited understory
         331.2   Primarily grass-forb understory
         331.3   Primarily low shrub understory
         331.4   Primarily shade tolerant midstory species in understory
         331.5   Well developed multi-layered understory
      332   Thinning, selection harvest
         332.1   Limited understory
         332.2   Primarily grass-forb understory
         332.3   Primarily low shrub understory
         332.4   Primarily shade tolerant midstory species in understory
         332.5   Well developed multi-layered understory
   340   Sawlog stand (more than 25 cm d.b.h.)
      341   Natural thinning only
         341.1   Limited understory
         341.2   Primarily grass-forb understory
         341.3   Primarily low shrub understory
         341.4   Primarily shade tolerant midstory species in understory
         341.5   Well developed multi-layered understory
      342   Thinning, selection harvest
         342.1   Limited understory
         342.2   Primarily grass-forb understory
         342.3   Primarily low shrub understory
         342.4   Primarily shade tolerant midstory species in understory
         342.5   Well developed multi-layered understory

350 Old growth (a stand older than "economic rotation age," usually characterized by an overstory of old trees of which many are suitable for cavity nesting species)
  351 Natural thinning only
    351.1 Limited understory
    351.2 Primarily grass-forb understory
    351.3 Primarily low shrub understory
    351.4 Primarily shade tolerant midstory species in understory
    351.5 Well developed multi-layered understory
  352 Thinning, selection harvest
    352.1 Limited understory
    352.2 Primarily grass-forb understory
    352.3 Primarily low shrub understory
    352.4 Primarily shade tolerant midstory species in understory
    352.5 Well developed multi-layered understory
400 Water influence zones
  410 Vegetation associated with perennial streams
  420 Vegetation associated with intermittent streams
  430 Vegetation associated with large reservoirs
  440 Vegetation associated with ponds, sinkholes, and springs

Originally, the majority of the eastern United States was a mature (old growth) deciduous forest. The exact pattern of the mosaic of successional stages is unknown. John J. Audubon and Alexander Wilson in their extensive travels throughout the region saw only a limited number of birds that are restricted to brushy successional stages (Griscom and Sprunt 1957). Their journals indicate that extensive tracts of old growth forests were common. Little information is available on bird population levels in climax forest stands. Most stands that have been studied are small fragments (forest islands) and bird population composition and density is strongly influenced by the "edge effect" (Table 3). Most forest interior bird species are able to breed in forest fragments as small as 35 acres (15 ha). However, MacClintock et al. (1977) stated that this is apparently only possible if the fragment is "subsidized" by a nearby major forest system.

Table 3.--Population of the common breeding bird species on two mature (possibly climax) forests: (a) oak-hickory forest in West Virginia and (b) oak-hickory hardwoods of the Southern Piedmont Plateau in North Carolina (Loery 1966)

Bird species	Forest habitat	
	A	B
	(Birds/40 ha or 100 acres)	
Red-eyed vireo	47	62
Ovenbird	37	26
Wood thrush	27	51
Cardinal	--	26
Carolina chickadee	--	23
Black-throated green warbler	20	--
Tufted titmouse	--	18
Black and white warbler	17	--
Cerulean warbler	17	--
Blue jay	--	14
Yellow-throated vireo	13	4
Solitary vireo	13	--
Hooded warbler	3	11
Acadian flycatcher	--	11
Brown-headed cowbird	--	11
Scarlet tanger	10	9
Blackburnian warbler	10	--
Eastern wood pewee	7	5
Downy woodpecker	7	--
Great crested flycatcher	7	--
Red-bellied woodpecker	--	7
Carolina wren	--	7
White-eyed vireo	--	7
Rufous-sided towhee	--	5
Common flicker	--	4
Hairy woodpecker	--	4
Summer tanager	--	4
White-breasted nuthatch	3	4
Blue-gray gnatcatcher	3	--
Worm-eating warbler	3	--
Black-throated blue warbler	3	--

BIRD-HABITAT ASSOCIATIONS

The study of habitat selection by birds
is a fascinating but complex subject. Each
bird seems to have a physiological and
behavioral preference for a certain set of
habitat attributes. Although there are
variations in the habitats chosen by differ-
ent individuals of the same species, there
are generally larger differences between
habitats chosen by different species. This
fact enables us to describe vegetation con-
ditions (types) that are preferred by
certain species. For example, we know that
killdeer prefer a bare ground type, that
yellow-breasted chats prefer a brushy area,
and that pileated woodpeckers prefer ex-
tensive areas of mature or over-mature
forests. But why should species have a
preferred habitat? Because the presence of
other species makes it necessary to special-
ize. This specialization more efficiently
utilizes all the components of the environ-
ment and lessens competition between species.
Any change in vegetation type or structure
throughout the oak-hickory or oak-pine for-
ests will change the bird species composition
(Tables 4 and 5).

Table 4.--Abundance of bird species found in various stages of oak-pine succession (adapted from Johnston and Odum 1956)

Bird species	Dominant plants and age in years of study area								
	Forbs	Grass	Grass-shrub		Pine forest				Oak-hickory climax
	1-2	2-3	15	20	25	35	60	100	150-200
Grasshopper sparrow	B[1]	A	A						
Eastern meadowlark	C	B	B	C					
Field sparrow			A	A	A	C	C		
Yellowthroat			B	B					
Yellow-breasted chat			C	B					
Cardinal			C	C	B	B	B	A	A
Rufous-sided towhee			C	C	B	B	B	B	
Bachman's sparrow				C	C	C			
Prairie warbler				C	C				
White-eyed vireo				C		C	C		
Pine warbler					B	A	B	A	
Summer tanager					C	B	B	B	B
Carolina wren						C	C	A	B
Carolina chickadee						C	C	C	C
Blue-gray gnatcatcher						C	B		B
Brown-headed nuthatch							C	C	
Eastern wood pewee							B	C	C
Hummingbird							B	B	B
Tufted titmouse							C	B	B
Yellow-throated vireo							C	C	C
Hooded warbler							C	A	B
Red-eyed vireo							C	B	A
Hairy woodpecker							C	C	C
Downy woodpecker							C	C	C
Great crested flycatcher							C	B	C
Wood thrush							C	C	A
Yellow-billed cuckoo								C	B
Black and white warbler									C
Kentucky warbler									C
Acadian flycatcher									C
Totals: (including rare species not listed above)	15	40	110	136	87	93	158	239	228

[1] A is most abundant, B is abundant, and C is common.

Table 5.--Abundance of bird species found in various age stands after clearcutting a mixed oak stand in Virginia (adapted from Conner and Adkisson 1975)

Species	1-year-old clearcut	3-year-old clearcut	7-year-old clearcut	12-year-old clearcut	Pole stand	Mature stand
Eastern bluebird	A[1/]	C	C	C		
Indigo bunting	A	B	B	C		
Carolina wren	B	C	C		C	
Common flicker	B	C	C	C		
Carolina chickadee	C		C			
Downy woodpecker	C					C
American goldfinch	C	C	C	C		
Brown-headed cowbird	B	C	C	C	B	C
Prairie warbler		B	B	A		
Field sparrow		B	B	C		
Rufous-sided towhee		B	B	B	C	
Yellow-breasted chat		C	C	B		
Hooded warbler		C	C	B		
Golden-winged warbler		C	C	C		
Cardinal		C	C	C		
Blue-winged warbler		C	C			
Brown thrasher		C				
Chestnut-sided warbler		C		C		
Ruby-throated hummingbird		C	C	C		
Hairy woodpecker		C				C
Catbird		C	C			
Worm-eating warbler			C	C		
Kentucky warbler			C			
Whip-poor-will			C			
White-eyed vireo			C			
Eastern wood pewee				C		C
Red-eyed vireo				C		B
Great crested flycatcher				C	C	C
Black and white warbler				C	C	
Scarlet tanager				C	C	C
Ovenbird					A	B
Blue-gray gnatcatcher					B	C
Wood thrush					B	B
Acadian flycatcher					C	C
Tufted titmouse					B	C
Pileated woodpecker						C
White-breasted nuthatch						C
Turkey						C
Ruffed grouse						C
Number of bird species observed	39	162	154	143	44	93

1/ A is most abundant, B is abundant, and C is common.

The word habitat is often used in reference to a specific mapable unit or obvious vegetation condition. Several species co-exist in any selected vegetation type (mapable habitat unit)--for example, an oak-hickory well stocked pole stand with limited understory (Table 2, number 331.1) might be inhabited by red-eyed vireos, tufted titmice, downy woodpeckers, blue-gray gnatcatchers, and many others. The Volterra-Gause principle asserts the two species cannot co-exist indefinitely if they are limited in their population size by the same factors. This principle implies that co-existing species are limited by different factors. These differences are often complex and subtle. Shugart et al (1975) touched on this principle when they listed groups of birds that co-existed in a given vegetation type, but used the resources differently. For example, kinglets, titmice, and chickadees have similar feeding behavior, but different food preferences; red-eyed vireos, Carolina wrens, and ruby-crowned kinglets eat similar foods, but have different feeding behavior. From a management point-of-view, I feel that it is important to indicate groups of species that will co-exist in one vegetation type without long discussions of the subtle differences (Tables 4 and 5).

One other idea pursued in the management guidelines is the recognition that bird species vary greatly in the specificity of their habitat requirements. The stenoecious species, those with limited adaptability to habitat variability, provide the greatest potential and challenge for management. These species require a specific habitat component (or components) to complete at least one phase of their life cycle. Most of the rare, endangered and threatened species are stenoecious.

Structure of vegetation tends to play a dominant role in bird habitat selection processes (Lack 1933, Miller 1942, Kendeigh 1945, Bond 1957 and others). For example, several warbler species will live in a mature lowland forest with an understory of giant cane but, as shown below they utilize different resource attributes.

Species	Height of nest or foraging area	Feeding sites
Cerulean warbler		Tree tops (canopy)
Yellow-throated warbler	15 m	Glean from small limbs
Black and white warbler		Glean from large limbs
Parula warbler	10 m	Generalist
Redstart		Second growth, large insect prey
Yellow warbler	7 m	Water edge
Prothonotary warbler		Cavity nester
Kentucky warbler	5 m	Feeds by gleaning
Hooded warbler		Feeds by hawking
Wormeating warbler		Steep slope
Swainson's warbler		In giant cane
La. waterthrush	0 m	Along streams

To maintain a full and natural complement of wildlife species, a full and natural complement of plant communities (habitats) must be retained in the landscape. Forest areas are in a continual state of flux and the distribution of comparable areas of vegetation varies with time (succession) and space (aerial extent). Land use, soil, and landform are each horizontal components of habitat heterogeneity whereas the abundance of forb, shrub, midstory, and canopy species are vertical components of habitat heterogeneity. The horizontal and vertical components are interrelated, both between the components and within the attributes of each component. A similar arrangement of components results in a stand. There will be variability within a stand, but generally management resolution will not be concerned with subtle variations. A sufficient number and arrangement of stands of each vegetation condition (seral stage) is necessary to harbor oganisms requiring specific habitats, because succession, land use options, and local disasters will continually cause areas to be unsuitable to some species.

A full vegetative complement including mature and dead standing trees, full understory and shrub layer and wide edges is necessary to maintain diverse breeding bird populations (Linehan et al 1967 and Verner 1975). Siderits (1975) indicated that plant species compositions, age-class and spatial coverage of stands are the most easily manipulated. Maximum diversity is a lower priority objective than maintaining a good distribution of the adapted communities. Communities should be delineated on the basis of plant species dominants, age, and stocking level. This type of management will benefit most species. The remaining species of interest--those with specific habitat components, endangered, threatened, or unique status, or those of economic importance-- will require specifically designed programs.

Specialized management plans could be initiated where one or more species requires "featuring" because of low population numbers, restricted range, or special interest. For example, a prescription might call for the control of understory shrub species in a mature forest to create a park-like stand for the Cooper's hawk, barred owl, prothonotary warbler, robin, and red-headed woodpecker. Another prescription would be to maintain an old field in low growing herbaceous cover to provide habitat for eastern meadowlarks, several species of sparrows, and bobwhites. Other birds that show definite habitat preferences include: those that depend on large trees (northern oriole and hooded warbler); those that depend on brushland (common yellowthroat, gray catbird, yellow-breasted chat, white-eyed vireo, and Kentucky warbler); and the forest edge species (mockingbird, yellow warbler, indigo bunting, and blue-winged warbler).

The oak-pine forests are of greater value to wintering bird populations than are the oak-hickory forests (Table 6). At least two major factors enter into this importance--the oak-pine forests are more southern and the coniferous tree component provides additional cover. The true importance of the oak-pine and oak-hickory forests in protecting and feeding wintering populations and, thus, maintaining breeding population is unknown.

Table 6.--Population levels of common wintering birds on three habitat types: (A) oak-hickory forest in Kansas, (B) mixed pine-deciduous forest in Louisiana, and (C) upland oak-hickory forest in Virginia (Ryder and Ryder 1976)

Species	Habitat type		
	A	B	C
(Birds/40 ha or 100 acres)			
Common grackle	-	132	-
White-throated sparrow	-	82	-
Ruby-crowned kinglet	-	50	+
Red-headed woodpecker	46	-	-
Tufted titmouse	25	14	7
Blue jay	17	23	+
Black-capped chickadee	25	-	-
Carolina chickadee	-	18	15
Pine warbler	-	23	-
Red-bellied woodpecker	8	14	7
Carolina wren	-	18	4
Common crow	-	-	15
Dark-eyed junco	8	14	-
American robin	-	14	-
Yellow-rumped warbler	-	14	-
Cardinal	-	14	-
White-breasted nuthatch	13	-	7
Golden-crowned kinglet	-	9	4
American goldfinch	-	9	-
Downy woodpecker	8	5	4
Brown creeper	+	5	4
Common flicker	-	5	+
Yellow-bellied sapsucker	-	5	+
Red-breasted nuthatch	-	5	-
Bobwhite	-	5	-
Eastern phoebe	-	5	-
Hermit thrush	-	5	-
Hairy woodpecker	+	+	4
Pileated woodpecker	-	-	4

MANAGEMENT GUIDELINES

The wildlife management profession has evolved through four distinct phases since its birth in the United States in the early 1900's. These phases are: (1) awakening of the public, (2) protection of a dwindling resource, (3) single species management, and (4) the presently favored "holistic" approach that involves intensive coordination with other program objectives. This last phase promises to be the most complex, but is potentially the most rewarding.

Setting specific management goals for a resource as large and diverse as eastern United States avifauna is complex, confusing, often contradictory, and maybe somewhat naive. Many approaches have been suggested and/or tried such as to: (1) maximize vertical and/or horizontal vegetational diversity, (2) maximize density of a featured species, (3) maximize number of species in a "key" area--from a recreational point-of-view this maximizes the probability of inter-specific encounter, and (4) manage for economic commodities and let the birds adapt.

In designing management programs, two assumptions should be applied. First, each species should be recognized for its intrin-sic value in ensuring the perpetuation of natural ecosystems. Therefore, all native species should be protected and efforts directed toward achieving and/or maintaining self-sustaining population levels. Second, different values can exist compatibly on the same area or in close proximity. There-fore, the needless sacrifice of any value is indefensible and the failure to make the most of all values is a dereliction of sound management. This still allows for areas where trees ought not to be cut, others where game ought not be harvested, and others where the public should be excluded.

I won't discuss the many forest management options that exist because these have been discussed in Zeedyk and Evans (1975) and Sander (1977). Three major options exist--even-aged management, uneven-aged management, and preservation.

With few exceptions (Marquis 1967) even-aged management is recommended by hard-wood silviculturists, primarily because other systems fail to produce adequate repro-duction and growth of desirable intolerant species (Sander and Clark 1971, Trimble 1970, Arend and Scholz 1969, Roach and Gingrich 1968). Three silvicultural cutting systems are employed to achieve even-aged stands--seedtree, shelterwood, and clearcutting. Stands typically pass through six recognizable stages--annual weed, brush, sapling, pole, small sawtimber, and mature sawtimber. The two types of operations in the life of an even-aged stand are the harvest cutting and intermediate treatments (thinnings). The impacts of these operations on bird populations are discussed in detail by Webb et al (1977).

For the purposes of this paper uneven-aged and all-aged management are lumped. Harvesting is done at scheduled intervals and the trees to be cut are selected, whether individually or in small groups. Selection is made on the basis of age, diameter, vigor, form, and species. Noncommercial treatment may follow commercial harvest to remove cull stems and undesirable species. Regulation is by volume and diameter rather than by area. Uneven-aged management tends to favor shade-tolerant species and to maintain a climax state or advance plant succession toward the climax community (Filip 1973). Intolerant or midtolerant species may sprout but fail to develop, thus the selection system is not recommended for oak silviculture. Some woodland owners practice uneven-aged manage-ment or "selection forestry" largely for aesthetic reasons.

Uneven-aged management tends to decrease tree species diversity and overstory biomass variations. Thus vertical diversity is en-hanced and horizontal diversity reduced. I found no direct information on how these changes influence bird populations but I can speculate on a few changes. The amount of edge habitats would probably decrease within a management unit. Some birds, like the cat-bird, seem to adjust to small openings (Bond 1957) and may utilize the edges resulting from group selection cutting. Birds that require larger openings would not adjust to uneven-aged management options. The non-commercial removal of snags and cull trees may influence cavity nesting species. Here again information is lacking on specific com-parisons of vertical and horizontal plant diversity.

Preservation as a management option has as its objective the development of a natural appearing forest, free from any evidence of logging. Presumedly the end result is the eventual development of old growth or climax plant community. Preservation is the selected objective of many Federal, State, and local agencies as well as private organizations and individuals. Like any other form of management, it has certain impacts upon wild-life habitat. Stand structure and composition will vary with climatic and edaphic conditions, overstory density, past use, fire history, wildlife and livestock browsing, and in the case of bottomland hardwoods, flood frequency, timing, and duration. Bond (1957), Odum (1950),

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and others have shown that the diversity of bird species is maximized at the preclimax or middle successional stage and that the number of species as well as total number of individuals is less at the climax stage. A group of forest-dwelling birds such as the red-eyed vireo and the cavity-nesting species of woodpeckers and owls would probably benefit from preservation objectives. Fire, storms, and site differences may create a mosaic of stands within a preservation framework.

I recommend that management adopt the following four-pronged approach, and that research strive to provide the information needed to accomplish this program.

1. Bring the birds to the people by developing habitats in and adjacent to recreational facilities and by enhancing bird viewing opportunities.

2. Bring the people to the birds by identifying unique birding areas, developing access to good birding spots, and educating the people in the art of bird appreciation.

3. Manage for ecosystem integrity by enhancing the structural complexity of physical and vegetational features of the landscape (Table 7), providing a variety of habitat components in a desirable combination to ensure fulfillment of individual species life requirements, and developing a program to identify and protect critical habitats of endangered, threatened, rare, and unique species.

4. Develop and initiate ways to enhance the habitat of the numerous cavity nesting species by accepting the idea that dead and dying trees are part of the natural stand development process. Thinnings should be done by girdling or herbiciding instead of felling. Regeneration goals could often be achieved without removing all dead, dying, and cull trees. Rotation age has a major influence on the cavity nesting bird species. These birds generally require mature forests for at least part of their life cycle. Short rotation cycles create young, vigorous, fast-growing timber stands with few natural cavities and dead trees. At least part of each management unit should be scheduled for a long rotation period--in excess of 100 years throughout the oak-hickory type. The pileated and red-bellied woodpeckers are two examples of birds that require extensive mature forest stands. The barred owls' preferred habitat is an oak woods that is free from understory brush and that has many dead or dying trees--conditions that are often present in over-mature forests.

Table 7.--A summary of the major habitat components considered in the management programs of the Mark Twain National Forest (USDA Forest Service 1973c)

Habitat component	Definition	Quantitative objectives	Qualitative objectives	Remarks
Age-size classes	The proportion of various ages or sizes represented ages 0-90; sizes-- sawlogs, poles, saplings, & reproduction	Balance of age-size by compartment, 34% sawlogs 44% poles, 11% saplings, and 11% regeneration size	A balance of age-size classes by vegetation types when adequate acreage present	Primarily commercial forest land, managed under an even-age system
Mast	Nuts and seeds from hardwood trees	40% of the compartment acreage in mast-producing stands (30% for pine compartments)	Hardwood vegetation types and species characteristics of the compartment	All hardwoods and hardwood-conifer types of commercial forest land and unproductive land
Old growth	Mature and overmature stands of all types	10% of the compartment acreage in old growth conditions	Vegetation types and sites representative of the compartment	All forested types and all land classes suitable for growing trees
Temporary forage	Tree reproduction less than 10 yrs. old	11% of the commercial land managed under even-age system (12% for pine)	Interspersion of regeneration areas among existing vegetation types and sites	All regeneration cuts and type conversion areas 0-9 years of age
Permanent forage	Areas managed for forbs, grasses, shrubs, or small trees	More than 9% of the compartment acreage (more than 8% for pine compartments)	A variety of permanent forage conditions and areas within compartments	Forest openings, grass lands (pasture and hay meadows), glades, upland drainages, rights-of-way, and savannas

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Cove Forests: Bird Communities and Management Options

Robert G. Hooper[1]

Abstract.--Over 60 species of birds regularly nest in cove forests. A primary goal for managing nongame birds is to provide suitable habitat, at some stage of the rotation, for each species that naturally occurs in a forest type. Even-aged stands up to 25 acres and rotations of 100 years should meet that goal in cove forests. Commercial thinnings benefit shrub nesting species but remove potential sites for cavity nesters.

INTRODUCTION

The forests of mountain coves, ravines, and adjacent moist slopes of the Southern Appalachians are among the most productive hardwood types of the North Temperate Zone. They have great esthetic value, protect water quality, and are of considerable botanical interest. Depending upon stand age and species composition, these forests provide habitat for many species of birds. In this paper I review existing information on breeding communities of birds in cove forests and predict possible effects of forest management options on these communities. Cove forests also may be important to winter bird populations, but data are lacking for an interpretation.

THE COVE FOREST

Cove forests are found at elevations between 1,000 and 4,500 feet in the Southern Appalachians of Virginia, Tennessee, North Carolina, South Carolina, and Georgia. They occupy coves, ravines, and adjacent moist lower slopes. An estimated 3.5 million acres of cove forest exist in the Southern Appalachians (D. E. Beck, pers. commun.). Some 30 tree species occur in cove forests; 6 to 8 may be prominent in any particular stand (Braun 1967, p. 199-205; Davis 1930; Whittaker 1956). At least 10 of these species are considered of high commercial value (table 1).

Various forest cover types have been recognized in coves (table 2). These types

grade into oak, oak-hickory, and oak-pine types on relatively dry sites. At high elevations, cove forests give way to northern hardwoods and spruce-fir. Hemlock commonly dominates on floors of ravines at all elevations and on broad valley flats around 4,000 feet above sea level.

Understory conditions vary tremendously: both open parklike and extremely dense understories occur. Rosebay rhododendron (*Rhododendron maximum*) generally forms dense understories near streams and beneath hemlock-dominated stands. In stands which are predominately hardwood, a large variety of shrubs and small trees occur in the understory. Many stands with an open understory have a lush herbaceous layer (Cain 1943).

While stands at or near climax contain primarily tolerant species--sugar maple, buckeye, hemlock, and beech (table 1)--even the intolerant but long-lived and fast-growing yellow-poplar occurs sparingly (Fowells 1965, p. 261). Climax stands are normally dominated by several species.

BIRD COMMUNITIES

General

All of the 62 species of birds known to nest in the different seral stages of cove forests (table 3) can be found nesting in other forest types in the Southern Appalachians or in other physiographic regions. Some stands have an unusually large number of species (table 4), but the average cove forest does not have more species than other types in the Southern Appalachians (Fawver 1950).

Table 1.--Major tree species of cove forests

Species	Potential commercial value	Tolerance to competition
Yellow-poplar *(Liriodendron tulipifera)*	High	Intolerant
Basswood *(Tilia spp.)*	High	Tolerant
Black cherry *(Prunus serotina)*	High	Intolerant
Black walnut *(Juglans nigra)*	High	Intolerant
White ash *(Fraxinus americana)*	High	Intolerant
White oak *(Quercus alba)*	High	Intermediate
Northern red oak *(Q. rubra)*	High	Intermediate
Cucumber tree *(Magnolia acuminata)*	High	Intermediate
Sugar maple *(Acer saccarum)*	High	Very tolerant
White pine *(Pinus strobus)*	High	Intermediate
Sweet birch *Betula lenta)*	Medium	Intolerant
Black locust *(Robina pseudoacacia)*	Medium	Intolerant
Chestnut oak *(Q. prinus)*	Medium	Intermediate
Hickories *(Carya spp.)*	Medium	Intolerant
Yellow buckeye *(Aesculus octandra)*	Medium-low	Tolerant
Beech *(Fagus grandifolia)*	Low	Very tolerant
Red maple *(A. rubrum)*	Low	Intermediate
Yellow birch *(B. lutea)*	Low	Intermediate
Fraser magnolia *(Magnolia Fraseri)*	Low	Intermediate
Silver bell *(Halesia monticola)*	Low	Tolerant
Hemlock *(Tsuga canadensis)*	Low	Tolerant
Blackgum *(Nyssa sylvatica)*	Low	Intolerant

Table 2.--Forest cover types of coves, ravines, and adjacent moist slopes in the Southern Appalachians

SAF type[1]	R-8 Wildlife habitat management handbook type[2]	R-8 Timber manage. types[3]
Yellow-poplar-white oak-northern red oak	Yellow poplar-white oak-northern red oak	Yellow poplar-white oak-northern red oak
Yellow-poplar-hemlock	White pine-yellow poplar-hemlock	White pine-yellow poplar
Yellow-poplar		Hemlock-hardwood
Hemlock		Yellow-poplar
White pine-hemlock		Hemlock
Northern red oak-basswood-white ash		

[1] Anon. 1967. Forest cover types of North America. Soc. Amer. For., Washington, D. C.

[2] Anon. 1971. Wildlife habitat management handbook. U. S. Dep. Agric., For. Serv., Region 8, Atlanta, Ga.

[3] Anon. 1972. Compartment prescription field book. U. S. Dep. Agric., For. Serv., Region 8, Atlanta, Ga.

Table 3.--Relative value of seral stages of cove forest as nesting habitat[1]

Species	Virgin		Second-Growth		
	Hardwoods	Hemlock	Sawtimber	Pole	Sapling
Broad-winged Hawk	X	X	X		
Ruffed Grouse	X	X	X	X	XX
Yellow-billed Cuckoo			X	X	
Screech Owl	X		X		
Barred Owl		X	X		
Ruby-throated Hummingbird					X
Common Flicker	X	X	X	X	
Pileated Woodpecker	XX		XX		
Hairy Woodpecker	X	X	X		
Downy Woodpecker	X		X		
Great Crested Flycatcher		X	X		
Eastern Phoebe			X		
Acadian Flycatcher	X	X	XX		
Eastern Wood Pewee		X	X	X	X
Blue Jay	X	X	X	X	
Black-capped Chickadee	X	X	X		
Carolina Chickadee		X	XX	X	X
Tufted Titmouse	X	X	XX	X	
White-breasted Nuthatch		X	X	X	
Red-breasted Nuthatch		X	X	X	
Brown-creeper		X	X		
Winter Wren	X	X	X	X	
Carolina Wren	X		X	X	
Gray Catbird		X	X	X	XX
Brown Thrasher				X	X
American Robin		X	X	X	X
Woodthrush	XX	XX	XX	XX	
Veery	X	X	X	X	X
Blue-gray Gnatchatcher			X		X
Golden-crowned Kinglet			X		
Cedar Waxwing				X	
White-eyed Vireo					X
Yellow-throated Vireo			X	X	
Solitary Vireo	XX	XX	XX	XX	X
Red-eyed Vireo	XX	X	XX	X	X
Black-and-white Warbler	X	X	XX	X	X
Swainson's Warbler			XX	X	
Worm-eating Warbler	X		X		
Golden-winged Warbler				X	X
Northern Parula	X	X	X	X	X
Black-throated Blue Warbler	XXX	XX	XX	XX	
Black-throated Green Warbler	XX	XXX	XX		
Blackburnian Warbler	X	XXX	X	X	
Yellow-throated Warbler			X		
Chestnut-sided Warbler				X	XX
Pine Warbler			X		
Prairie Warbler					X
Ovenbird	X	X	XX	X	
Louisiana Waterthrush			X		
Common Yellowthroat					X
Yellow-breasted Chat				X	XX
Hooded Warbler	X	X	XX	X	X
Canada Warbler	XX	XX	X	X	X
Scarlet Tanager	X	X	X	X	X
Cardinal	X		X	X	X
Rose-breasted Grosbeak		X	X	X	X
Indigo Bunting				X	X

Table 3.--Continued

| Species | Virgin | | Second-Growth | | |
	Hardwoods	Hemlock	Sawtimber	Pole	Sapling
American Goldfinch				X	X
Rufous-sided Towhee			X	X	XX
Dark-eyed Junco	XX	XX	XX		
Chipping Sparrow				X	X
Field Sparrow				X	X
Song Sparrow				X	XXX

1/   X = Species occurs at low frequencies and densities. Also occurs in
          other habitats at greater densities.
      XX = Species occurs at medium densities but also occurs at equal or
          greater densities in other habitats.
     XXX = Species occurs at highest densities within the region.

   The table is based on literature cited in the text and personal observation
   by the author.

Table 4.--Densities and numbers of species of birds in cove forests[1]

Stand condition	Bird density (pairs/100acres)	Number of species	Number of censuses
Seedling and sapling	66–321	8–13	3
Poletimber	270–296	21–35	2
Sawtimber	333–510	17–30	3
Virgin Hemlock	230–430	13–23	4
Hardwoods	183–370	9–19	4

   1/ Values in table taken from literature cited in text.

A 1-year-old clearcut had 66 pairs of breeding birds per 100 acres (Lewis and Smith 1975). The mean for all other cove forests reported (Fawver 1950; Holt 1974; Mellinger 1969–1975, 1977; Odum 1950) was 314 pairs per 100 acres, and the highest was 510 pairs per 100 acres. These densities are greater than for other forest types in the Smoky Mountains (Fawver 1950) and for most other forest types in the South and Southeast.

Virgin Stands

Fawver (1950) censused four virgin cove forests that were dominated by hardwoods and two that were dominated by hemlock. Odum (1950) and Holt (1974) censused a virgin hemlock stand at a 12-year interval. Density of pairs of breeding birds per 100 acres ranged from 183 to 370 in the hardwood stands and from 230 to 430 in the hemlock stands (table 4). The virgin hardwood areas had 13 to 23 species of breeding birds and the virgin hemlock had 9 to 19 species. A total of 28 species nested in the virgin stands. Each of these species nests in other habitats, both in the region and in other regions.

Species most dependent on virgin stands appear to be the Black-throated Blue Warbler, Black-throated Green Warbler and Blackburnian Warbler. Although these species occur in seral stages of the cove forests and in other forest types, they reach high densities in the virgin cove forests. The Black-throated Blue Warbler was the most abundant species in the hardwood-dominated cove forests, accounting for up to 59 percent of the density of

breeding individuals: one area had 185 breeding pairs per 100 acres (Fawver 1950). Although densities of the Black-throated Blue Warbler were less in hemlock-dominated forests, it was still an abundant species. The Blackburnian Warbler and the Black-throated Green Warbler were associated mostly with hemlock stands.

Twelve cavity nesters used the virgin stands but were usually more abundant in the second-growth stands.

Second-Growth Stands

Mellinger (1969-75, 1977, pers. commun.) censused a mature sawtimber stand for 9 consecutive years. Odum (1950) and Holt (1974) censused a poletimber stand in 1946-47 and in 1959-60; they revisited the stand in 1971-72 when it was in a sawtimber stage. They also censused a stand in the sapling stage in 1946-47 and 1959-60, and again in 1971-72 when in a pole stage. Lewis and Smith (1975) censused a stand 1 growing season after clear-cutting.

Population density and number of species in the second-growth pole and sawtimber stands were similar to those of the virgin stands (table 4). Bird species found in the virgin stands were well represented in the second-growth sawtimber stands (table 3). The second-growth stands did not have the high densities of Black-throated Blue Warblers that Fawver (1950) reported for the virgin stands. Holt (1974) found 44 pairs of Black-throated Blue Warblers per 100 acres--the highest reported in second-growth stands.

The pole stands had surprisingly large bird populations (table 4). This abundance may have been due to a light stocking of trees, the occurrence of hemlock, and a well-developed rhododendron understory (Odum 1950; Holt 1974). Pole stands of yellow-poplar and other hardwoods would probably have much lower densities.

The composition of bird species was considerably different in sapling plots than in older stands (table 3). For example, Odum (1950) reported a percentage difference (which takes into account the abundance of each species) of 97.9 between a sapling and a virgin stand.

TIMBER MANAGEMENT PRACTICES

Cove sites are highly productive and are typically classed as good to excellent for timber growth. Oaks grow 65 to 90 feet and yellow-poplar grows 90 to 140 feet in 50 years (Trimble 1973; Beck and Della-Bianca 1972). At 80 years, well-stocked stands of second-growth hardwoods contain about 37,000 board feet per acre on the best sites and 25,000 board feet per acre on lower quality sites (Frothingham 1931).

Since the majority of desirable timber species are relatively intolerant of competition (table 1), cove forests are generally managed for timber under even-aged silvicultural systems (Trimble 1973).

The individual selection silvicultural system, leading to all-aged stands, may be used where disturbance to the canopy must be minimized to protect esthetic values or stream banks. Because selective cutting favors tolerant species like buckeye, hemlock, beech, and sugar maple, it may reduce stand diversity. Of the tolerant species, only sugar maple and basswood have high commercial potential. Selection cuts heavy enough to encourage regeneration of intolerant species may result in understocked stands and high-grading (Trimble 1973).

Group selection cuts as small as 0.25 acre can regenerate the intolerant species, but openings of 0.5 to 1.0 acre are more desirable for growth of the regeneration (Trimble 1973). However, the impact of deer browsing upon the reproduction can be severe in openings that small (Harlow and Downing 1969).

Shelterwood cuttings are silviculturally feasible and could be used to maintain a forested canopy. The shelterwood system may be especially suited to securing advanced regeneration of heavy-seeded species such as oaks. The seed tree method is unnecessary in cove forests because many of the hardwoods sprout readily, advanced regeneration is normally present, and the light seeds of certain species carry long distances (Trimble 1973).

Clearcutting offers the greatest potential for intensive timber management. Maximum reproduction and growth of the desirable timber species are provided under this system (Trimble 1973). Clearcuts as small as 1 acre (essentially overlapping the group selection system) can be used. Silviculturally there is no upper size limit for clearcuts, but on forests under multiple-use management upper size limits are imposed to enhance wildlife and other values.

Rotation length for maximum wood production is about 70 years for yellow-poplar and 80 for oaks. Most landowners use rotations of 70 to 100 years. The National Forests currently use 100-year rotations to enhance scenic values.

Precommercial thinnings increase growth rate and improve stand composition and stem distribution. Such treatments are costly, however, and gains must be high to justify them. Production of palatable browse may be a partial justification for precommercial thinning (Della-Bianca 1975). On some areas, there is a need to release crop trees from grapevines (McGee and Hooper 1975). Rosebay rhododendron is so dense in some areas that it severely inhibits tree regeneration, but no practical means of control is available (Della-Bianca and McGee 1972).

Stands containing high percentages of yellow-poplar are usually quite dense, and wood fiber yields are highest when these densities are maintained. If the major goal is to enhance growth of saw logs and veneer bolts, however, periodic thinnings are required. A rule of thumb for maximum board-foot growth in thinned stands 30 to 70 years old is to match residual basal area to site index, e.g., 90 square feet basal area on site 90 and so on (Beck and Della-Bianca (1975).

MANAGEMENT IMPACTS AND RECOMMENDATIONS

Goals

If a manager wants to encourage birdlife, his goal should be to provide suitable habitat for each indigenous species for some period during the timber rotation. Further, he should ensure that these sets of conditions are always present at some point in the forest. Any practice that alters vegetation will benefit some species of birds and be detrimental to others. It is impossible to have all bird species nesting in the same stand at the same time, but suitable habitat conditions for each species can be provided in some part of the forest all the time. This approach will provide for more bird species than any attempt to maximize the species and bird density on each acre.

Recommendations for bird management are provided below. These recommendations are based on the best available information. They are, however, largely untested.

Rotation Age

Rotations of 100 years seem adequate to provide habitat for the bird species associated with virgin stands. Specific studies on stand age as it relates to bird communities in cove forests are lacking, but none of the second growth stands reported were greater than 100 years old. Certain species, such as the Black-throated Blue Warbler, Barred Owl,

and Pileated Woodpecker may require longer rotations for habitat conditions approaching their optimum.

Shorter rotations of say 70 to 80 years may provide habitat for most, if not all, of the species that were found in virgin stands, but some of these species would probably be existing under marginal habitat conditions that have unknown impacts on the species.

Stand Regeneration

Clearcutting

Clearcuts as small as 1 acre will provide habitat for all the species in table 3 listed under the Second-Growth Sapling Stage except the Prairie Warbler, Yellow-breasted Chat, and Field sparrow. These three species are by far more abundant in the early seral stage of the oak-hickory and oak-pine types adjacent to the cove types so they would not be eliminated from the forest (Hooper 1967).

Larger clearcuts of say 25 acres would provide suitable habitat for larger and less fragmented populations of the early seral species. Birds requiring mature stands would be better provided for, in the long run, by the larger clearcuts since the older stands would also be larger in area. Clearcuts exceeding 30 acres in cove forests seem unnecessary in managing bird populations: all species using sapling and mature stands should find habitat in stands of that size.

Shelterwood Cuts

Shelterwood regeneration areas with a residual basal area of 40 to 50 square feet per acre would probably provide habitat for most of the species of the sapling stage. Species using edge habitats, such as Chestnut-sided Warblers and Indigo Buntings would be especially attracted to shelterwood areas. Some of the species of the mature forest would continue to use the shelterwood area until the residual trees were removed. Due to the layering of the vegetation, a larger number of bird species would be expected on these areas than on the clearcut areas.

Group Selection Cuts

Group selection cuts approaching 1 acre would have effects similar to the smallest clearcuts discussed above. Smaller cuts of 0.25 to 0.50 would probably have effects similar to the individual selection cuts discussed below.

Individual Selection Cuts

Individual selection cuts with a residual basal area of 80 square feet or less per acre and group selection cuts of 0.25 to 0.50 acres would probably result in high densities and numbers of species. Species requiring either a continuous canopy or sparse canopy might be at a disadvantage under these conditions.

Thinnings

Commercial thinnings on these good sites result in prolific growth of the understory (D. E. Beck, pers. commun.). Both the number of species and number of individual birds should increase (Hooper and others 1973) following thinnings.

Thinnings, and possibly individual and group selection cuts, could have a severe impact on the Pileated Woodpecker. Pileated nest trees in Virginia (Conner and others 1975) were on mesic sites and in stands with an average basal area of 137 square feet per acre. Most nest cavities were in dead trees or in dead portions of live trees. Such trees are usually removed in thinnings. Although pileateds have territories of 100 to 200 acres and larger, leaving as little as 1 acre per 100 acres of cove forest unthinned (but regenerated in the normal rotation) could greatly improve conditions for the pileated and other woodpeckers in intensively managed cove forests. Thinning in the usual manner but girdling and leaving several of the less valuable trees might be a more economical alternative.

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A Comparison of Avian Community Structure in the Northern and Southern Appalachian Mountains

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Abstract.--The structure of avian communities along elevational gradients is examined. A descriptive analysis of community-level properties, contrasting northeastern and southeastern communities, is presented. Hypotheses sufficient to explain differences in community organization are proposed and examined by analysis at the population-level. Emphasis is placed on shifts in species habitat utilization subsequent to changes in species composition and habitat availability. Suggestions for the development of workable habitat management schemes are presented.

INTRODUCTION

Numerous studies have recently been conducted in an attempt to understand niche patterns within animal communities, the correlations between various niche dimensions and species diversity, and the contribution of critical dimensions to achieving species coexistence. Many of these studies have dealt explicitly with the importance of habitat usage in ecological communities, particularly bird communities (MacArthur and MacArthur, 1961; MacArthur et al., 1966; Cody, 1968; Wiens, 1969; James, 1971; Shugart and Patten, 1972; Anderson and Shugart, 1974; Whitmore, 1977; and others). Of particular relevance to this symposium is the almost unanimous consensus that bird species diversity is strongly correlated with structural habitat diversity and that for the majority of species there is a cause and effect relationship between these variables.

MacArthur and his coworkers initially established the importance of habitat structure when they discovered the strong positive correlation between foliage height diversity, an index of the vertical distribution of foliage biomass, and species diversity (MacArthur and MacArthur, 1961; MacArthur and Preer, 1962). The major significance of this finding was that a single index was such a powerful predictor of species diversity in a variety of geographically distinct locales.

Following MacArthur, many additional studies aimed at understanding the connection between habitat structure and species diversity have been conducted (reviewed in Balda, 1975). In recent studies there has been a movement away from analyses of single habitat variables towards multivariate analyses of habitat data (i.e., Shugart and Patten, 1972; Whitmore, 1977). The complexity has been expanded primarily for two reasons: 1) to understand bird species diversity patterns in those communities for which foliage height diversity (and other indexes such as percent vegetation cover) had not been a good predictor (i.e., Balda, 1969; Karr, 1971; Pearson, 1975; Willson, 1974); and, 2) to discover the specific features of habitat structure which were contributing to species diversity.

From studies of avian communities occupying temperate forests, some general patterns of resource partitioning have emerged. The most important of these is that habitat selection is the dominant factor determining bird distributions and habitat features are more important than food availability in avian resource division (Schoener, 1974; Shugart et al., 1975). Further, a review of multivariate studies of habitat partitioning in forest bird communities (James, 1971; Shugart and Patten, 1972; Shugart and James, 1973; Anderson and Shugart, 1974; Whitmore, 1975, 1977) reveals a consistently

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dominant role for a small subset of structural habitat variables. The extensive discriminatory power contained in just a few variables is best illustrated by Whitmore (1977) who was able to significantly separate a community of 24 species by considering only 10 habitat variables.

The consistency apparent in these findings indicates that a few structural features of the habitat may be the dominant determinants of species diversity. Further, they argue for a general pattern of forest community organization independent of geographical location within the temperate zone. The unique features of temperate avian species which result in regular patterns of community organization may primarily be a consequence of the migratory nature of the majority of breeders. These characteristics and their implications for the evolution of strong habitat selection have been discussed by Able and Noon (1976).

In the discussion which follows we will examine the organization of eastern montane forest bird communities. We will first present a descriptive analysis of community-level properties, comparing northeastern and southeastern montane communities. From these analyses we generate hypotheses about community structure that are sufficient to explain differences in community-level organization. As a test of our hypotheses we will present results of a population-level analysis of a subset of these avian communities. We examined the ground-foraging thrush guild which, particularly in the Northeast, is a dominant component of these montane communities. We conclude by synthesizing the results of both the community and population-level studies into a tentative scheme for habitat management which, hopefully, will maintain the integrity of natural bird communities.

METHODS

Species Distribution Patterns

On the northeastern and southeastern study sites sampling stations were established approximately every 100m along the elevational gradient. Censusing data was collected during a 3 - 4 hr interval beginning immediately after dawn and again in the late evening 1 - 2 hr prior to sunset. At each sampling station two observers walked in opposite directions recording all bird species seen or heard while progressing at a steady pace for a prescribed length of time (usually .5 - .75 hr). On successive days the order in which stations were sampled was altered so as to minimize bias introduced by time of day. In general, 1.5 - 2 hr of sampling time was accumulated for each sampling station. Finally, the counts were normalized to the number of individuals of

each species per hour of sampling time at each station (see Able and Noon 1976, for further details).

Habitat Analyses

The habitat data quantifying the structural parameters of the thrush species' territories were obtained by sampling 0.04 ha (0.1 acre) circular plots centered upon the point at which a bird was seen performing a specified behavior. The sampling methods closely followed quantification techniques proposed by James and Shugart (1970). The design of the techniques is such that all strata of the forest breeding habitats are thoroughly measured.

A total of 250 habitat quantifications was done on the five thrush species at the northeastern montane site, 94 quantifications were obtained on two thrush species at the southeastern montane site and 56 quantifications were done in a nonmontane site in northern New York. No attempt was made to stay within homogeneous stands of forest when sampling but all samples were collected so as to avoid "edge" situations. All habitat quantifications at both montane sites were done to include habitats covering the full range of a species' elevational distribution. In addition, the sampling intensity, as a function of elevation, reflected the distributional abundance of the species along the elevational gradient.

Study Areas

The northeastern montane study area was Mount Mansfield, the highest mountain in the Green Mountains of Vermont, with an elevation of 1339m. The mountain is located approximately 65 km east of Burlington, Vermont (44° 31'N, 84'W). The study site covers an area of approximately 10 km^2 on the eastern face of the mountain.

Relatively undisturbed forest extends from 550m to 1200m, the last 200m of elevation being alpine meadow and exposed rock. The eastern exposure of the mountain is criss-crossed with numerous ski trails; however, they have had a negligible effect on the composition, abundance and distribution of the avian populations (Able and Noon, 1976). The extent of the edge effect between ski trail and undisturbed forest is slight and we avoided areas of extensive disturbance in all cases. The vegetation of the mountain is basically mature second growth forest, although some areas of virgin spruce-fir remain at high elevations (Siccama, 1968). The mountain is composed of four major vegetation zones. Successively, these zones are: 1) sugar maple (Acer saccharum) and beech (Fagus grandifolia) forest; 2) yellow birch (Betula lutea), paper birch (B. papyrifera) and red

spruce (_Picea rubens_) forest; 3) red spruce and balsam fir (_Abies balsami_), and 4) alpine tundra.

To the casual observer the mountain gradient appears to consist of at least two discrete vegetational units: pure deciduous and pure coniferous with a zone of mixed vegetation at mid-elevations. However, Siccama (1968) showed that the vegatation of the Green Mountains is actually a complex continuum of species populations rather than a mosaic of discrete communities (see Whittaker, 1967). Deciduous forests characteristic of the low elevation forests are not found above mid-elevations, but species characteristic of upper slopes are found in small numbers on the lower slopes. In the zone between the two major vegetational units species characteristic of both occur, but no species is confined to mid-slope forests. Despite the essential continuity which characterizes the vegetational community of this gradient, we have distinguished three major changes in vegetational physiognomy: 1) the area on the gradient in which beech and sugar maple disappear. Concomitantly, yellow birch and red spruce increase markedly. 2) the virtual disappearance of deciduous trees along with an increase in the proportion of balsam fir. 3) tree line. In practice, ecotones 1) and 2) could be localized within zones of about 100m of elevation or less, and tree line was considerably more abrupt.

The southeastern montane study area was the Great Smoky Mountains National Park located on the border between Tennessee and North Carolina (83° 37'N, 84° 30'W). This montane site covered an elevational gradient extending up to 2025m on Clingman's Dome on the Tennessee side of the main mountain ridge. The gradients studied had primarily a north to north-northwest exposure and for the most part were characterized by mesic to submesic forest types.

The Great Smoky Mountains supports a particularly diverse forest of varied community types. Whittaker (1952, 1956) gave an exhaustive description of the forest communities. In general, the vegetational communities in which studies were done are of three major types: 1) mesic cove forests; 2) submesic oak forests; and 3) subalpine forests.

In the mesic cove forests the principal canopy trees were yellow buckeye (_Aesculus octandra_), white basswood (_Tilia heterophylla_), silverbell (_Holesia monticola_), sugar maple, eastern hemlock (_Tsuga canadensis_), tulip tree (_Liriodendron tulipifera_), yellow birch and beech (Whittaker, 1952, 1956). Above 1370m the composition of the mesic forest changes into a subalpine forest dominated by red spruce and Fraser fir (_A. fraserii_). Outside of the

range of the spruce, or where ravines cut into the mountain ridge, mesic stands above 1370m are dominated by gray birch.

In spite of the fact that this transect, like the northeastern one, is also a complex continuum of species and not easily divisible into discrete vegetational communities, two ecotones were recognized: 1) the area on the gradient in which red spruce and yellow birch become significant components of the canopy. This zone is characterized by a substantial decrease in canopy height. 2) the virtual disappearance of deciduous trees along with an abrupt increase in the percentage of red spruce and the appearance of Fraser fir. Both ecotones correspond with areas where gross changes in the structural physiognomy of the forest occurred.

The non-montane northeastern study site included the islands and shoreline areas on the Cranberry Lake Biological Station, Saint Lawrence County, New York (44° 15'N, 74° 45'W). The study site covered an area of approximately 10 km^2.

Relatively undisturbed second growth forest covered most of the areas studied, though some areas of virgin forest were also included. The range of forest types and vegetational dominants encountered in this region were very similar to those on Mount Mansfield with the notable absence of extensive stands of balsam fir and stunted coniferous vegetation. Elevation at this study site ranged from 450 - 550m.

RESULTS

Community Patterns

Species Composition

We have previously described the community structure patterns on four mountains in New York and Vermont (Able and Noon, 1976). There were great similarities among the four gradients; for this comparison we have used data only from Mount Mansfield, Vermont, the gradient we studied most extensively.

The Mt. Mansfield and Smoky Mt. elevational gradients encompassed a similar (structural) range of forest habitats and each gradient had the same number of species, 41. There were, however, considerable differences in the species composition on the two transects; they overlapped in slightly less than two-thirds of their species. Sixteen species (39 percent of the total) on the Smoky Mt. gradient were not present on Mt. Mansfield (Com. Flicker, _Colaptes auratus_; Pileated Woodpecker, _Dryocopus pileatus_; Acadian Flycatcher, _Empidonax virescens_; Carolina Chickadee, _Parus carolinensis_; Tufted Titmouse, _P. bicolor_; Carolina Wren, _Thryothorus ludovici-_

anus; Blue-gray Gnatcatcher, Polioptila caerulea; Yellow-throated Vireo, Vireo flavifrons; Worm-eating Warbler, Helmitheros vermivorus; Cerulean Warbler, Dendroica cerulea; Yellow-throated Warbler, D. dominica; Chestnut-sided Warbler, D. pensylvanica; Louisiana Waterthrush, Seiurus motacilla; Kentucky Warbler, Oporornis formosus; Hooded Warbler, Wilsonia citrina; Cardinal, Richmondena cardinalis). Fourteen species (34 percent) absent on the Smoky Mt. gradient were found on Mt. Mansfield (Least Flycatcher, E. minimus Raven, Corvus corax; White-breasted Nuthatch, Sitta carolinensis; Hermit Thrush, C. guttatus; Swainson's Thrush, Catharus ustulatus; Gray-cheeked Thrush, C. minimus; Cedar Waxwing, Bombycilla cedrorum; Nashville Warbler, Vermivora ruficapilla; Yellow-rumped Warbler, coronata; Blackpoll Warbler, D. striata; Mourning Warbler, O. philadelphia; Common Yellowthroat, Geothlypis trichas; Purple Finch, Carpodacus purpureus; White-throated Sparrow, Zonotrichia albicollis). Many of these differences between the two localities involved abundant and broadly distributed species. When one considers a spectrum of habitats such as occurs on these elevational gradients, the southern avifauna cannot be considered an included subset of the northern as Rabenold (1976) found when only spruce-fir forests in the two areas were examined.

Figure 1 compares patterns of species diversity on the two gradients. Species richness and two indices of diversity are plotted. In both regions, the three measures of diversity tend to be highly correlated, but there are obvious differences in pattern. On Mt. Mansfield both diversity indices closely parallel the trend in species richness and

all generally declined with elevation. In the Smoky Mountains, species richness fluctuated greatly but still showed a downward trend with elevation. N_1 and N_2 also showed considerable variation over the length of the gradient, but if a trend similar to that of species richness is present it is very slight. The relative flatness of the diversity curves is in marked contrast to those for Mt. Mansfield.

Because the species richness of the Smoky Mt. communities is essentially the same as on Mt. Mansfield the marked differences in diversity must be due to differences in equitability. This can be seen graphically in Fig. 2 which compares dominance-diversity curves for the two gradients. The Smoky Mt. communities are characterized by much higher dominance and a greater increase in dominance over the span of habitats relative to Mt. Mansfield. Figure 3 presents an analysis of dominance comparing the Smoky Mt. communities with those on Mt. Mansfield and nearby Camel's Hump Mt. by Wiens' (1975) method. For a community with a given number of species, the samples from the Smoky Mts. had significantly higher dominance (p<.025; Mann-Whitney, one-tailed) than the two northern mountains.

The overall difference in dominance in the two regions appears to be due to higher relative abundances of the commonest one or two species in the Smoky Mt. communities rather than to a difference in numbers of rare species. This can be seen in Table 1 which ranks the relative abundances of the four commonest species at selected elevations on the two mountains. At all but one of these sampling stations, the dominant Smoky Mt. species had much higher pi's than their northern counterparts. Mean proportional abundances of all the species comprising
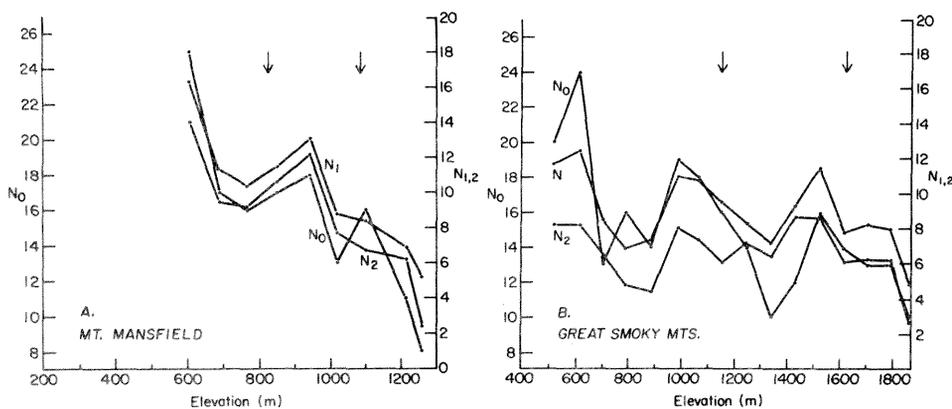
Figure 1.--Plots of species richness (N_0) and diversity with elevation on Mt. Mansfield, Vermont (A) and Great Smoky Mountains (B). $N_1 = Exp(H')$; $N_2 = 1/\Sigma p_i^2$.
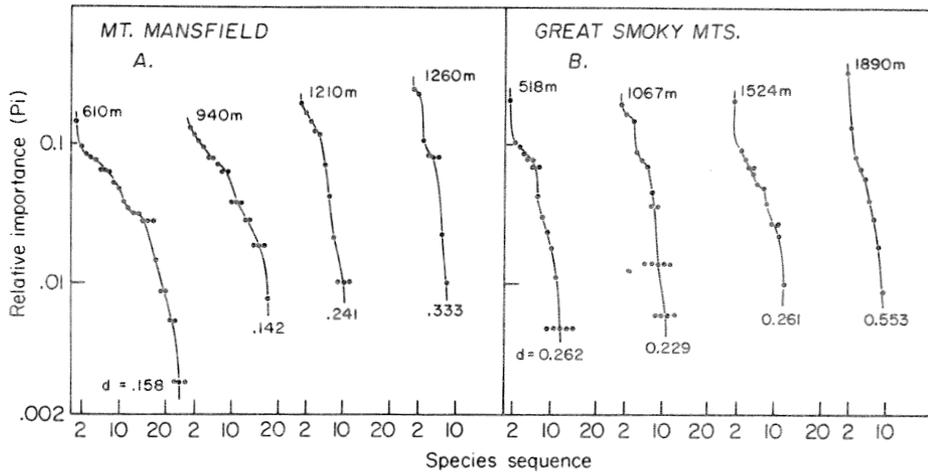
Figure 2.--Dominance-diversity curves for selected elevation on Mount Mansfield, Vermont (A) and Great Smoky Mountains (B). Each species is represented by its proportional abundance in the sample (p_i) on the ordinate, and its rank in the sequence of species from the most to the least abundant on the abcissa. Indices of dominance, $d = N_{i_{max}}/N$, are given for each curve.
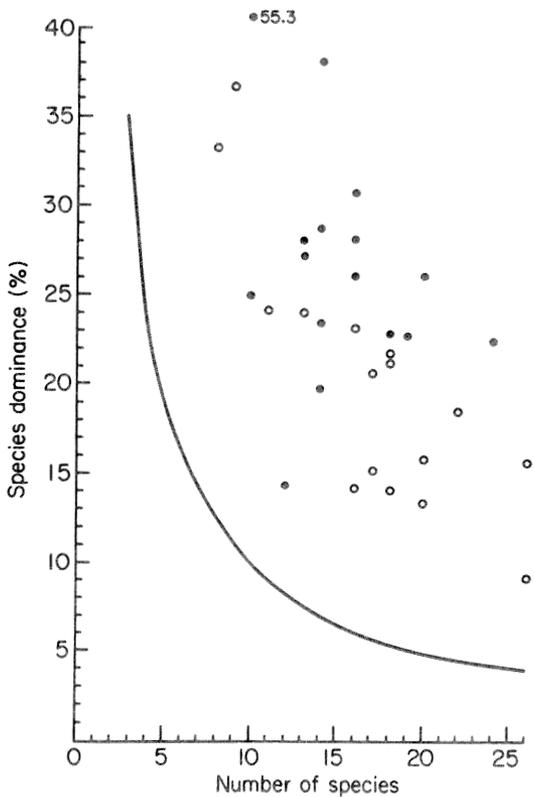
Figure 3.--Comparison of degree of dominance for given numbers of species in communities on Mount Mansfield and Camel's Hump Mountain, Vermont.

a census was always higher and generally more variable on Mt. Mansfield than in the Smokies.

The major differences in species composition between the two regions precluded a paired comparison, but the abundances of the less common species were generally similar. The great difference in dominance was largely due to the much greater nos. of the most abundant species. As a result of this, nearly all elevations in the Smoky Mts. supported a significantly larger number of individuals than comparable sites on any of the northeastern gradients (mean no. indivs./hr., all stations, Smoky Mts. = 170.7, S.D. = 28.3; Mt. Mansfield $\bar{X}$ = 100.0; S.D. = 33.5; Whiteface Mt. $\bar{X}$ = 148.4; S.D. = 55.7).

Species Amplitudes

On both northern and southern elevational gradients a few species with very generalized habitat preferences were found over nearly the entire transects (Table 2). In the Northeast, the Dark-eyed Junco (Junco hyemalis) and White-throated Sparrow ranked among the top five species on all four mountains (Able and Noon, 1976). Three of the six broadest species on Mt. Mansfield were among the five broadest in the Smoky Mts. In addition, the Black-throated Green Warbler (Dendroica virens) ranked fifth on Whiteface Mt. in the Adirondacks of New York. Thus there appears to be considerable similarity in the amplitude patterns of the habitat generalists in the two regions.

Table 1.--Ranking and proportional abundances of the four most abundant species at selected elevations on Mount Mansfield, Vermont, and the Great Smoky Mountains. Mean p_i values for all species at each elevation are also given.

Species	p_i	Species	p_i	Species	p_i	Species	p_i
Mount Mansfield							
El. 610m		770m		1020m		1260m	
Red-eyed Vireo	.1573	Red-eyed Vireo	.1770	Blackpoll Warbler	.2353	Wh.-thr. Sparrow	.3333
Amer. Redstart	.0941	Dark-eyed Junco	.1416	Wh.-thr. Sparrow	.1765	Blackpoll Warbler	.2941
Ovenbird	.0787	Amer. Robin	.1416	Winter Wren	.1029	Nashville Warbler	.1078
Wood Thrush	.0754	Hermit Thrush	.1327	Swainson's Thrush	.1029	Yel.-rump. Warbler	.0784
$\bar{P}_i$	.0400		.0625		.0769		.1250
S.D.	.0362		.0555		.0664		.1214
Great Smoky Mountains							
El. 610m		976m		1524m		1798m	
Red-eyed Vireo	.2706	Red-eyed Vireo	.2258	Dark-eyed Junco	.2611	Dark-eyed Junco	.2896
Ovenbird	.1882	Bl.thr.Blue War.	.1935	Veery	.0887	Gold.-cr.Kinglet	.1639
Bl.-thr.Green War.	.1353	Bl.thr.Green War.	.0774	Bl.-cap.Chickadee	.0887	Bl.-thr.Green War.	.1585
Amer. Redstart	.1000	Ovenbird	.0701	Blackburnian War.	.0887	Solitary Vireo	.1148
$\bar{P}_i$	.0392		.0490		.0625		.0716
S.D.	.0558		.0599		.0598		.0837

Table 2.--Elevational amplitude rankings of the five species on each mountain with the broadest distributions on the gradients.

Amplitude Rank	Mount Mansfield			Great Smoky Mountains		
	Species	Amplitude (m)	Proportional Amplitude	Species	Amplitude (m)	Proportional Amplitude
1	Dark-eyed Junco	660	.943	Hairy Woodpecker	1372	.994
2	Winter Wren	660	.943	Amer. Robin	1372	.994
3	Bl.-cap.Chickadee	610	.871	Bl.-thr.Green War.	1372	.994
4	Wh.-thr. Sparrow	495	.707	Solitary Vireo	1098	.796
5	Hairy Woodpecker	495	.707	Dark-eyed Junco	1098	.796
6	Amer. Robin	495	.707			

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In general, species in the Great Smoky Mts. occupied a larger proportion of the elevational gradient. However, in both areas a few species whose distributions appeared not to be artificially truncated by the ends of the gradient were nonetheless characterized by very narrow ranges. In the Northeast, the Golden-crowned Kinglet (Regulus satrapa) and Canada Warbler (Wilsonia canadensis) were found in the middle elevations, but had narrow amplitudes of between 100-150m (about 18 percent of elevational range). In the Smoky Mts., the Kinglet was again among the narrowest species with an amplitude of about 275m (about 20 percent of elevational range) and Brown Creeper (Certhia familiaris) was similar.

In both regions, the mean amplitude of the species at each sampling station increased with elevation and decreased with species richness (Fig. 4). These relationships say that the high elevation faunas of these mountains are made up largely of habitat generalists which dominate the depauperate communities at the tops of the mountains. The high elevation community is basically a subset of lower elevation avifaunas and at high elevations the most abundant species attained both greater dominance and absolute abundances than lower elevation dominants. Among all species on the gradients there is a positive correlation between amplitude and abundance (Able and Noon, unpubl. data). Of the 10 most numerous species, all but two also ranked among the 10 species with the largest amplitudes on the gradient.

Community Structure

Patterns of species turnover on environmental gradients can give insight into mechanisms producing community structure. We have examined the similarity of species composition and relative abundance at sampling stations along the gradients using a dissimilarity index (MacArthur, 1972, p. 189):

$$M = \frac{2}{1 + \dfrac{2\Sigma p_i q_i}{\Sigma p_i^2 + \Sigma q_i^2}} ,$$

where p_i and q_i are the proportions of species i in samples p and q, and $1 \leq M \leq 2$. Figure 5 compares Mt. Mansfield and the Smoky Mts. by plotting the similarity between the lowest stations and each successively higher station. In general, the functions should increase as the distance between stations being compared increases. An increase in the slope of the line indicates a greater change in community composition between two stations.

On the four mountains studied in the Northeast, increases in dissimilarity (i.e.,

increases in M) were associated with ecotones. Mt. Mansfield, the steepest of the four, was slightly atypical in that the two ecotones appeared to have been treated as a single discontinuity, at least as far as our analysis was able to discriminate. The pattern on the Smoky Mt. elevational gradient was very similar, with a very large and abrupt faunal change between the stations at 1067m and 1158m. The data from both areas suggest a major influence of habitat discontinuities in determining the distributional limits of species on these gradients. Whereas there are obvious and large changes in species composition and relative abundances on the Smoky Mt. transect, the magnitude of the effect is not as great at the species level as in the Northeast (Table 3). Only about one-third of the species' distributional limits coincided with ecotones in the Smoky Mts. compared with slightly more than half of such limits in the Northeast. In fact, the proportion of species limits associated with ecotones in the Smokies does not differ from that found by Terborgh (1971) in Peru (with data normalized for number of sampling stations associated with ecotones). However, ecotones still exerted a large effect in the Smokies through changes in relative abundances.

In our earlier paper (1976) we failed to find any evidence of overt competitive exclusion in the distribution patterns of the species. Further detailed studies of the five thrushes on these gradients has also failed to reveal any interference competition (e.g., interspecific territoriality) (Noon, 1977). In the Great Smoky Mts., cases suggestive of spatial competitive exclusion were even rarer. The Wood Thrush (Hylocichla mustelina) and Veery (Catharus fuscescens) and the Red-eyed (Vireo olivaceus) and Solitary Vireos (V. solitarius), as well as a host of parulid species, overlapped broadly on the gradient. Among congeners, only the Carolina (Parus carolinensis) and Black-capped Chickadees (P. atricapillus) were continguously allopatric, although neither reached near maximal abundance adjacent to the contact zone. Thus with respect to evidence of interspecific competition in the form of intra-habitat spatial exclusion, the pattern in the Smokies appeared to be virtually identical to that in the Northeast.

The species comprising the breeding avifaunas of both regions are predominantly migratory, inhabiting these forests only during the relatively short breeding season. There are, however, noticeable differences between the two areas with respect to the proportions of species and individuals that are long-distance migrants. About three-fourths of the species included in our censuses of New England mountains are migrants that leave the region in winter. In the Smoky Mts. only 62 percent of the species make migrations more extensive than short-distance altitudinal movements. A much more striking
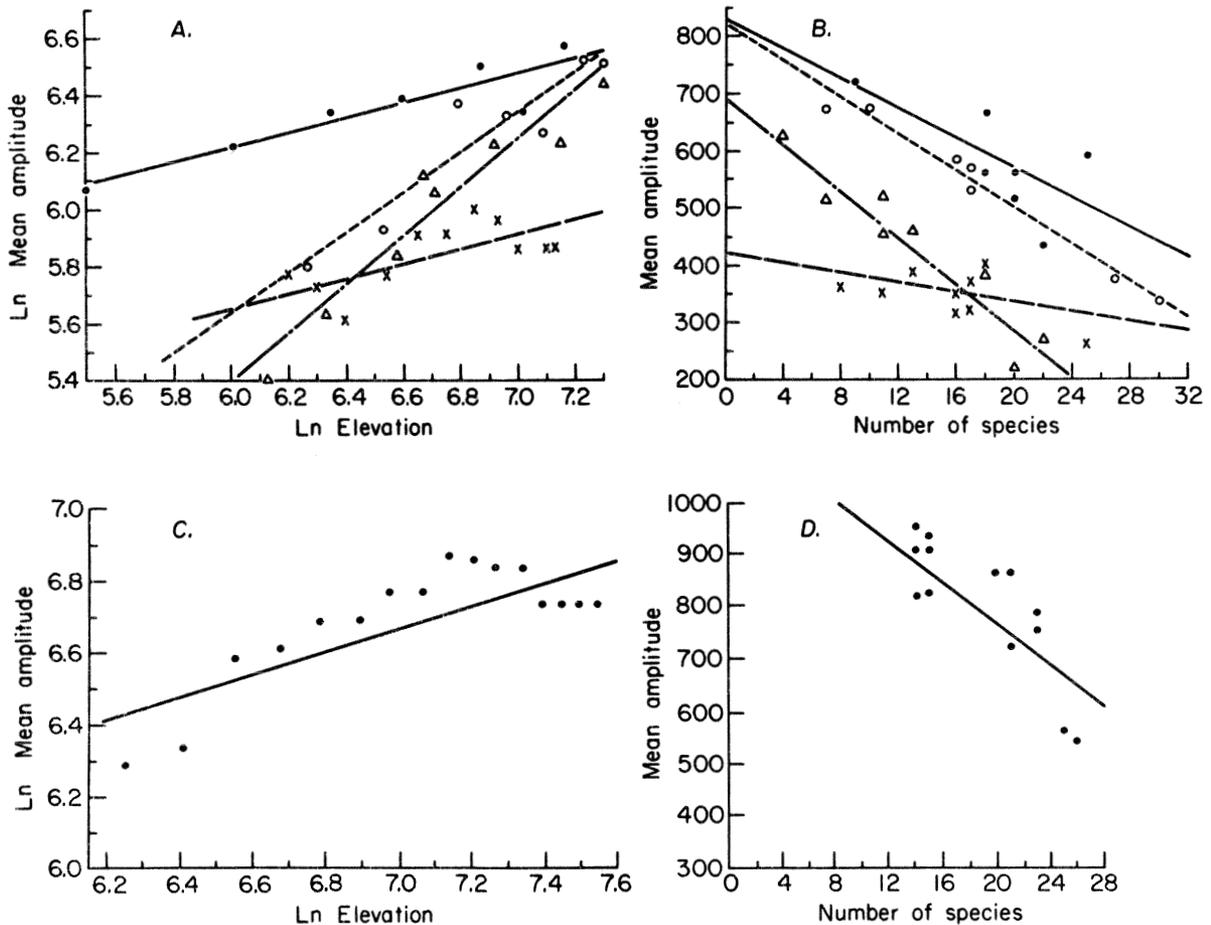
Figure 4.--Regressions of mean species amplitude at given sampling stations on elevation and the species richness at the station. A and B, northeastern mountains: X Mount Mansfield; ● Camel's Hump Mountain; O Whiteface Mountain, New York; Δ Nippletop Mountain, New York. C and D, Great Smoky Mountains.

difference can be seen if one compares proportions of individuals that belong to essentially resident species. On Mt. Mansfield, this figure varies between about 12 percent (lowest elevation sampled) and 2 percent (highest station) (mean = 7.2 percent). In contrast, the proportion of individuals belonging to resident species ranged from about 4 percent (884m station) to 66 percent (highest station) (mean = 29.7 percent) and generally increased with elevation.

The difference between the two regions was due almost entirely to the high importance of Dark-eyed Junco, Black-capped Chickadee, Golden-crowned Kinglet and Red-breasted Nuthatch above the first ecotone at around 1160m. In general, resident species did not reach higher abundance nor did they have larger amplitude than migrants (some examples are shown in Table 1).

Population Patterns

Northeastern Montane

Distributional Analyses.-- A particularly interesting pattern of our northeastern montane censuses was the diversity of thrush species (Hylocichla and Catharus) occupying these
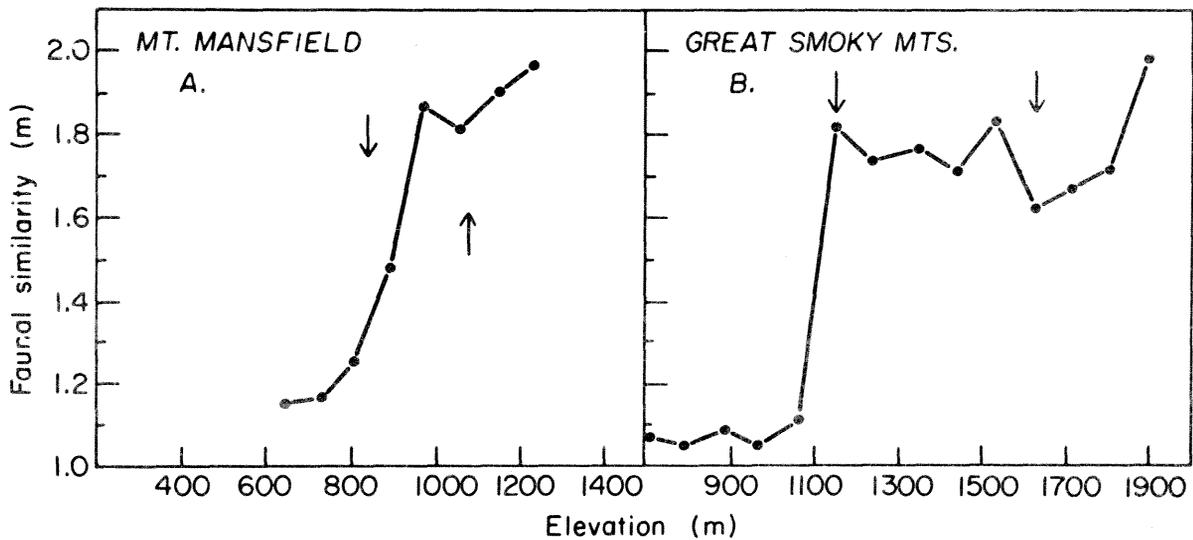
Figure 5.--Plots of the index of faunal dissimilarity (M) between the lowest elevation station and each succeeding higher one on Mount Mansfield (A) and between the lowest two stations combined and each succeeding higher one in the Great Smoky Mountains (B).

Table 3.--Elevation limits of species distributions in relation to ecotones on five mountains.

Mountain	No. of limits excluding termini	No. at ecotones	Proportion at ecotones	Proportion of limits/ ecotone station
Whiteface (NY)	35	20	0.570	0.285
Nippletop (NY)	34	18	0.530	0.177
Mansfield (VT)	39	20	0.510	0.170
Camel's Hump (VT)	39	20	0.510	0.255
Gr. Smoky (Tenn.)	40	13	0.325	0.081

gradients. When the relative abundances of the four most abundant species at each sampling station were calculated, one or more thrush species ranked in the top four at the majority of sampling sites. Figure 6 illustrates the distributional patterns of the thrush species on Mount Mansfield. Plotted are abundances, normalized and expressed as the number of individuals of species i censused per hour. The patterns illustrated here were qualitatively similar for all four northeastern elevational gradients.

From the figure it is apparent that the Wood thrush and Veery had very similar distributions being most abundant at low elevations and reaching their upper limit together at the lower ecotone. The Hermit thrush bred at low elevations but showed variable abundance, extending beyond the lower ecotone into mid-elevations. At higher elevations the Swainson's and Gray-cheeked thrushes inhabited mutually ex-
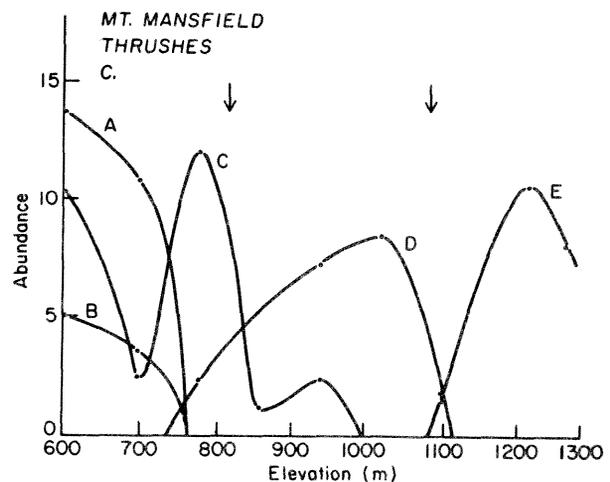
Figure 6.--The abundances of the thrush species on the Vermont elevational gradient, species of thrushes are denoted as: (A) Wood thrush; (B) Veery; (C) Hermit thrush; (D) Swainson's thrush; (E) Gray-cheeked thrush.

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clusive ranges. The Swainson's thrush over-
lapped extensively with the hermit thrush at
the lower end of its distribution, but had
mimimum overlap with the gray-cheeked at its
upper extent. The truncated distributions
of these two species at their zone of contact
suggests interference competition except
that this point coincided with the upper ele-
vational ecotone.

Habitat Analyses.--During the breed-
ing seasons of 1975 and 1976, habitat quan-
tifications were done for the five thrush
species breeding on Mount Mansfield. Fifty
habitat quantifications were done for each
species with each quantification consisting
of measurements on 58 structural habitat
variables (details given in Noon, 1977).
Each species was represented in the data
matrix by 50, 58-element observation vec-
tors.

Univariate analyses (one-way analysis of
variance) of the structural habitat vari-
ables revealed patterns of intrahabitat
separation for overlapping species and
interhabitat separation for species with dis-
junct elevational distributions. Each of
the variables measured was regarded as a
continuous gradient quantifying some aspect
of the breeding territories selected by
these species. Overlap was extensive along
most of these gradients, but all species
showed patterns of separation along a unique
complex of variables. Simultaneous differ-
ences along a multitude of gradients re-
sulted in a significant increase in se-
paration. However, many of the variables
measured were highly correlated, and the
danger of achieving a distorted picture
of the nature and extent of group differ-
ences increases as the correlations among
the variables increases.

An alternative way to describe group
differences is to use discriminant function
analysis which constructs a linear combina-
tion of the set of variables that will maxi-
mally discriminate the groups. The linear
combination is a new, transformed variable
composed of the original variables each
weighted according to its power to dis-
tinguish the groups. Species' positions are
then examined in terms of their ranking
along this linear combination. By this pro-
cess, species' positions on several inde-
pendently measured univariate gradients
(which may be highly redundant) are reduced
to a single position along a multidimen-
sional gradient of habitat structure. This
reduction in dimensionality simplifies elu-
cidation of species' differences and facili-
tates quantitative comparisons among the
species in terms of a few highly significant
variables. For an indepth discussion of the
applications of discriminant analysis to eco-

logical problems see Green (1971, 1974).

The use of discriminant function analysis
as a powerful tool for forest managers was
proposed at a previous meeting of this group by
Shugart et al. (1975). The specific advantage
of this type analysis is that it reduces com-
plex multivariate data to a manageable and sig-
nificant subset of the original data. In
addition, it goes beyond ambiguous univariate
correlational studies (such as the relationship
between foliage height diversity and bird species
diversity) to identify specific features of
habitat structure strongly correlated with a
species' presence.

The results of multiple step-wise discrim-
inant analysis of the thrush guild are presented
in Table 4. The number of variables needed to
significantly distinguish the structural habi-
tats of these species has been reduced from over
50 to nine. A test of the discriminatory power
of the subset of nine variables prior to the
removal of any discriminant functions indicated
that they contained a highly significant amount
of discriminatory power (Wilk's lambda = 0.0379;
associated chi-square = 792; p<.001). In addi-
tion, 96 percent of the variability in the pre-
dictor variables can be explained by group dif-
ferences (ω^2 multi = 96).

The proportion of the discriminatory power
contained in the subset of predictor variables
attributable to the ith discriminant function
is given by the ratio: $p_i = \lambda_i /(\lambda_1 + \lambda_2 + ... \lambda_n)$.
where λ = the eigenvalue of the ith discriminant
function. P_i is an index of how the total dis-
criminatory power of the predictor variables
is apportioned to each discriminant function.
Thus, 85 percent of the discriminatory power of
the predictor variables is accounted for by the
first discriminant function, 7.9 percent by the
second, and so on. The discussion which follows
confines itself to an analysis of the first two
functions which collectively account for over
90 percent of the discriminating power contained
in the analysis.

Additional information essential for an
understanding of the analysis are the stand-
ardized discriminant function coefficients
given opposite each variable in the table. The
absolute value of each coefficient is propor-
tional to the relative contribution of its
associated variable to group separation along
that discriminant axis. The sign merely indi-
cates whether the variable is making a positive
or negative contribution. These coefficients
may be used to interpret the functions by iden-
tifying the dominant characteristics by which
separation occur.

The positions of the species' mean habitat
vectors in discriminant two-space, as well as
the 95 percent confidence limits around these
points, are shown in Fig. 7. The relative

Table 4.--Summary of Multiple Stepwise Discriminant Analysis

	Discriminant Function			
Characteristic:	I	II	III	IV
Eigenvalue	7.94	0.736	0.395	0.220
Relative percentage of eigenvalue associated with the function	85.5	7.90	4.3	2.3
Cumulative percentage of eigenvalue across all discriminant functions	85.5	93.4	97.7	100.0
Chi-square statistic for testing significance of discriminant function	792.0	262.0	129.0	48.0
Significance (degrees of freedom)	$p <\!\!< .001$ (36)	$p <\!\!< .001$ (24)	$p <\!\!< .001$ (14)	$p <\!\!< .001$ (6)
Standardized Discriminant Function Coefficients				
CPCR	.4877	-.8273	.0134	1.3435
GDCR	-.0322	-.4870	-.4177	-.0701
RDBA	.1205	-.2947	-.6126	.0099
USCF	-.1224	-.4182	-.7317	-.1562
ADDC	.0766	.5365	-.2234	.0055
TALL	.2309	-.7188	.3561	-.6737
SBDY	.0110	-.6947	.6158	.3175
NOTS	.9431	-.3890	-.3571	-.1726
AVDI	.0131	.1559	-.0105	-1.0300

ADDC - absolute density of deciduous trees
AVDI - average diameter of trees
CPCR - percent canopy cover
GDCR - percent ground cover

NOTS - number of tree species
RDBA - relative basal area of deciduous trees
SBDY - shrub density
TALL - canopy height
USCF - percent of understory coniferous

positions of the group centroids reflect individual responses to structural niche variables as well as the difference among the species in their response to habitat gradients. The magnitude of the distances separating species in this plane reflects the degree to which their habitat selection patterns differ. The further apart any two species' mean observation vectors are in this space, the less similar are their structural niches.

To understand the manner in which significant segregation is achieved and the contribution of each variable to separation, it is instructive to look at each discriminant axis independently (Fig. 8).

Canopy cover (CPCR), canopy height (TALL), and percent understory coniferous (USCF) were the dominant variables describing DF-I. The function is in effect a gradient reflecting canopy features and the deciduous to coniferous continuum which parallels the gradient of elevation. The discriminant function represents a macrohabitat description of the change in forest structure and composition as one proceeds from low to high elevations. The extremes of this gradient are occupied by habitats selected by the Wood thrush and Gray-cheeked thrush. The habitats selected by the Wood thrush are characterized by high canopy cover and height and low percentage of coniferous understory, whereas the Gray-cheeked

Figure 7.—95 percent confidence ellipses about the means on DF-I and DF-II for the five northeast thrush species. Species of thrushes are denoted as: (H.m.) Wood thrush; (C.f) Veery; (C.g) Hermit thrush; (C.u.) Swainson's thrush; (C.m.) Gray-cheeked thrush.

thrush selects stunted spruce-fir forests where the relative magnitudes of these variables are reversed. Species positions along this discriminant axis are consistent, and in the same sequential order as, their distributional pattern along the elevational gradient. For example, the Gray-cheeked thrush is widely separated from all other species which in turn are clustered along the positive portion of the axis. The Wood thrush and Veery have almost coincident centroids on this axis reflecting their complete overlap along the elevational gradient. Extensive overlap occurs because variables reflecting interhabitat differences are unable to discriminate these two species.

Canopy cover and height were again the most dominant variables characterizing DF-II, but in addition, shrub density (SBDY) and the absolute density of deciduous trees (ADDC) contributed substantially to group separation along this axis. The pattern of covariance among these variables describes a gradient of habitats from those characterized by relatively high canopy cover and height, dominated by deciduous trees, to habitats of dense shrubs with an open and often low canopy. Species' positions along this gradient are again interpretable in terms of the continuum of forest types which characterize the species' elevational distributions, but, in addition, variables reflecting intrahabitat separation are important for group discrimination. For example, the relative positions of the Wood thrush and Veery centroids are significantly separated along this axis primarily because of the contribution of shrub density. The most extensive separation occured between the Swainson's and Hermit thrushes
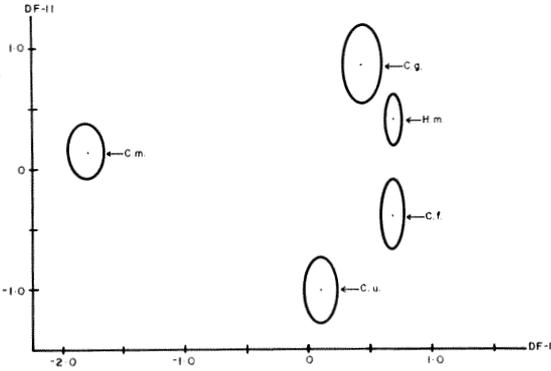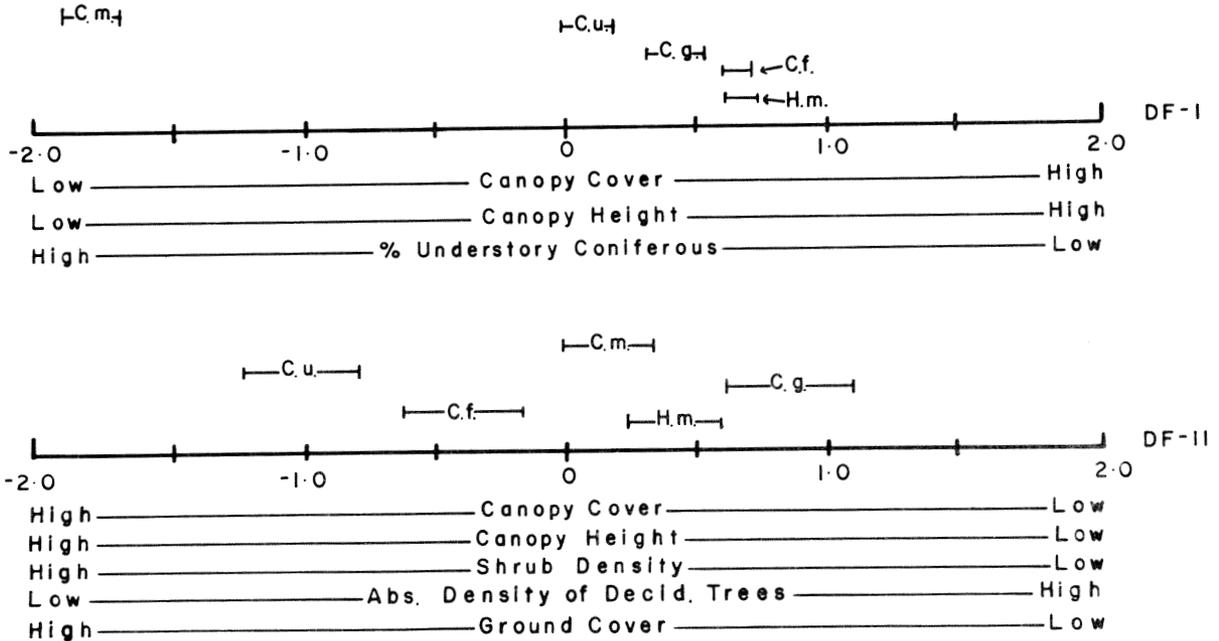
Figure 8.—Thrush species positions on each independent discriminant axis. Species denoted as in Fig. 7.

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primarily because of the influence of shrub density coupled with ground cover: both microhabitat variables reflecting the mosaic structure of the habitat in the area in which these species overlap.

The most direct way to test the discriminating power of the variables selected by the analysis is to determine their effectiveness at accurately assigning the observations to the correct species' group. If a large number of misclassifications occur, then the variables selected are poor discriminators. In practice, the actual and predicted group membership results are compared for those observations actually used to derive the functions. The power of the discriminating variables is empirically determined by the proportion of correct classifications. The results for the five northeastern thrush species are summarized in the classification matrix given in Table 5.

By employing a subset of nine of the original 50 structural variables over 77 percent of the 250 individual quantifications have been assigned to the correct species' group. The accuracy of assignment varies among the species and this in turn supplies information on the degree of ecological similarity of the various species pairs. The number of groups to which a species is misclassified and the extent of this misclassification is a crude index of habitat niche breadth for the species. For example, of the five species considered here the Hermit thrush occupies the widest range of habitat types and thus would have the largest niche breadth.

From the perspective of habitat assessment the results presented here indicate that by quantifying just nine structural habitat variables, the forest manager could predict with 77 percent accuracy what thrush species occupies a particular patch of forest. Of course this statement may need to be qualified because this pattern of habitat selection may be unique to northeast montane forests or, perhaps, solely to Mount Mansfield. In order to develop a workable management scheme to increase the breeding status of the Veery, for example, it is necessary to test the generality of the habitat selection model developed from the Mount Mansfield study area. For avian species, an assessment of their habitat associations in vegatationally similar communities, adjacent and geographically distinct, would constitute a powerful test of their generality of habitat selection. To this end we performed identical habitat analyses of thrush species in the Smoky Mountains and in non-montane areas in northern New York State. In essence, we will test the accuracy with which the classification functions (based on the nine discriminating variables) derived from the Vermont study assign thrush individuals breeding in other locales to their correct species group. The proportion of correct classifications is an empirical index of the generality of their habitat selection.

Southern Montane

Distributional Analyses.—During May 1977 an extensive elevational transect on the Tennessee side of the Great Smoky Mountains National Park was censused. As discussed earlier, the census results included information on the

Table 5.—Classification Matrix

Actual group	N	Predicted Group Membership				
		Wood thrush	Veery	Hermit thrush	Swainson's thrush	Gray-cheeked thrush
W.T.	50	78% (39)	14% (7)	8% (4)	0% (0)	0% (0)
Vy.	50	22% (11)	66% (33)	8% (4)	4% (2)	0% (0)
H.T.	50	22% (11)	2% (1)	62% (31)	14% (7)	0% (0)
S.T.	50	4% (2)	10% (5)	0% (0)	84% (42)	2% (1)
G.C.T.	50	0% (0)	0% (0)	0% (0)	2% (1)	98% (49)

Percent of observations correctly classified: 77.6%

species composition and distributional patterns of these montane avian communities. At all sampling stations thrush species were a significant component of the species complement. The Wood thrush generally had lower relative absolute abundance than on northeastern gradients while the Veery had comparable abundance (Fig. 9). Some of the decrease in the Wood thrush density may be attributable to time of sampling. The early spring of 1977 was unusually warm and the species may have been sufficiently advanced into its breeding cycle as to be vocalizing less frequently.
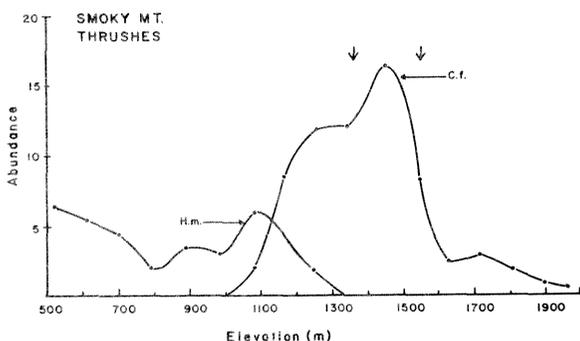
Figure 9.--The abundances of the thrush species on the Smoky Mountain elevational gradient. Species denoted as in Fig. 7.

Note from Fig. 9 that the Wood thrush distribution pattern in the Southeast was comparable to the northeastern pattern. It occupied the lower altitudes along the gradient and its upper elevational terminus coincided with the lower ecotone as on Mount Mansfield. However, the distribution pattern of the Veery was markedly different. It did not appear on the gradient until mid-elevations (but below the first ecotone) and extended all the way to the upper terminus of the gradient. Unlike their northeastern distributions, the Wood thrush and Veery tended to inhabit mutually exclusive ranges along southeastern mountains. In addition, both species showed evidence of amplitude expansion. The Wood thrush and Veery occupied 37 percent of the northeastern gradient but occupied 56 percent and 68 percent respectively of the southeastern transect.

Habitat release indicates shifts in a species' structural habitat niche to include areas of niche space occupied by putative competitors in sympatry (e.g., Crowell, 1961, 1962; Diamond, 1970; Yeaton, 1974; Terborg and Weske, 1975; and others). The amplitude expansion and elevation distributional patterns of the two southeastern thrush populations, particularly the Veery's shift to high elevations, implies that habitat release has occurred for these species. However, to convincingly argue that release has occurred, it is necessary to establish that niche shifts have occurred along critical niche dimensions. Optimally, these will be dimensions quantifying proximate cues used to assess habitat suitability. Operationally, they are usually dimensions derived from multivariate statistical analyses and thus potentially both highly correlated with and powerful predictors of a species' presence.

Habitat Analyses.-- To rigorously test the specificity of the species' habitat selection, and thus the generality of our model, each of the southeastern observation vectors were individually classified by their highest probability of species membership. By classification is meant the process of identifying the likely group membership of an observation vector according to its values on the discriminating variables. Classification is achieved through the use of linear classification equations derived during discriminant analysis from the pooled within-groups covariance matrix and the centroids for the discriminating variables (Klecka, 1975). A separate equation is derived for each group in the analysis. The classification score for each observation for each group is determined by multiplying the raw variable values by their associated coefficients, and adding these together along with the group constant. The observation is then assigned to the species group with the largest classification score.

The results of the classification of the southeastern Wood thrush and Veery populations, according to the functions derived from the northeastern guild, are presented in Table 6. Only 45 percent of the Smoky Mountain Wood thrush individuals were classified as selecting habitats structurally comparable to their northeastern counterparts. Contrast this value with the 78 percent correct classification for northeastern Wood thrushes. Smoky Mountain Wood thrush most frequently select habitats like those selected by northeastern montane Veeries.

Fifty-one percent of the southeastern Veery observation vectors have structural niche configurations consistent with their northeastern conspecifics. Thirty-two percent of the population selected habitats structurally comparable to those selected by the Swainson's thrush, whereas only four percent of the population selected habitats of this type on Mount Mansfield. This represents a substantial expansion

Table 6.--Classification of Smoky Mountain observation vectors by Mount Mansfield classification functions.

		Predicted Group Membership				
Actual Group	N	Wood thrush	Veery	Hermit thursh	Swainson's thrush	Gray-cheeked thrush
W.T. (S)	47	45% (21)	49% (23)	4% (2)	2% (1)	0% (0)
Vy. (S)	47	8.5% (4)	51% (24)	8.5% (4)	32% (15)	0% (0)

into the habitat types which are not utilized in the presence of the Swainson's thrush.

The extensive habitat release observed for both **these** species suggests a strong role for interspecific competition in shaping the specific habitat selection patterns detected for the northeastern montane populations (see Noon, 1977). The most pertinent issue relative to the topic of this paper, however, is the lack of consistency in structural habitat selection between these geographically distinct montane thrush populations. Changes in a species composition as well as structural habitat may result in significant shifts in habitat utilization. The model of habitat selection generated from the study of northeastern montane thrush populations cannot be generalized to vegetationally similar southeastern montane forests. Development of habitat management scheme for forest species may become greatly complicated because of niche shifts which accompany changes in a species' biotic environment.

The niche shifts observed in southeastern thrush populations may have been predicted to some extent because of potential genetic and/or phenotypic differences in populations occupying opposite extremes of the species distributions. In addition, there may be subtle structural changes in forest physiognomy which precludes the species selecting identical structural habitats at these two geographically distinct areas. However, foliage height diversity profiles for spruce-fir forest in northern Maine and the Smoky Mountains are almost identical (Rabenold, 1976), indicating the structural differences may be slight.

To more rigorously test the generality of the habitat selection model established from Mount Mansfield, we studied thrush populations at a comparable latitude but occupying non-montane forests. This comparison may control for significant genetic or phenotypic population differences as well as subtle

structural differences in vegetation structure. This study area was occupied by all of the northeastern montane thrush species except the Gray-cheeked thrush. The methods of locating individuals and quantifying their breeding territories were identical to those previously employed.

The classification results for the 56 habitat quantifications are presented in Table 7. All thrush species, except the Swainson's thrush, are predominantly classified into their correct species group. However, the accuracy of classification has dropped substantially for most species, particularly for the Swainson's thrush which is strongly misclassified as Wood thrush. The **pattern** of misclassification for the Swainson's thrush is particularly surprising because this species and the Wood thrush show virtually no spatial overlap on any of the northeastern elevational gradients (Able and Noon, 1976). The results imply that the habitat selection model cannot be readily applied to adjacent non-montane axes.

We propose two tentative hypotheses to explain the lack of generality in habitat selection for these thrush populations. The first of these concerns the distribution of vegetational patches with particular structural attributes. Habitat patches with the appropriate structural configuration for a specific thrush species appear to be smaller in spatial extent and more randomly distributed in the Cranberry Lake region than on adjacent mountains. This difference between montane and non-montane areas is most likely the result of stricter vegetational zonation on mountains; a consequence of rapid change in abiotic influences which control plant species distributions. If the species respond to this change in grain by increasing territory size (in order to keep the amount of suitable structural habitat relatively constant) then their habitat selection will not appear to be as specific as on mountains. Two types of data are needed to test this hypothesis: first, it will be necessary to document that habitat types are more patchily distributed in this locale than on mountains, and second, to es-

Table 7.--Classification of Cranberry Lake observation vectors by Mountain Mansfield classification functions.

Actual Group	N	Wood thrush	Veery	Hermit thrush	Swainson's thrush	Gray-cheeked thrush
					Predicted Group Membership	
W.T.	13	62% (8)	23% (3)	15% (2)	0% (0)	0% (0)
Vy.	13	8% (1)	54% (7)	31% (4)	8% (1)	0% (0)
H.T.	13	23% (3)	15% (2)	46% (6)	15% (2)	0% (0)
S.T.	17	59% (10)	12% (2)	18% (3)	12% (2)	0% (0)

tablish a relative increase in territory size from montane to non-montane areas. Data of this sort will be collected over the next few breeding seasons.

The second hypothesis concerns historical factors. The geographical range of the Wood thrush has dramatically expanded over a short period of time. Only since 1890 has this species become a regular component of the breeding avifauna in the northeastern United States and Canada (Bent, 1949). Evidence supplied by Morse (1971), from an area in northern Maine recently invaded by the Wood thrush, indicated that the thrushes may be interspecifically territorial. In those aggressive encounters reported, the Wood thrush was behaviorally dominant and may have preempted territories previously occupied by other thrush species. However, in areas studied by Dilger (1956) and Noon (1977), where the Wood thrush was not a recent invader, there was no evidence of interspecific territoriality. In the Cranberry Lake region the Wood thrush may be a recent addition to the breeding avifauna (Adams, 1923) and its abundance is still substantially lower than any of the other thrushes. Because covert competitive interactions contribute strongly to these species' patterns of specific habitat selection (Noon, 1977), the Cranberry Lake region may not have reached a competitive equilibrium. Non-equilibrium patterns of resource utilization may be sufficient to explain the observed degree of habitat misclassification (though not the specific pattern of misclassification).

To summarize, tests in other locales of the habitat selection model developed from an extensive multivariate study of the breeding habitats of the northeastern montane thrush guild have indicated a lack of generality. In southeast mountains where two of the five guild members remain, habitat niche shifts

have occurred as the result of changes in their competitive environment (Noon, 1977). In non-montane, but adjacent, areas in the northeast shifts in habitat utilization for some species are hypothesized to be the result of vegetational and historical factors. The implications are, at least for some forest birds, that habitat management schemes will have to be tailored to local conditions.

DISCUSSION

Habitat selection in passerine birds appears to be influenced by the physical structure of the vegetation without particular regard to the plant species present. In a variety of multivariate studies of avian habitats differences in a few structural variables were sufficient to significantly discriminate even very diverse communities (Whitmore, 1977). This consistency argues for some overriding patterns of community organization. Comparisons of community-level patterns of organization for northeastern and southeastern elevational gradients have been presented. In general, the patterns of organization for these communities are quite similar, but with noteable exceptions. The similarity of organization may most likely be a consequence of the migratory nature of the majority of breeders on these gradients.

Perhaps the most striking feature that emerged from the comparison of community structure on elevational gradients in the northern and southern Appalachian Mountains is their strong similarity. In terms of species richness, whether viewed over the entire gradient or on a station by station basis, the two gradients were virtually identical although there were many differenced in species composition. Rabenold (1976) compared the breeding birds of spruce-fir forests in Maine and North Carolina and concluded that the southern fauna was a depauperate subset of the northern. We did not find such a striking

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difference and Rabenold's species list suggests that the Maine site may have contained greater horizontal heterogeneity. This coupled with the presence of spruce budworm specialists can account for at least part of the difference. Based on our data, the montane avifauna of the southeast does not follow the general trend of lower species richness southward discussed by Tramer (1974).

The communities were also quite similar with respect to the absence of obvious competitive exclusion patterns, the effect of ecotones on species turnover patterns (though somewhat reduced in the Smoky Mountains), and the pattern of species amplitudes on the gradients. These similarities imply that there is some generality to certain structural features of predominantly migratory temperate forest bird communities. In some of these same ways, both communities are quite different from tropical forest ones as discussed previously (Able and Noon, 1976). Most notably, the apparent absence of altitudinal segregation of putative competitors suggesting interference competition, and the large changes in community composition coincident of ecotones are in sharp contrast to the patterns described by Terborgh (1971), Terborgh and Weske (1975) and Diamond (1973) in two widely separated tropical areas.

In many ways the differences between the communities of the two areas are more interesting than their similarities. Whereas species richness was very similar, the communities in the Smoky Mountains were more extensively dominated by one or a very few species. This difference was not accomplished at the expense of the abundance of the rarer species. In fact, abundances of most species averaged higher in the Smoky Mountains than on the northern gradients and this difference was merely greater in the dominants. Rabenold's (1976) data reveal the same difference which he attributed to reduced competition in the depauperate southern fauna. Our data don't admit this explanation, but there are other possibilities, none of which are yet tested. The breeding season is elongated in the southern mountains, allowing more double-broadedness and at least the potential of staggering breeding and thereby reducing competition. Differences in resource abundance, variety or temporal availability between the two regions could also effect changes in the competitive regime.

If competition across the community is relaxed in the southern mountains (and we do not assert that this is generally so), both the higher abundances of species and the smaller turnover of species at ecotones could be explained. Distributional boundaries coincident with ecotones are likely a product of habitat selection evolved and reinforced by competitive pressure. If ecotones were less sharp in the Smoky Mountains our results with regard to distributional limits would be explained. However, we have no evidence that this was the case. In addition, it must be emphasized that whereas a smaller proportion of species limits occurred at ecotones than in the Northeast, large changes in the relative abundance of species were still obvious.

If we examine the species which are dominants at various elevations on the Smoky Mountain gradient a common characteristic emerges. The most abundant species are also those that occupy the greatest elevational ranges on the gradient. The list of these abundant and broadly distributed species includes both migrants and residents, low- and high-elevation species, representatives of at least five families, and a variety of trophic specializations. The only feature they appear to have in common is that they are habitat generalists.

This relationship between "niche" width and abundance has been found in several kinds of communities, including birds (McNaughton and Wolf, 1970; but cf. Ricklefs, 1972). The causal factors in this relationship are by no means clear although it seems reasonable that species with broad habitat tolerances could reach and maintain larger local populations.

A final major difference between the communities on the two gradients is the ratio of migrants to regional residents. Superficially, the Smoky Mountain avifauna is more similar to a tropical one. However, many of the individuals of these species move at least to lower elevations in winter and those that do not apparently wander extensively (Stupka, 1963). Thus they are not sedentary in the sense that many tropical species are thought to be (e.g., Diamond, 1973; but cf. Karr, 1976, and references cited therein). Because in both areas virtually all individuals occupy their breeding territories for only a small fraction of the year, interspecific territoriality leading to the repulsion interactions described by Diamond (1973) and Terborgh (1971) may be impractical. As we argued previously, competitive pressures in these migratory temperate communities seem to have been resolved primarily through differential habitat selection. Under these conditions overt evidence of competition may be leacking as shown theoretically by Rosenzweig (MS), and empirically by Noon (1977).

Differences in community-level patterns reflect differences in population-level responses. Even if these distinctions are slight they may have important consequences for effective habitat management. If southeastern species are more generalized than their northeastern counterparts then they should be less adversely affected by specific changes in habi-

tat structure. On the otherhand, if south-
eastern species diversity is limited by
peak resource abundance then attempts to
increase local diversity by increasing lo-
cal habitat heterogeneity will have only
limited success.

Variability in a species' habitat sel-
ection may imply behavioral plasticity in
response to proximate cues used to assess
habitat suitability. Specificity of habitat
selection in any one locale may by in re-
sponse to interspecific competition (Noon,
1977) or simply to a lack of alternative
suitable habitat. Effective habitat manage-
ment for a specific species will depend
upon accurately ascertaining these subtle
influences. Managing structural habitat
components to positively influence a par-
ticular species will most likely have nega-
tive influences on other species. The chal-
lenge for the habitat manager is to minimize
these negative repurcussions.

Present land-use practices often re-
sult in the generation of small blocks of
forest. The dramatic consequences of this
forest fragmentation on avian communities
has recently been reported (Whitcomb, 1977).
Although these fragments contain patches of
habitat structurally appropriate for cer-
tain species, those species are absent. In-
variably these species are neotropical mi-
grants which appear to be extremely size-
sensitive. Proper management to insure the
presence of these species means not only
insuring appropriate habitats but that these
habitats be contained within large tracts of
continuous forest.

The analysis of the thrush habitat sel-
ection patterns have demonstrated the use
of a multivariate analysis technique and its
potential application to habitat management
schemes. For example, using the results
of discriminant function analysis a given
location within a forest could be measured
using the same subset of variables as were
used in the habitat niche descriptions of
the thrushes. Subsequent to plotting this
point in discriminant space the location
could be assessed according to its proba-
bility of containing a particular thrush
species. If the forest site were not con-
tained within the probability ellipse of
the desired species, or if it would not sup-
port the theoretical maximum species comple-
ment, then, in theory, the habitat could be
altered to include this (and other) species.
An area with high structural diversity should
generate a point in discriminant space that
would simultaneously be contained within the
probability ellipses of several species.

The consequences of habitat perturba-
tions or successional changes would be re-

flected by movement of a forest's mean habitat
vector in discriminant function space. Any
habitat alteration which would move the mean
vector closer to a species' centroid should be
beneficial to that species since the population
would have more suitable habitat available (An-
derson and Shugart, 1974). Conversely, movement
away from a species' centroid should have a neg-
ative effect on its population size and if moved
sufficiently could cause local extinction.

The accuracy with which predictions of pop-
ulation change can be made depends upon the
regularity of a species' habitat selection pat-
tern independent of changes in its competitive
environment. The more invariant a species'
habitat selection the more accurately its popu-
lation dynamics can be modeled. The results
presented above represented a test of the gener-
ality of habitat selection of the northeastern
montane thrush guild. They indicate that subtle
changes in a species environment may generate
substantial niche shifts. The successful man-
agement of avian wildlife will require a de-
tailed understanding of the species' habitat
requirements as well as the dynamics of its
interactions with the rest of the community.
Our data indicate that changes in community-
level attributes may generate significant
changes in a species' habitat utilization.

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Specialized Bird Habitats and Management

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Snag Management for Cavity Nesting Birds

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Abstract.--Availability of snags on forest lands affects
abundance, diversity, and species richness of cavity nesting
birds. The effect of timber rotations, harvesting techniques,
and fungal heart rots on nest site availability is examined.
Research needs are surveyed and management recommendations
suggested.

INTRODUCTION

Increases in availability of snags on
forest lands have been shown to increase the
abundance, diversity, and species richness of
cavity nesting birds (Balda 1975b). If forest
management is to favor these species and the
production of snags as suitable nest sites, it
must consider length of timber rotation, har-
vest techniques, fungal heart rots, and bird
species.

This paper examines interactions that af-
fect production of suitable nest sites and
offers management recommendations that could
increase snag availability.

SNAGS AND SNAG USE

In this paper, a snag will be defined as
any dead, dying, or living tree suitable as
a nest site for a cavity nesting bird. Snags
are produced naturally by a variety of envi-
ronmental factors, all of which stress and
kill living trees. Fire, tree disease,
lightning, flooding, and drought are some of
the more obvious forces that stress trees
(Keen 1955).

Birds use snags for a variety of pur-
poses. Woodpeckers, chickadees, nuthatches,
and brown creepers (Certhia familiaris) com-
monly use snags as foraging substrate. Fly-
catchers, shrikes, red-headed woodpeckers
(Melanerpes erythrocephalus), bluebirds, and
hawks regularly use open-area snags as
perches to watch for prey. Many species of

passerine birds that occupy edge or open habi-
tats use snags as singing perches for terri-
torial advertisement. Woodpeckers often use
resonant undecayed portions of snags as drum-
ming sites for territorial announcements.

Primary cavity nesters, such as wood-
peckers, typically excavate their own nest
and roost cavities in snags. Secondary
cavity nesters use natural cavities and aban-
doned woodpecker excavations (Table 1). For
example, owls often use woodpecker cavities
as daytime roost sites, occasionally before
they are vacated by woodpeckers (Conner
1973). Therefore, factors that cause trees
to become suitable, potential nest sites for
primary cavity nesters are the most important
management parameters in snag production.

Natural cavities and woodpecker excava-
tions are also used by animals other than
birds (Gysel 1961, Kilham 1968, Dennis 1971,
Erskine and McClaren 1972). Squirrels, mice,
wood rats, bats, raccoons (Procyon lotor),
and opossum (Didelphis virginianus) use
cavities for winter and summer dens. Less
noticeable residents are various species of
funnel-web spiders, skinks, and tree frogs.
Cavities provide dry shelters for these small
predators as they wait for insects (Conner
1974).

SUITABILITY OF SNAGS AS NEST SITES

Recent studies demonstrate that even
primary cavity nesters cannot nest in just
any tree. These birds largely depend upon
trees infected by fungal heart rots; such
trees have softened heartwood that makes it
easier for the birds to excavate a cavity
(Odum 1941a and b, Steirly 1957, Shigo and
Kilham 1968, Dennis 1969, Ligon 1970, Kilham
1971, Conner et al. 1975, Crockett and Hadow
1975, Conner et al. 1976, Jackson 1977b).

Table 1.--Selected list of cavity nesting birds (Robbins et al. 1966, Dennis 1971, Erskine and McLaren 1972, Mowbray and Goertz 1972).

Species	Primary or secondary cavity nester	Specific references on nesting sites
Wood Duck (Aix sponsa)	secondary	Bent 1923, Bellrose et al. 1964.
American Kestrel (Falco sparverius)	secondary	Bent 1938
Screech Owl (Otus asio)	secondary	Bent 1938
Common Flicker (Colaptes auratus)	primary	Burns 1900, Bent 1939, Conner et al. 1975, Conner et al. 1976, Conner and Adkisson 1977.
Pileated Woodpecker (Dryocopus pileatus)	primary	Bent 1939, Hoyt 1957, Conway 1957, Jackman 1974, Conner et al. 1976, Conner and Adkisson 1977, Bull and Meslow 1977.
Red-bellied Woodpecker (Melanerpes carolinus)	primary	Bent 1939, Reller 1972, Jackson 1976.
Red-headed Woodpecker (Melanerpes erythrocephalus)	primary	Bent 1939, Reller 1972, Conner 1976, Jackson 1976, Conner and Adkisson 1977.
Yellow-bellied Sapsucker (Sphyrapicus varius)	primary	Bent 1939, Kilham 1971.
Hairy Woodpecker (Picoides villosus)	primary	Bent 1939, Lawrence 1966, Kilham 1968, Conner et al. 1975, Conner et al. 1976, Conner and Adkisson 1976, 1977.
Downy Woodpecker (Picoides pubescens)	primary	Bent 1939, Lawrence 1966, Conner et al. 1975, Conner et al. 1976, Conner and Adkisson 1976, 1977.
Red-cockaded Woodpecker (Picoides borealis)	primary	Bent 1939, Steirly 1957, Ligon 1970, Thompson (ed.) 1971, Jackson 1977a and b, Kilham 1977.
Great Crested Flycatcher (Myiarchus crinitus)	secondary	Bent 1942.
Tree Swallow (Iridoprocne bicolor)	secondary	Bent 1942.
Black-capped and Carolina Chicakdees (Parus atricapillus and P. carolinensis)	both	Bent 1946, Odum 1941a and b.
Tufted Titmouse (Parus bicolor)	both	Bent 1946.
White-breasted, Red-breasted, and Brown-headed Nuthatches (Sitta carolinensis, S. canadensis, and S. pusilla)	both	Bent 1948.
Brown Creeper (Certhia familiaris)	secondary	Bent 1948.

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Table 1.--Continued

Species	Primary or secondary cavity nester	Specific references on nesting sites
Carolina Wren (Troglodytes ludovicianus)	secondary	Bent 1948.
Eastern Bluebird (Sialia sialis)	secondary	Bent 1948, Conner and Adkisson 1974a, Pinkowski, 1976.

Many of these studies also suggest that woodpeckers can excavate nest cavities in non-infected trees. In such studies, however, the presence of fungal fruiting bodies on tree exteriors was relied on to indicate heart rot. But species of fungi that cause primary infection of heart rots do not typically fruit on the exterior of nest trees, and in many cases there is no other sign of decay on the outside of a nest tree with heart rot (Conner et al. 1976). In such cases, aseptically removed chips of heartwood from the tree core near the nest cavity should be cultured in the laboratory to check for fungi.

SEQUENCE OF HEART ROT INVASIONS

Heart rot fungi commonly enter through dead branch stubs (Hepting and Chapman 1938, Baumgartner 1939, Conner et al. 1976), but can also enter through tree bark damage. Wind-blown spores then come in contact with favorable growing conditions (Shigo and Larson 1969).

Once a fungus has entered a tree it usually decays a small area and then spreads throughout the heartwood. Woodpeckers apparently detect heart rot by pecking the tree and distinguishing a particular resonance (Conner et al. 1976).

Woodpeckers often start cavities but may abandon an excavation site when sound, undecayed heartwood is encountered (Conner et al. 1976, E. L. Bull pers. comm.). Jackson (1977b) has suggested that red-cockaded woodpeckers (Picoides borealis) excavate nest cavities slowly in areas where suitable potential nest trees are lacking. The woodpeckers can only excavate until they reach sound heartwood and must wait for fungal activity to decay wood tissue. In such cases, excavation may take more than a year.

IDENTIFICATION OF POTENTIAL NEST TREES

Potential nest trees for primary cavity nesters are those infected with "top rots," heart rot fungi that invade the trunk or main limbs in upper regions of the tree. If a tree is to be classified as a suitable, potential nest tree, heart rot must be detected at the range of heights and stem diameters where woodpeckers normally nest (Table 2). Possible existence of suitable nest site conditions could be detected by observing:

1. Fungal conks (fruiting bodies) of species known to cause heart rots (Shigo and Larson 1969, Hepting 1971, Miller 1972, Conner et al. 1976).

2. Dead branch stubs (Shigo and Larson 1969, Baumgartner 1939, Conner et al. 1976).

3. Old wounds or scars on trees resulting from mechanical, lightning, or fire damage (Hepting 1935, Hepting and Hedgcock 1937, Stickel 1940, Toole 1959, Shigo and Larson 1969). With sufficient time butt rots will grow high enough in the heartwood of trees to create suitable nest site conditions (Toole 1959).

4. Discolored or soft, decayed wood in increment borer corings (Toole 1959, Shigo and Larson 1969, Conner et al. 1976, Jackson 1977b).

5. Existing woodpecker holes or cavities.

6. Obvious dead portions of trees.

7. Testing the tree with a "Shigometer" --Northeastern Forest Experiment Station--photo story No. 29, Upper Darby, Pa. 19082.

Table 2.--Nest site characteristics of several primary cavity nesters. Values presented are a subjective estimate of optimal conditions based on data in the literature (see individual species list, Table 1). CAUTION--These values will vary for tree species and geographical areas different from those where initial data were collected.

Species	Nest cavity height (m)	Tree diameter at nest (cm)	Preference for live or dead section of trees[1]	DBH of nest tree (cm)	Age of nest tree (yrs.)
Red-cockaded Woodpecker	3-12	unavail. in lit.	live	26-60	70-100
Downy Woodpecker	2-11	15-30	dead (both)	17-60	60-70
Hairy Woodpecker	3-17	20-40	both	22-60	85-95
Red-bellied Woodpecker	3-18	15-35	dead (both)	30-76[2]	60-200[2]
Red-headed Woodpecker	4-20	24-36	dead (both)	70-110[3]	140-300[3]
Common Flicker	3-18	26-60	dead (both)	30-120	60-300
Pileated Woodpecker	5-17	30-45	both	35-85	100-180
Black-capped Chickadee	2-9	9-15	dead	unavail. in lit.	unavail. in lit.

[1] - This parameter shows extreme geographic variation.

[2] - Conner, unpublished data in oak-hickory timber type (n = 4)

[3] - Based on mature oak-hickory wood lots--values probably less in southern pine types.

8. Identification of fungi from culture of wood obtained by coring trees with an increment borer (Davidson et al. 1942, Nobles 1965, Conner et al. 1976.

Conks on the outside of a tree do not always indicate a heart rot, and thus a potential nest tree. Sap rots which infect and kill living xylem and phloem tissue also produce conks. The condition of the sapwood, however, may influence suitability of trees as nest cavity sites for certain species. Downy woodpeckers (Picoides pubescens) and common flickers (Colaptes auratus) in eastern U.S. rarely excavate nest cavities in oaks (Quercus spp.) and hickories (Carya spp.) with a living cambium at the nest areas. Eastern pileated (Dryocopus pileatus) and hairy (Picoides villosus) woodpeckers often excavate through a living hardwood cambium to reach a decayed heartwood core (Conner et al. 1975). Downies and flickers apparently need sap rots to soften outer portions of trees as well as heart rots when hardwoods and possibly pines (Pinus spp.) are used.

EFFECTS OF TIMBER MANAGEMENT ON NEST TREE PRODUCTION

Rotation time, or time between clear-cutting, affects nest tree production. At present, rotation times are often established to maximize timber production and minimize loss of products to decay and similar factors (Hepting 1971). Short rotation times that maximize timber production may reduce the chance of trees growing large enough to house nest cavities (Table 2). Sufficient time must also pass to allow fungal heart rots to adequately decay trees. However, there is no information available to define the time needed for various heart rot fungi to decay trees to the extent required for nest excavation.

Based on U.S. Forest Service guidelines (Forest Service Manual, Section 24-10, and 24-15) rotation times for pines on National forest lands in southern forests are about 65 to 70 years. At that age stands range from 40 to 55 cm dbh depending on site condition and can be used for pulpwood and/or sawtimber. When this dbh range is compared with trees selected as nest sites by the seven woodpecker species, the Forest Service

rotation scheme falls within the dbh ranges used (Table 2). Nest trees are apparently being produced. However, only the downy, red-bellied, and flicker nest regularly in trees younger than 65 to 70 years. This suggests that more time is needed for trees to become suitably infected with fungi.

A study of Fomes pini in southern pines demonstrates an increase in fungal activity with age (Hepting and Chapman 1938). Only one out of 40 trees was sufficiently infected with rot to be culled after 80 years, ten years beyond the Forest Service rotation for southern pines. Forest Service rotation on bottomland hardwoods is 100 years, perhaps a bit more favorable for cavity nesters.

Rotations practiced by private paper companies are shorter than those set by the Forest Service. Where southern pines are managed for pulpwood production, rotations of 20 to 30 years are preferred (Johnson in Slusher and Hinckley 1974). If both pulpwood and sawlogs are desired, rotations are 35 to 40 years.

Timber harvest techniques also influence cavity nesters. In the National Forests of southwestern Virginia, snags and nest trees were left standing during clearcutting operations and a variety of wildlife used these trees: bluebirds (Conner and Adkisson 1974a), woodpeckers (Conner and Crawford 1974, Conner et al. 1975), and red-tailed hawks (Buteo jamaicensis) (Conner and Adkisson 1974b). Ages of these stands when clearcut ranged between 100 and 150 years (Conner unpublished data), apparently a sufficient time for fungi to create suitable nest sites. However, snags are highly susceptible to fire and have the potential to fall; they are therefore considered undesirable by many forest managers (McClelland and Frissell 1975).

Firewood collections on national forests remove many snags. The Forest Service occasionally opens up sections of land so that the public can pick up or cut any dead or fallen trees at no cost. In areas where nest sites are limited, such practices should be discontinued if cavity nesters are to be favored.

CALCULATIONS OF MINIMAL SNAG DENSITY

Several formulas have been devised to calculate the minimum snag density needed by a cavity nesting species. Based on data collected in Arizona, Balda (1975a) calculated the number of snags needed to support secondary cavity nesters in ponderosa pine (Pinus ponderosa) forests. The Forest Service has developed guidelines for additional formulas

(Bull and Meslow 1977). Factors used in the calculations include: (A) maximum bird species density in pairs per square mile, (B) number of snags used annually for nesting and roosting, and (C) a reserve of snags: 15 for each one used. These three figures are then multiplied times each other (A x B x C = Y), where Y equals the number of suitably sized snags required per square mile by the species.

If the timber on an area is to be cut, the number of snags to be left can be calculated with the following formula (Bull and Meslow 1977): $S = T(L-R) + Y$
Where S = number of snags to be left per square mile
T = years to next harvest
L = annual snag loss per square mile
R = annual snag recruitment per square mile
Y = number of suitably sized snags required.

Snags fall, and a sufficient number should be left to insure an adequate supply for cavity nesters until replacements become available. When leaving snags it is best to choose those that will last the longest (McClelland and Frissell 1975) as well as those with cavities that are of immediate use. It should also be noted that snags in clearcuts benefit species that select open environments but do not favor cavity nesters that require deep woods habitat.

ARTIFICIAL PRODUCTION OF NEST TREES AND SNAGS

Nest trees and snags could perhaps be created artificially during timber harvest operations and in uncut forest stands. Silvicide injections are often used to kill unwanted trees during clearcutting to eliminate competition for light, moisture, and nutrients.

Research is needed to determine if heart rot fungi are inhibited by the silvicides. The effect of silvicides on insect invasions as well as toxicity to wildlife (e.g. dioxin in 2,4,5-t) also needs to be examined since snags are regularly used as foraging sites. Several studies have already shown that certain herbicides have a toxic and teratological effect on insects, wildlife, and the ecosystem (Orians and Pfeiffer 1970, Galston 1971, President's Scientific Advisory Comm. 1971, Westing 1971, Moffett et al. 1972, Morton et al. 1972, Lichtenstein et al. 1973, Wilson 1973, Kenaga 1974).

If silvicides do not prevent production of suitable, potential nest sites and do not harm wildlife, injections might be made in uncut stands and during lumbering operations to increase snag density.

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Frill girdling of trees and inoculation with sap rots may be an alternative method of eliminating unwanted trees and making nest sites.

Artificial nest sites might be produced even more rapidly through a technique suggested by Affeltranger (in Thompson (ed.) 1971). Trees could be bored and possibly inoculated with an appropriate species of fungus at heights and positions where woodpeckers normally excavate nest cavities (Table 2). Consideration must be given to the orientation of woodpecker nest entrances (Burns 1900; Bent 1939; Lawrence 1966; Dennis 1969, 1971; Baker in Thompson (ed.) 1971; Kilham 1971; Reller 1972; Conner 1975; Inouye 1976; Conner 1977). Bore holes should be placed on the underside of leaning trees so that the openings point 10 degrees below the horizontal (Conner 1975). The preference of individual woodpecker species for either live or dead sections of trees as nest sites must also be considered (Table 2).

The general habitat requirements of cavity nesters should be considered when artificially creating nest trees. Treated trees should be located in habitats with basal areas, vegetation densities and heights, etc., that are acceptable for a particular cavity nester (See references in Table 1).

MANAGEMENT RECOMMENDATIONS

If forest management is to favor nest sites for cavity nesters, the following recommendations can be employed:

1. If timber on an area is to be harvested, increase silvicultural rotation times to a minimum of 100 years for most cavity nesters, and to 150 years for the pileated woodpecker (benefits forest cavity nesters). (Note--total habitat requirements of individual species must also be considered.)

2. When harvesting timber leave a sufficient number of suitable snags for present and future use by cavity nesters (See Bull and Meslow 1977) (optimizes open area cavity nesters).

3. If timber is not to be harvested, manage the area as wilderness (optimizes mature forest cavity nesters).

4. Discontinue removal of dead, dying, and decayed trees for use as materials or firewood in areas where nest cavity sites are limited.

5. Create suitable nest sites by frill girdling trees and inoculating them with sap rots.

6. Pending results from further research, bore holes in suitably sized trees and inoculate with a suitable heart rot fungus. (Local bird clubs could help in this management practice.)

7. When managing for individual species, be aware of specific nesting habitat (basal area, vegetation density, etc.) and nest tree requirements, i.e., living, dead, top broken off, etc. (See references for individual cavity nesting species, Table 1).

RESEARCH NEEDED

Further research is needed on the following subjects before snag management for cavity nesters can be optimized:

1. Determine the fungi species responsible for producing suitably decayed nest trees in southern forests.

2. Investigate the utility of silvicide injection and frill girdling as methods of producing suitably decayed trees for cavity nesters. The effect of silvicides on fungal heart rots, insects, wildlife, and the ecosystem must be determined.

3. Determine the time period necessary for each particular sap and heart rot species to invade and suitably infect different tree species. (See Toole (1959), butt rot invasion sequence versus time.)

4. Determine the effectiveness of bore holes and subsequent inoculations with an appropriate fungi species for artificially creating suitable nest trees.

5. Determine how long snags of various tree species will remain standing.

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Raptor Management[1]

Malcolm G. Edwards[2]

Abstract.--Interest in raptors and their preservation
has resulted in state and federal laws protecting them from
trapping, shooting and poisoning. While many of man's ac-
tivities are destructive, some can be modified to lessen
their impact on raptors.

INTRODUCTION

Until recent times, the white man has
considered all raptors vermin and they were
shot, trapped and poisoned. This persecu-
tion resulted from competition with man
for prey species and from occasional forays
into domestic birds and animals. As more
information on the predator-prey relation-
ship was disseminated, the farmer and
the hunter slowly changed. The crash in
the population of many hawks due to the
widespread use of toxic insecticides in
the 40's and 50's attracted the attention
of bird fanciers, biologists and other
groups. Consequently, state and federal
laws were passed protecting raptors.

The goal of raptor management is
difficult to define. It has been
characterized as having three points of
view: economic, recreational and
scientific (Snyder 1975). In the Southeast,
most poultry is raised under cover and
direct losses to farmers are slight. Com-
mercial shooting preserves, however, may
have serious problems with individual
red-tails and Cooper's hawks. Most impor-
tant are the economics of preserving
habitat threatened by developers. Rec-
reation needs vary, with nature enthusiasts
wanting many species in a natural setting
while falconers are primarily interested in
the larger accipiters, buteos and falcons.

With a few exceptions, management has
consisted mostly of protection from shoot-
ing, disturbance and poisons. In many cases
this protection is sufficient to sustain a
viable population. More comprehensive manage-
ment strategies have been developed for the
bald eagle (Mathieson et. al. 1977) and the
peregrine falcon (Cade 1975a). A proposal
for saving an endangered or threatened pop-
ulation has been developed (Olendorff and
Stoddart 1974).

The management of raptors sometimes
seems futile due to their mobility. If con-
ditions are unsuitable in one place, they
simply move until they find what they need.
However, manipulation of habitat, urban
growth and other activities of man have re-
duced the total habitat. The more adaptable
red-tailed hawk has not been affected as much
as the less adaptable bald eagle. The bird
hawks (peregrine falcon, Cooper's and sharp-
shin hawk) have suffered heavy losses due to
the ingestion of toxic chemicals.

MAN'S IMPACT ON RAPTORS

Some species of raptor is found in almost
all situations, including the center of large
cities. The impact of man's activities on
raptors results from--

--timber management

--shooting

--pollution of water, damming,
 channelization

--urban sprawl

--pesticides

--falconry

Timber Management

Timber management may damage or enhance habitat, depending on the type of cut and the raptor. A newly cut timber stand is rich in passerines (Hooper 1967) and small mammals and attracts the accipiters and buteos. However, most buteos and owls need large, mature trees for nesting and perching. Screech owls and kestrels nest in tree hollows, usually found in mature or overmature timber. A number of safeguards can be built into timber sale operations to protect raptors and maintain suitable habitat.

When a stand of timber is regenerated or has an intermediate cut, all known active hawk and owl nests should be tied into a special zone such as a water influence zone or into a clump of trees being retained for future den trees. If any of the historical peregrine falcon eyries become active, timber operations should be stopped within 1/2 mile of the base of the cliff during the nesting period of March 1 through June 30. Special considerations are unnecessary when eyries are inactive. To encourage raptors, at least one perch tree for hunting should be retained in each 5 acres of cutover area. Preferably this will be a den tree. In stands where prescribed burning may be practiced, a large healthy pine should be retained. With most agencies and many commercial timber managers, it is customary to leave strips of trees along streams and lakes. The larger trees in these strips are important for eagle and osprey nesting. As large dens develop slowly and are critical to some of the owls, all den trees with an opening of 5" or over should be retained, regardless of location.

A balance of age classes and timber types with good dispersion of both will provide habitat for many raptors. Pure stands of pine provide very little for raptors so both upland hardwoods and bottomland hardwood stringers are needed. An exception is newly thinned and burned pine stands which are known to be used by golden eagles. In site preparation prior to seeding or planting, den and perch trees, buffer zones and other key areas must be protected. In planted pine stands, wider planting intervals are preferred because the grass and forbs growing between rows provide better habitat for small mammals.

Bald eagle nesting sites require protection. In the absence of a survey of territory size, a tentative area of 120 acres has been assumed on Southern Forests (U. S. Forest Service 1974). Within this zone, land use practices that alter habitat are prohibited. Disturbance will be held to the present level or reduced. Any cutting will be by the selection method. Activities such as timber harvesting, cultural improvements and road construction will not be conducted within one-half mile of nests during the time of egg laying, incubation and the first month after hatching (Chamberlain 1974).

Shooting

While most raptors are protected by both state and federal law, many are still crippled and killed by gunshots each year. The Eagle Rehabilitation Center at Auburn University received 5 crippled eagles in 1977. Generally crippled birds are picked up by state or federal law-enforcement personnel and taken to a veterinarian or falconer who is interested and has a permit for rehabilitation. No one knows how many are shot and left. There is no question though, that shooting is on the decline due to law enforcement and education.

There are many individuals, including veterinarians, who are interested in rehabilitating raptors. In some cases, the bird can be returned to the wild. Disposition of the others which are permanently crippled from gunshot wounds is a problem. Most zoos and museums have all they want and some of these volunteers find themselves keeping 5 or 6 hawks and owls on a permanent basis. Euthanasia is the only practical solution but is very distasteful. Rehabilitating the more common hawks and owls is not really practical, but human nature being what it is, these efforts will continue.

Water Pollution and Channelization

Water pollution, channelization and dredging affects both eagles and ospreys by reducing the supply of fish. Studies have shown a reduction of 68% of the fish population in channelized streams (Tarplee, Louder, Weber 1971). Investigations have also shown that fish from polluted waters introduce toxic chemicals into these birds (Anonymous 1970). Dredging and thermal pollution also have far reaching effects in reducing the fish population (Smith 1971). Manmade reservoirs, however, may contribute to the habitat of ospreys and eagles.

Urban Sprawl

The preemption of forests and fields for factories and subdivisions has caused problems for many raptors as it reduces their total habitat. On the other hand, the interstate system that has accompanied

this development has improved conditions
for the red-tailed hawk. The seeded cuts
and fills are prime habitat for cotton rats
and other small mammals and few people will
shoot from or across an interstate. Here
in Georgia, a wintering red-tail for each
linear mile of interstate has been noted
often. Conversely, screech and barred owls
seem particularly susceptible to being
struck by automobiles.

Pesticides

There has been so much written about
the effects of the toxic chemicals on raptors
that this paper will not discuss this in de-
tail. Although DDT is no longer used in
this country, it is still a threat as it is
widely used in South America and wintering
raptors ingest these poisons with their
prey (Lincer, Sherburne 1974). A further
threat is the return to North America of
prey species which carry heavy concentra-
tions of these dangerous chemicals. How-
ever, the problem doesn't seem as serious as
it was when these poisons were used in the
Continental United States. The number of
immature arctic peregrine falcons seen and
banded has remained static for the last 5
years, indicating good reproduction.

Falconry

The number of raptors taken by fal-
coners is insignificant. The birds kept
are marked and replacements are closely
monitored. To illustrate the extent of
falconry in the Southeast, South Carolina
has 3 registered falconers, Georgia has 12,
Alabama has 3, and the practice is illegal
in North Carolina. No falconer is permitted
to keep more than 3 birds and only immature
birds may be trapped. There is much inter-
est in captive breeding of hawks and falcons
for use by falconers. The drain on wild
birds is quite small.

ENDANGERED SPECIES

Endangered raptors in the Southeast
are the southern bald eagle and the eastern
and arctic peregrine falcons. Other than
captive birds in breeding projects, the
eastern peregrine is apparently no longer
present as a breeding population. The arctic
peregrine is observed in large numbers in its
fall migration down the Atlantic coast and
in lesser numbers throughout the East. A
breeding bird census of ospreys and bald
eagles taken annually on Southern National
Forests and adjoining lands shows an in-

crease in number of nests and number of
young birds fledged since 1972.

DIRECT HABITAT IMPROVEMENT

Little has been done in the Southeast
that can be defined as a direct habitat im-
provement. For many years there has been a
wintering population of 4 to 6 golden eagles
in the high plateau along the Blue Ridge
Parkway on the Pisgah National Forest in
North Carolina. The area is open country with
scattered shrubs and trees and abundant cotton-
tail rabbits and other small mammals. Each
year a part of this land is burned to retain
the old-field stage of succession. This both
perpetuates the large mammal population and
keeps it open enough for eagles to maneuver.

Studies are also being made on the practi-
cality of creating tree dens in pole size tim-
ber with the use of a power drill. The prem-
ise is that dens started in young trees will
be large enough for raptors and other den
dwellers when the trees are 60 or 70 years of
age. Natural large dens take much longer to
develop. Artificial nest boxes have been
successfully used by kestrels (Hammerstrom,
Hammerstrom, Hart 1973) and screech owls.
Plans exist for reestablishing peregrine fal-
cons on historical eyries in the Southern
Appalachians (Cade 1975a). Conceivably new
artificial eyries may be created in suitable
habitat where cliff faces do not provide
natural ledges.

For several years, a pair of golden
eagles has wintered on the Lake Burton Game
Management Area on the Chattahoochee National
Forest in North Georgia where they are sus-
tained on the carcasses of deer killed il-
legally or accidentally and gathered by the
Game and Fish Commission.

Artificial nest structures have been
erected for osprey use but without success in
North Carolina and Florida.

SUMMARY

Raptor management is new and few proven
practices are known which result in increased
populations.

Raptors have been impacted for many years
by the activities of man resulting in death
due to shooting, poisoning and reduction of
habitat and prey base. Timber management de-
creases habitat for some raptors and creates
it for others. Modifications of timber oper-
ations can lessen this impact. Shooting and

pesticides poisoning have decreased although
too late for the eastern peregrine falcon.
The banning of toxic pesticides, protection
against shooting and education has resulted
in stable and increasing populations of some
raptors.

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COMMON SOUTHEASTERN RAPTORS

COMMON NAME	ZOOLOGICAL NAME	HABITAT [1]
Arctic Peregrine Falcon	Falco peregrinus tundrius	Migrant and occasional winter resident along all coast
Barn Owl	Tyto alba pratincola	Fields and sparse woods
Barred Owl (Northern)	Strix varia varia	Oak-pine, oak-hickory, oak-gum-cypress, white-red-jack pine, maple-beech-birch
Barred Owl (Florida)	Strix varia alleni	Palmetto hammocks oak-gum-cypress
Black Vulture	Coragyps atratus	Not restricted to any timber type
Broadwinged Hawk	Buteo platypterus	Oak-hickory, oak-pine, oak-gum-cypress, maple-beech-birch
Burrowing Owl (Florida)	Speotyto cunicularia	Prairies of central and south Florida
Cooper's Hawk	Accipiter cooperi	Broken woodlands of oak-hickory, oak-pine, white-red-jack pine, maple-beech-birch
Everglade Kite	Rostrhamus sociabilis	Swamps and marshes of Florida
Golden Eagle	Aquila chrysaetos canadensis	Winter resident, may be found in all types
Great Horned Owl	Bubo virginianus	Oak-hickory, oak pine, oak-gum-cypress, maple-beech-birch, white-red-jack pine, spruce-fir
Marsh Hawk	Circus cyaneus hudsonia	Marshes, fields and meadows including coastal areas
Mississippi Kite	Ictinia misisippiensis	Open areas in lowlands, oak-gum-cypress, longleaf-slash pine
Osprey	Pandion haliaetus carolinesis	Around lakes and reservoirs throughout Southeast
Pigeon Hawk	Falco columbaris	Migrant and occasional winter resident throughout Southeast including coastal areas
Red-tailed Hawk	Buteo jamaicensis	Field borders, oak-hickory, oak-pine
Red-shouldered Hawk	Buteo lineatus	Oak-gum-cypress, Oak-hickory
Screech Owl (Eastern)	Otus asio	Fields and broken woodland oak-hickory, oak-pine, maple-beech-birch

Screech Owl (Florida)	Otus asio floridanus	Peninsular Florida, oak-hickory, oak-gum-cypress, longleaf-slash pine
Sharpshinned Hawk	Accipiter striatus	Broken woodland, oak-hickory, oak-pine, oak-gum-cypress, maple, beech-birch, spruce-fir
Shorteared Owl	Asio flammeus	Fields, meadows, cut over areas in winter
Sparrow Hawk	Flaco sparverius	Fields, meadows, coastal areas
Southern Bald Eagle	Haliaeetus leucocephalus	Coast and inland waters, nests in large pines
Swallow-tailed Kite	Elanoides forficatus	Marshes and swamps, oak-gum-cypress
Turkey Vulture	Cathartes aura	Not restricted to any timber type

1/Timber types from National Atlas, USGS, 1970.

Wading Birds and Wetlands Management

Mary C. Landin[1/]

Abstract.--Management of wetlands for wading birds is
a little known research area. Prior research has primarily
been directed toward estuarine and coastal areas. Fresh-
water wetlands in the Southern United States have declined
dramatically in the past 150 years, as have populations of
the bird species dependent upon those areas for habitat.
Human recreational activities, fill and drain efforts,
channelization, and dredging are primary causes of wetlands
decline. Pesticides and poor water quality as well as the
forementioned factors contributed to the decimation of bird
populations. Habitat development and management practices
would benefit all marsh users as well as the 27 species of
wading bird species discussed. Five management techniques
are set forth: (1) preservation and management of all
existing wetlands; (2) creation of new wetlands areas;
(3) expansion of some temporary wetlands to permanent areas;
(4) maintenance of high water quality; (5) year-round pro-
tection of wetlands areas from humans and predators.

INTRODUCTION

Management of wetlands for wading birds
is a little known research area which has
historically not been given much consideration.
This is especially true in freshwater wetlands,
although research efforts have been made con-
cerning protection and development of habitat
in coastal areas by the U. S. Army Engineer
Waterways Experiment Station (WES), the U. S.
Fish and Wildlife Service (USFWS), the National
Oceanic Atmospheric Administration (NOAA)
through the Sea Grant Program, the National
Park Service, the National Audubon Society, and
to a limited degree, some state conservation
agencies, and private citizens.

Past and present research by these
agencies or groups have been tailored to meet
the needs of each agency. The WES studies are
nation-wide efforts to determine the extent of
use (nesting, loafing/roosting, and feeding)
of dredged material islands by colonial nesting
sea and wading birds throughout the United
States coastal, riverine and Great Lakes water-
ways. Their objective is the establishment of
guidelines for management and development of
these 2000+ Corps-made islands (Landin and
Soots 1977).

The USFWS Coastal Ecosystems Team is
presently making a survey of Eastern and Gulf
Coast colonies of wading birds with the inten-
tion of mapping these colony locations
(Portnoy 1977, Custer, unpublished data).
Their objective is to be better able to
protect the colonies through their refuge
systems, land aquisitions, and other means.

NOAA through Sea Grant has sponsored
research at state levels. The most outstand-
ing study in terms of wading bird habitat
management was conducted by Soots and Parnell
(1975) in the North Carolina estuaries.

State efforts have usually been in coop-
eration with state universities and have been
more localized, site-intensive research
(Williams and Martin 1968; Ryder 1977; John
Smith 1976, Texas Parks and Wildlife, personal
communication).

The National Park Service has funded
research efforts of Buckley and Buckley (1976)
which has resulted in a general guidelines
manual for protection of existing sea and
wading bird colonies on the East Coast.

The National Audubon Society established
sanctuaries for wading and sea birds years ago
in key locations. Most of their protected
areas have been coastal (Mills 1934, Dunstan
1977) but a few sites are inland. These areas
are generally only nesting/roosting sites

however, and can offer no protection from destruction of feeding habitat outside the sanctuaries. Only when colonies of wading birds are established in large refuges with accompanying wetlands to ensure feeding habitat are they a successful and continuing entity.

HISTORIC REVIEW

One hundred fifty years ago, before the intensive efforts to fill, drain, or dredge the wetlands and waterways, there existed in the interior Southeastern United States large expanses of freshwater swamps and marshes such as the Big Cypress and the Everglades in Florida; the Great Dismal Swamp of Virginia; Grand Bay, Okefenokee and Altamaha Swamps in Georgia; White River Bottoms, Swan Lake, and Slovac Thicket in Arkansas; I'On Swamp in South Carolina; Reelfoot Lake in Tennessee; and the Tensas Bottoms of Louisiana (Goodwin and Niering 1971, Niering 1966). These areas still exist today on a much reduced, altered scale. However, there had also been numerous other smaller wetlands scattered throughout the South that have totally disappeared through fill and drain efforts for farmland or city expansion.

These freshwater wetlands had supported a large and varied wildlife population, not the least of which were tremendous colonies of eleven species of herons, egrets, ibises, and cormorants that nested at Reelfoot Lake, Swan Lake, Okefenokee Swamp, the Everglades and other suitable areas (Audubon 1944, Bent 1926, Meanley 1972). In addition, they provided habitat for numerous song birds and solitary nesting marsh birds such as the bitterns, rails, American coots (Fulica americana), wood ducks (Aix sponsa), gallinules, limpkins (Aramus guarauna), sandhill cranes (Grus canadensis), and marsh wrens. They also provided resting and feeding areas for migratory ducks, geese, and swans, and 20 species of shorebirds as they moved between breeding and wintering grounds (Errington 1966, Niering 1966).

Since the 18th century man has ditched and attempted to drain wetlands, and since the 1930's has succeeded in draining for agricultural use in the South alone some 20-30 million hectares (Stransky and Halls 1967). Thousands of wetland hectares have been inundated by reservoirs. Along with the drastic diminishing of Southern wetlands, populations of marsh birds declined as well (Bent 1926, Meanley 1972). Some bird species whose ranges and occurrences were reported by Audubon (1944) and Bent (1926) are now listed as extinct or endangered throughout much of their former range and other species' ranges have been drastically reduced (Meanley 1972; USDI 1977).

Our present day Southern interior wetlands consist of isolated pockets of swamps and river bottoms that could not be drained for agriculture by ditching or stream channelization. Channelization was even more detrimental to wetlands than mere ditching (Wharton 1970) because the destruction and restructuring of a biotic community occurred when streams were straightened and cut clean of protective vegetation (Alexander 1963). If any thought to wildlife was given in prior channelization practices, it was to game fish populations. No consideration to water quality nor non-game wildlife was given and as Russell (1966) pointed out, wildlife is now suffering the consequences of this lack of thought. He suggests that laws be enacted requiring a 17-meter buffer zone between all streams and waterways and agricultural and forestry operations. This would provide for cleaner water, and more and better habitat for both fish and wildlife populations.

Dredging of waterways have had an effect on declines in inland wading bird populations by the increase in turbidity of water (USAEDSL 1975). Water turbidity and quality are key factors in declines, since wading birds are visual fish-eaters, and must be able to see their prey.

Another very important practice in the South is the heavy use of pesticides on agricultural crops. Residues from fields wash and leach into lakes, streams, and wetlands, and contaminate these areas. These areas have become sinks for these contaminants, unsafe for fishing, boating, and swimming; and in some areas these activities have been prohibited temporarily (the Mississippi Delta oxbow lakes are examples of this). The most visible evidence of problems with pesticide and fertilizer contamination is fish kills and depletion of game fish species. Less apparent but just as deadly is the biomagnification resulting from continued use by fish-eating birds of the contaminated fish sources. Numerous cases of population decline of bald eagles (Haliaeetus leucocephalus), ospreys (Pandion haliaetus), other raptors, and wading and sea birds have been noted by many authors due to eggshell thinning from contamination which results in unsuccessful nesting attempts. Indeed, even though its use has been banned for several years, the continued spector of DDT/DDE contamination haunts our Southland and other heavily agricultural areas.

Forest harvest practices in the past, although not having the wide-reaching effects of agronomic practices, have also played a role in wildlife population declines (Clawson 1975). Clear cutting, which allows greater erosion and stream pollution unless carefully managed, has

contributed to the problem. Stream bank cutting and ditching to drain hardwood bottomlands and bald cypress (Taxodium distichum) stands for forestry equipment access have changed stream temperatures, ground water levels, sediment and chemical loads in streams (Clawson 1975).

Urban and industrial development cannot escape blame in the decline in wading/marsh bird populations. As the human population has grown, pressures from industrial sites and their wastes, human recreation activities (boating, fishing, hunting, and even birdwatching), human housing needs, and other uses generally termed as "progressive" in our eyes, have all contributed to disruption of life cycles and destruction of habitat necessary for birds' survival.

HABITAT REQUIREMENTS

Life requirements of the six major bird groups using southern wetlands are quite different (Robbins et al. 1966). These six groups are: 1) migrating and overwintering shorebirds; 2) migrating and overwintering waterfowl, including the resident wood ducks and hooded mergansers (Lophodytes cucullatus); 3) the fish-eating raptors that generally overwinter, although some nesting still occurs; 4) the wetland nesting and feeding passerines, woodpeckers, and belted kingfishers (Megaceryle alcyon); 5) the solitary nesting rails, gallinules, coots, limpkins, sandhill cranes, and bitterns; and 6) the colonial nesting herons, egrets, ibises, and cormorants. For the purposes of this paper only Groups 5 and 6 which include 27 species (Table 1) will be considered and discussed, although in general any habitat preservation or development will help all wetlands users.

Colonial Nesters

Nesting Requirements

Colonial nesting wading bird species generally require a tree-shrub nesting substrate, although in Texas they have been known to nest on the ground as well as in shrubs and trees (Chaney et al. 1977). All of the species listed on Table 1 will nest together in mixed colonies in varying percentages although some pure colonies of great blue herons (Ardea herodias) do occur in inland areas (Thompson 1977). Chaney et al. (1977) noted as many as eight species nesting together. Meanley (1956 and 1972) reported a colony of little blue herons (Florida caerulea), snowy egrets (Leucophoyx thula), great egrets (Casmerodius albus), green herons (Butorides virescens), and anhingas (Anhinga anhinga) nesting at

Table 1

Wading bird species that use freshwater wetlands for nesting and/or feeding and loafing.

Colonial Nesters

Great egret(Casmerodius albus)
Snowy egret(Leucophoyx thula)
Great blue heron(Ardea herodias)
Little blue heron(Florida caerulea)
Green heron(Butorides virescens)
Black-crowned night heron(Nycticorax nycticorax)
Yellow-crowned night heron(Nyctanassa violacea)
Wood ibis(Mycteria americana)
White-faced ibis[1](Plegadis chihi)
Glossy ibis[1](Plegadis falcinellus)
Double-crested cormorant(Phalacrocorax auritus)
Anhinga(Anhinga anhinga)
White ibis(Eudocimus albus)
Cattle egret[2](Bubulcus ibis)

Solitary Nesters

King rail(Rallus elegans)
Virginia rail[1](Rallus limicola)
Sora[1](Porzana carolina)
Black rail(Laterallus jamaicensis)
Yellow rail[1](Coturnicops noveboracensis)
Limpkin(Aramus guarauna)
Whooping crane[1](Grus americana)
Sandhill crane(Grus canadensis)
American coot[1](Fulica americana)
Common gallinule(Gallinula chloropus)
Purple gallinule(Pophyrula martinica)
American bittern(Botaurus lentiginosus)
Least bittern(Ixobrychus exilis)

1/ Feeding/loafing use only
2/ Nesting only---species feeds in upland areas

Swan Lake, Arkansas. Gersbacher (1939) reported large numbers of great egrets, double-crested cormorants (Phalacrocorax auritus), great blue herons, black-crowned night herons (Nycticorax nycticorax), and anhingas nesting together at Reelfoot Lake (colony now extinct; Gersbacher 1964).

Nesting substrate in Southern freshwater wetlands generally can be expected to consist of bald cypress, tupelo gum (Nyssa aquatica), swamp privet (Forestiera acuminata), black willow (Salix nigra), button-bush (Cephalanthus occidentalis) and other Southern swamp shrubs and trees (Bent 1926; Meanley 1972). Great blue herons have been known to nest in pecans (Carya illinoensis) in Texas (John Smith 1976, Texas Parks and Wildlife Department, personal communication). The birds generally will build their nests at or near the top of the canopy at heights ranging from

1-30 meters, depending on the nesting substrate. They select secluded sites for their colonies that offer protection from predators and isolation from humans. Frequently they nest on islands, or the sites will have insular characteristics such as being surrounded by impenetrable marsh or thickets. They also usually nest near their feeding areas, but if hard pressed for nesting sites they will select sites several miles away. Scharf (1976) reported a large colony of waders which nested on an isolated island in Lake Erie but that flew as far as 30 kilometers away to feed.

Nesting chronology varies with locality, but generally begins for all species by March and all young have usually fledged by September. Cattle egrets (Bubulcus ibis) are the latest nesters, will be the last species to enter a heronry, and have increased in population while other species declined. This may be attributed to the fact that they are wetlands nesters but upland feeders, and therefore do not suffer the limitations imposed by diminishing wetlands (Davis 1960). Great blue herons will nest in February in most localities. In south Florida, most species are late winter-early spring nesters, especially wood ibises (Mycteria americana) (Kushlan 1976; Browder 1976). Roosting areas are usually in the same area as the nesting colony.

Feeding Requirements

All wading herons, egrets, and ibises feed almost solely on fish, crustaceans, amphibians, and insects (Martin et al. 1951). These birds were much persecuted as being predators of game fish until research (Cottam and Uhler 1945) proved that 75% of their diet consists of non-commercial fish, frogs, snakes, crayfish, mice, and similar prey. Obviously, they are feeders in an aquatic environment, and any decrease in wetlands area decreases these species' feeding habitat proportionally.

Solitary Nesters

Nesting Requirements

Rails, limpkins, bitterns, gallinules, coots, and sandhill cranes are all prone to nest in isolated pairs in tall marsh grasses, cattails (Typha latifolia), and sedges (Bent 1926). They build their nests in secluded spots above the water level by matting together the vegetation or by fastening the nest to the stems of vegetation. They will also nest on old stumps, in mats of vines, or low shrubs. They too will choose insular situations for nest sites, as this affords them protection from predation and disturbance, but they hide their nests carefully in comparison to the colony nesters.

These species usually begin nesting in March and all young fledge by August. These birds roost in the same habitat in which they nest: tall marsh grasses, cattails, sedges, and low shrubs.

Feeding Requirements

Feeding requirements are varied for this group of birds. Sandhill cranes usually are vegetarian, consuming marsh vegetation such as chufa (Cyperus esculentus), bulrush (Scirpus spp.), waterlily (Nymphea spp.), and other wetland plant leaves, stems, tubers, and seeds. They do eat some insects, frogs, snakes, and toads (Walkinshaw 1949).

Limpkins almost always only eat the soft bodies of snails, and rails are solely consumers of insects and crustaceans (Martin et al. 1951). Gallinules are opportunists and change with the season. In spring they consume 35% and in fall 83% plant foods (grasses, millet (Echinochloa spp.), and rice (Oryza sativa). They will also eat aquatic insects, mollusks, and other insects (Bent 1926). All species are directly dependent upon wetlands for their food sources.

HABITAT: WHAT CAN BE DONE

Given the background of massive, universal impact on Southern wetlands and the wildlife that inhabits them, a very gloomy picture emerges. "Most land and water investments are terribly permanent. What is done cannot be undone by us or our children" (Clawson and Fox 1961). The wetlands that have become agricultural lands, reservoirs, and urban sites in years past will undoubtedly remain as they are now. Even as most biologists realize the vital need to protect our remaining wetlands, pressures from both private and public sources to alter our wetlands are still felt. In Mississippi less than five percent of the productive hardwood bottomlands in the Delta area remains, yet private land owners still are draining and clearing as fast as permits are available.

Section 404 regulations giving the U. S. Army Corps of Engineers biologists authority to determine wetlands areas before permits will be issued for land alteration should slow down the destruction of more wetlands. New guidelines are being established, and research is under way at WES to determine indicator species and other identifiers of wetlands and transition zones that will be extremely useful to field biologists responsible for permit determinations.

Where does the present situation leave the

wading bird populations so badly decimated by pesticides, habitat destruction, and human encroachment? Remedies are not fast and clear-cut. Realistically, the manager of a wetlands area must be prepared to accept the fact that he cannot expand the wetlands outside the land he can control (refuges, management areas, game farms, commercial forest lands). Therefore he will have to settle for limited results. But the cumulative efforts of all managers could be a modest expansion of wetlands in the South that would increase available habitat not only for the wading birds in question, but other marsh users such as the economically attractive waterfowl species.

Several habitat development and management practices will need to come into use when consideration is given to providing freshwater habitat for wading birds. First, all existing wetlands areas should be protected and managed very carefully to ensure that their quality is not decreased by pollutants (sediments, chemicals, pesticides, excess nutrients) from outside sources. This is a difficult assignment, since it would require enforcement of water quality standards and education of surrounding land owners as to proper conservation and farming practices to prevent erosion, over-fertilization and over-spraying of chemicals and pesticides.

Second, permanent wetland areas should be created where none exists that meet the following requirements: 1) varying water depths with large areas of shallow marsh, 2) good water quality, and 3) year-round protection, especially in spring and summer. Temporary greentree reservoirs and flooded fields are an established practice for wintering waterfowl. Something of this nature on a permanent basis is needed for wading birds that will provide a habitat for the prey of wading birds. The key here is to provide more feeding habitat, as nesting habitat has usually not been found to be a population-limiting factor. A temporary water-retaining structure for waterfowl only helps wading birds during the months of actual flooding (winter). The rest of the year, and especially during the critical nesting season when quality foods are needed in abundance, flooded habitat is simply not available to wading birds in a management system for waterfowl.

Third, some areas on all refuges and management areas should be converted to permanent shallow water ponds and marshes for year-round use by waders as feeding areas. Deeper water is needed for cormorants' fishing.

Fourth, a very important requirement for all species is clean, clear water so that the birds can see their prey. Rivers, lakes, streams clouded with sediment and contaminated with chemicals are useless to visual feeders. It is

no accident or coincidence that the colonies and populations of herons and egrets decline in the Mississippi River system from north to south (Thompson 1977). Pesticides and sediment loads in the river which increase as it flows southward have taken a deadly toll on historic populations.

Finally and of equal if not greater importance, is the absolute necessity of providing protection in wetlands areas from humans and predators that would disturb a wading bird colony. Signs prohibiting entry to colony areas, education of the public, fences, and tough laws are required to ensure the protection these species must have to exist. Shooting of nesting herons and egrets occurs for sport and for malice, and must be controlled by law enforcement officials.

SUMMARY

In summary, neither wetlands nor wading bird populations will ever regain what has been lost to man. Only by preservation and management of existing wetlands and as much expansion as is possible of historic wetlands will wading birds survive and increase. Pesticides, excess nutrients, and sedimentation have taken tolls in bird populations and disrupted their reproductive processes. Human disturbances have caused tremendous upheavals in nesting colonies. Five practices are recommended for management of wading birds in freshwater wetland habitats:

1) All existing wetlands should be preserved and managed
2) New permanent wetland areas should be created
3) Expansion of some temporary wetlands into permanent areas on refuges and management areas should be done as rapidly as possible
4) High water quality should be maintained in all wetlands areas to ensure feeding habitat for fish-eating birds
5) All areas must be protected from humans and predators to be of real value to wading birds year-round, but especially during the nesting season (February-September).

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Census Techniques for Forest Birds

Chandler S. Robbins [1]

Abstract.--The spot-mapping method is generally acknowledged to be the most dependable of the several census methods for forest birds in the breeding season. Transects and point counts, especially when well standardized and corrected for biases, may be preferable if large areas must be sampled in a short period of time.

INTRODUCTION

With the increasing emphasis on nongame birds as an important natural resource, forest managers are looking for efficient ways to document their populations, for both research and educational purposes. This paper will summarize and comment upon the principal techniques that have been used successfully at various seasons of the year.

CHOICE OF TECHNIQUES

Unfortunately, there is no quick and easy way to measure bird populations in forest habitats. Indices that can be used for comparing one plot with another are relatively easy to obtain, but it is seldom practical to attempt an actual head count on even a small sample plot of 6 to 10 hectares. Almost any attempt to obtain a population estimate must be a compromise between the degree of accuracy sought and the amount of time and trained personnel available.

CHANGING POPULATION

The average adult songbird has only a 40% to 60% probability of being alive one year later. For young birds, the likelihood is considerably less. Thus, bird populations are continually changing through production of young, death of young and adults, local wandering in and out of study plots, and for most species, migration. Mortality of young birds is highest in their first one or two weeks after fledging. Mortality of adult birds of most species is highest during migration, or periods of severe weather, which are most likely to occur in midwinter.

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OPTIMAL SEASONS FOR CENSUSING

Bird census work can be done with greatest accuracy during the peak of the breeding season, which for most species is in May and early June in the Southeast. At this time, most male birds are defending territory and are strongly attached to a very small area of a specific habitat for four or more weeks. During the peak of the nesting season most male birds are in song every day, at least during early morning hours, and are much more easily detected than later in the summer. In winter and during the migration seasons, birds are much more mobile and less attached to a specific habitat type.

DOCUMENTARY STUDIES

Any census work undertaken should be initiated with one or more particular objectives in mind. If one wishes only to document the species that are using a forest, help can frequently be enlisted from local experienced amateurs.

Since I work primarily with amateur ornithologists on cooperative programs to monitor populations, I naturally think of the vast resource of qualified help that is available to assist with bird population studies.

For example, nearly all of the national wildlife refuges have lists of birds of their area that are available for free distribution to visitors. Some of these lists were compiled entirely by amateur volunteers, and in almost all cases amateurs contributed many of the records. Most of the national parks also have publications on their wildlife resources. Comparatively few national, state, or other forests, however, have made lists of birds and other fauna available to the public. I believe that provision of such lists is one of the first steps toward arousing public
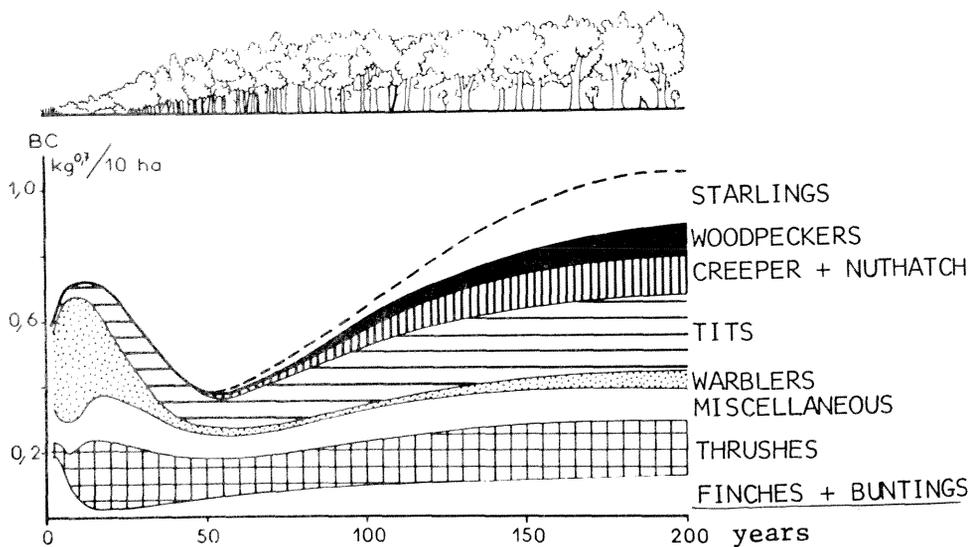
Figure 1.--Changes in consuming biomass as represented by
the principal bird families during a 200-year succession
in an oak forest in France. From Ferry and Frochot (1970).

interest in the biological resources of a
forest. Volunteer cooperators should be able
to prepare such lists, and furthermore, assist
later with quantitative studies of bird
populations.

Parts of many of the national and state
forests are included within 15-mile diameter
Christmas Bird Count circles. An easy way to
enlist volunteers to assist in the preparation
of a list of species for a specified forest
would be to contact the Christmas Count
compiler (whose name and address are always
given in the published report in American
Birds) and get from him the name of the person
or persons responsible for covering the
forest. By asking this observer to keep a
separate record of birds seen in the forest,
one can not only start to build up a file of
information on the winter avifauna of the
forest, but one can also generate the interest
necessary for continued assistance through all
seasons of the year. If help is needed in
documenting presence of endangered species,
this also can often be done by enticing
qualified amateurs to join in the search.

COMPARATIVE STUDIES

For comparing bird populations of two or
more sites, we must turn to methods that will
yield numerical estimates of bird population,
or at least index values. Such studies would
include the need to document populations
before and after some particular management
program, timber harvest procedure, fire,
pesticide treatment or other event that might
influence bird populations (Kendeigh 1947,

Hager 1960, Michael and Thornburgh 1971,
Conner et al. 1975, Webb et al. 1977,
Schweitzer 1978). Such studies can also be
used to document population changes during
successional stages (fig. 1) or during
recovery from fire, surface mining, or other
ecological changes (Johnston and Odum 1956,
Ferry and Frochot 1970, Hamilton and Noble
1975, Shugart and James 1973, Shugart et al.
1975). Comparative studies can also be used
to assist management decisions. For example,
one may wish to choose among several areas for
a particular management program, or even for
preservation of a unique ecosystem such as to
provide habitat for a particular endangered or
threatened species.

Williamson (1970), for example, has used
spot-mapping censuses to show that density and
diversity of bird-life in coniferous planta-
tions can be increased by providing a fringe
of deciduous trees or leaving small "island
refuges" of scrub or deciduous trees. Such a
practice might even provide additional
benefits by reducing insect damage.

BREEDING SEASON TECHNIQUES

Spot-mapping Census

The spot-mapping technique, also called
the plot census or, simply, mapping census,
was first employed in North America by
Williams (1936) and in Sweden by Enemar
(1959). Basically, this technique consists of
making 8 or 10 census trips through a plot of
known size, and preferably of uniform habitat,
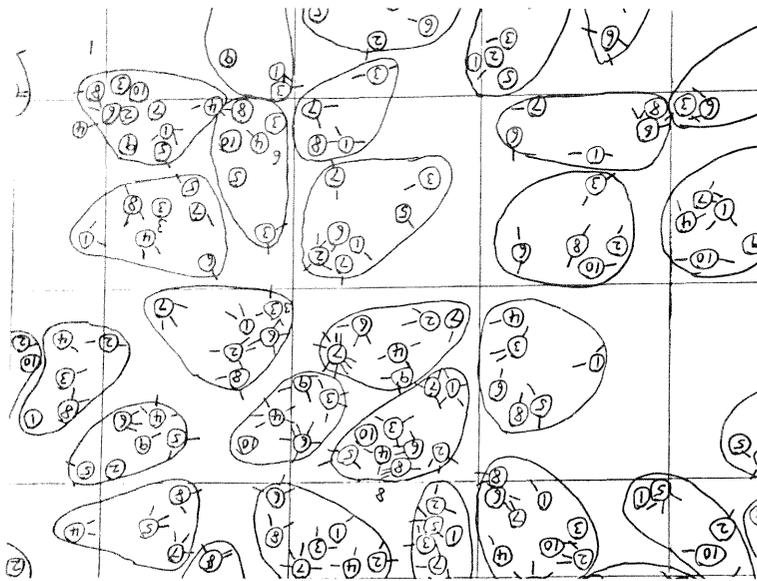that has been surveyed and mapped with a grid

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Figure 2.--Section of species map for Red-eyed Vireo at the Patuxent Wildlife Research Center. Numbers designate the 10 trips. Singing males are circled; simultaneous registrations are indicated by pointers. Each square is 1 ha.

system. On each visit the position of each bird seen or heard is recorded on the plot maps. Kendeigh (1944), Lack (1937), and Udvardy (1957) give good historical accounts, describe the method in detail and include comprehensive bibliographies. An important feature of the spot-mapping technique is to designate with appropriate symbols those individuals of a species that are heard singing at the same time (simultaneous registrations). These, in conjunction with clusters of single registrations, make it possible to outline the approximate territorial limits of each male bird and make a reasonable estimate of the total number of territorial males of each species present in the area (fig. 2).

This technique has now been widely adopted in Europe and North America. Procedures have been standardized by the International Bird Census Committee (1970a,b) so that results obtained in different countries can be compared. Spot-mapping has been widely used in England since 1962 to monitor bird population changes (Batten and Marchant 1977a,b). A quantitative description of the habitat (James and Shugart 1970) is now a standard feature of many of the breeding bird censuses in forest habitats published in American Birds.

The spot-mapping method is the technique used by most census workers (Kendeigh 1944, Bond 1957, Oelke 1974, Yut 1974). It is generally acknowledged to be the most accurate of

the various bird census methods because: 1) it gives the greatest opportunity to record all species that are breeding in the area, 2) it most closely approximates the absolute number of breeding pairs, 3) there is a minimum of error in estimating whether the birds recorded are within or outside of the plot boundaries, and 4) observer bias is minimized. The chief disadvantage of the technique is the amount of time required to set up the plot and conduct a minimum of eight census trips.

Critique

The spot-mapping method is not without its pitfalls. Most plots censused are within the 6 to 20-hectare range, and do not permit accurate measurement of territories of wide-ranging species. Year-to-year variation in plots as small as 6 ha is greatly exaggerated by birds that move short distances into or out of the plot boundaries from one year to the next.

Svensson (1974) had 58 persons with various levels of experience estimate breeding populations using census maps from 37 plots. He reported that the coefficient of variation ranged from 6% to 56% (15 to 30% for most plots), and that it varied among species (from 16% to 36%). Variability would have been less if the participants had had field experience in the plots. Svensson concluded that considerable variation does exist among persons in the evaluation of species maps, and he recommends that when plots from different

habitat types or different regions are compared a check should be carried out on a sample of maps to see if there are any differences in the evaluation procedures applied.

Nilsson (1977), in an evaluation of the mapping method, believed that more than 10 visits, and perhaps as many as 20, may be required for accurate censusing of certain difficult species. He suggested that the number of visits might be reduced if more time were spent on each visit.

Berthold (1976) published a comprehensive critique of bird census methods with emphasis on the mapping method. He concluded that there are almost no methodologically perfect tests of census methods; that errors of 50% or more are common; and that although many errors and sources of errors have been recognized in the literature, they have not sufficiently been taken into consideration. He recommended abandoning relative census methods in favor of more absolute methods, and he proposed using nest finding and banding to supplement mapping. He stated that census methods should be more standardized and that calculations or justified estimates of errors should be included in published results. A. J. Erskine, who has translated Berthold's critique into English for the Canadian Wildlife Service (unpublished manuscript), points out that "Berthold is not himself a worker in bird census studies but rather an environmental physiologist accustomed to the careful regulation of variables often possible in laboratory studies. Many of the criticisms he advances are long familiar to census workers, whose experience would have prevented some of the sweeping generalizations in his review." Berthold does include an excellent bibliography, especially of German, English, and Scandinavian titles.

The mapping method was recently criticized by Best (1975) as not yielding results that can be interpreted consistently by different experienced observers; but this criticism was unfair because the author apparently failed to follow standard procedures and neglected to obtain data on simultaneous registrations of the single species considered--data that are essential to proper interpretation of the results.

To fairly test reliability, different observers must do the field work as well as determine the number of territories on each map. This was done in a mature floodplain forest plot at the Patuxent Research Refuge in Maryland by Robbins and Bridge. They conducted independent censuses of 8 visits each in a 40 ha plot from 15 May to 3 June 1962. One observer censused from north-south trails

through the plot while the other used east-west trails. After making independent estimates of the breeding population, the two observers combined their maps and made a revised estimate based on all 16 visits. With 8 visits the observers had detected 89% and 92% of the birds that were detected on 16 visits.

Diehl (1974), who made 27 and 21 visits, respectively, to two grassland plots totaling 43.5 ha found that between 32% and 44% of the pairs present were detected on a single visit, and 95% to 98% on one or more of 10 visits. However, a great many of these birds were detected on only one or two visits and would not have been recognized as distinct pairs; thus while nearly all of the pairs had been observed and recorded, the population estimates from 10 visits would have been only 53% to 66% of the number of pairs present.

Other authors (Davis 1965, Jones 1974, Erskine 1974) have discussed problems in using the spot-mapping technique for certain species that are difficult to census, such as those that do not sing regularly, are not territorial, or range over areas much larger than the size of most census plots. Nevertheless, spot-mapping is still the most generally accepted method and the one most frequently used to calibrate the results of less time-consuming, but relatively less accurate methods.

Census Summaries

Three catalogs (Erskine 1971, 1972, 1976) have summarized the results of 228 Breeding Bird Censuses that have been conducted in Canada. Censuses that have been published from 1937 through 1977 in American Birds have been put on magnetic tape at the Migratory Bird and Habitat Research Laboratory where they provide a valuable comparative resource that may be accessed either by habitat, by bird species, or by a number of the other variables that are included in the computer record. This file presently contains information on 1,101 plots.

Transects

The transect method involves counting birds on one or both sides of a line through one or more habitats; in most instances either the width of the transect is defined or the distance to each bird encountered is estimated. The transect method was first used extensively in the United States in 1906-09 by Forbes and Gross (Graber and Graber 1963) and in Finland in 1941-56 by Merikallio (1958). In both instances, the transect results were used to estimate total populations by habitat for an entire state or nation. The Forbes and

Gross study was later repeated by Graber and Graber (1963) to show bird population changes over a 50-year period.

One advantage of the transect method is that it may be used throughout the year, but the results are less accurate outside the breeding season. Another advantage is that a relatively large area can be sampled in a short time. Flack (1976), for example, used 150-foot-wide transects to compare breeding bird populations in 41 aspen forests in 9 western states and provinces, 1966-69.

The chief disadvantage of the method is that a single coverage of a transect does not permit a good estimate of the number of birds missed. Anderson and Pospahala (1970), using data from 1600 miles of transects, generated a curvilinear (quadratic) equation to show the fraction of waterfowl nests missed at various distances from the center line of the transect; but they pointed out that to adequately correct for the number of fixed objects missed one needs a large sample and one must also make the assumption that all of the objects closest to the center of the transect are detected.

Emlen (1971) also has considered how the

	A	B	C	D	TOT
WIDTH OF STRIP (FT)	50	50	100	212	412
NO BIRDS DETECTED	60	42	41	12	155
PROJECTED NO PRESENT	60	60	120	250	490

C D 412 = 155/490 = .316
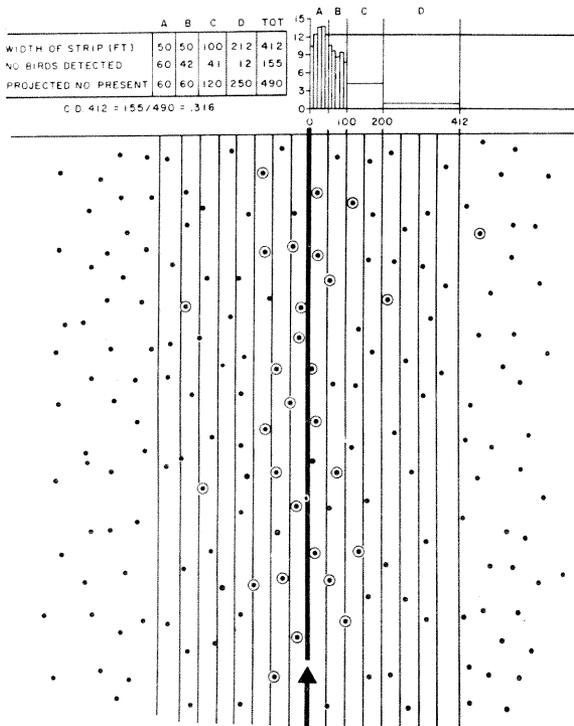
Figure 3.--Schematic model showing birds detected (circled dots) at various distances from the transect (heavy line). From Emlen (1971).

error inherent in the transect count may be minimized by first estimating the lateral distance to each bird encountered (fig. 3), and then deriving a coefficient of detectability. He assumes that no bird close to the observer goes undetected. In actual practice, the number of birds within a few meters of the transect line that are undetected may be quite large (Järvinen and Väisänen 1975), especially in a mature forest habitat. Even during the height of the breeding season there is an enormous difference in singing behavior and conspicuousness among the various species. A noisy, active species such as the Tufted Titmouse may be recorded on 68% of the visits if within 50 meters of the observer, whereas species such as the Ruby-throated Hummingbird, Worm-eating Warbler, and even the American Redstart may be recorded only 36% to 39% of the time (Stewart et al. 1952, pp. 269-270). Emlen (1977) estimated the number of unrecorded males of common species by running each transect five times, plotting all singing birds on maps, outlining the territory of each, and determining what European workers call the "effectivity" of a single trip for each species. He then used the computed effectivity for correcting his breeding season transect results.

The transect method is quite effective for comparing the abundance of a given species among two or more plots of similar habitat. Also, unless visibility is strongly influenced by the structure of the habitat, the transect method may be used to compare abundance of a given species from one habitat to another. It is not, however, a desirable method for comparing abundance of two species that may not be equally conspicuous, unless appropriate corrections are made, species by species. These corrections can be made by taking a series of transect counts through plots where the population has been estimated by other methods (Ferry and Frochot 1970), Enemar and Sjöstrand 1970).

Although most transect workers record birds per kilometer (or per mile) or per square kilometer (or per 100 acres), a few have preferred to use units of time such as birds per 10 hours (Colquhoun 1940).

Transects are especially effective along hedgerows and wood margins where it may seem impractical to establish mapping plots or make point counts. Johnston (1947) did, however, use spot-mapping in two isolated woodlots to compare distribution of forest-edge and forest-interior species.

The IPA or Point Count Method

The IPA (Indices Ponctuels d'Abondance)

method was developed by Ferry and Frochot (1970) as a means of obtaining indices of abundance for comparing bird populations of different habitats (or of the same habitat in different locations) during the breeding season.

The IPA counts by the French ornithologists consist of the establishment of a network of points regularly distributed through the habitat to be studied. The observer then stands at each designated spot for 20 minutes in the early morning in good weather and notes all birds heard and seen. Each spot is censused twice in the breeding season. The higher of the two counts of pair numbers is used as an index of abundance for each species. Each singing male, occupied nest or family of birds out of the nest counts as one pair, while a bird merely seen or heard calling counts as half a pair. The efficiency of a 20-minute stop seems satisfactory to the French investigators because during the last 5 minutes only 3% more species and 9% more individuals were recorded in forest habitats.

Ferry (1974) quotes Schwartz (1963, p. 139) as stating that with a sample of 30 or more the mean may be compared with another number, whatever the type of distribution. Thus, it is possible to calculate whether the mean IPA of a species is statistically different from zero, and so have an objective way of eliminating species whose occurrence in the habitat is due to chance or whose presence is unimportant. (In actual practice, of course, some of the scarcer species may be the ones most in need of attention from forest managers.) Ferry (1974) has determined which species have statistically significant population differences in two habitats as indicated by the IPA method. He has then computed a percentage of difference as a final comparison of the two plots. In this way, numerical similarity indices could be computed among an entire matrix of different plots with a minimum of field work. Ferry also points out that by conducting IPA counts within a mapping census plot, one can determine the effectivity of the IPA method, species by species, and thus obtain correction factors to convert indices to population estimates.

In Denmark, Jørgensen (1974) conducted 81 IPA censuses on 8 mornings from mid-May to mid-June. The 13 1/2 hours of effective field work was about 50% less than would have been needed for covering one census plot by the mapping method. Jørgensen compared the density of each species among different habitats,

using the Mann-Whitney U-test. He concluded that the IPA method was well suited to a study of forest succession, in which it is desired to make statistical comparisons. He summarized habitat utilization (based on 15 to 18 counts in each habitat) in terms of a list of dominant species, each comprising 5% or more of the registrations, and sub-dominants (2% to 5%). Then, using only the dominant species, he computed similarity indices among the various habitats using the formula $s=2c/(a+b)$ where s is the index, a and b are the numbers of species in each sample, and c the number of species common to the two samples.

In the United States, the IPA method has been further refined by Whitcomb and Robbins 2/ who make three 20-minute counts (each composed of four 5-minute segments) at each point. The three samples are taken at different times in the nesting season (generally early, middle, and late June) and at three different periods in the early morning hours in order to maximize the likelihood of recording all species present.

Density-Frequency Relationship

Blondel (1975) has introduced a further modification of the IPA method (Echantillonnage Frequentiel Progressif: EFP). The EFP method uses the presence or absence of a species on each of the 20-minute IPA counts to determine frequency of that species in each plot (fig. 4). Comparison of the IPA and the EFP figures allows one to determine for each species the relationship between its density and its frequency. The frequency of a species is shown to be closely correlated with the logarithm of its density (fig. 5); the lower the frequency the better the correlation. "Thus, frequencies of occurrence can be used as an objective measure of the number of individuals included in the community." Rotenberry and Wiens (1976) found a similar correlation between density and frequency using roadside transect (BBS) data.

Blondel claims that the EFP method, which is highly standardized, is very useful for a rigorous statistical interpretation of data. He used the EFP method to calculate ecological profiles and niche breadth for each species. He analyzed the structure of bird communities according to the structure of the vegetation. For each community, he determined the species richness, the species diversity index (H'), the equitability (J'), and the level of fit to Galton's log-normal model. He also discussed the influence of reforestation on bird communities. "In many instances, conifer plantations, especially Cedar (species not stated), seem successful in the rebuilding of communities." Blondel concludes that the

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2/ In preparation

Parus ater

Parus major

Altitude: < 500m | 500-1000m | 1000-1400m | >1400 m

Fréquence: >75% | 75>F>50% | 50>F>25% | F<25% | F=0

Echantillon insuffisant | Presence observée
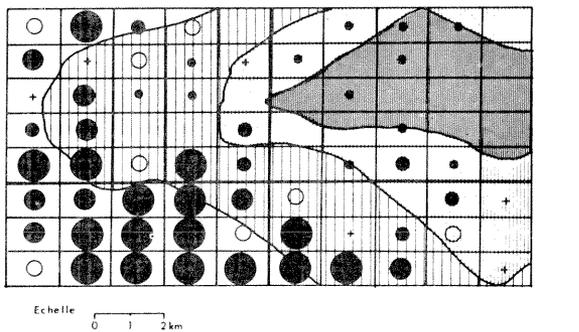
Echelle 0 1 2km
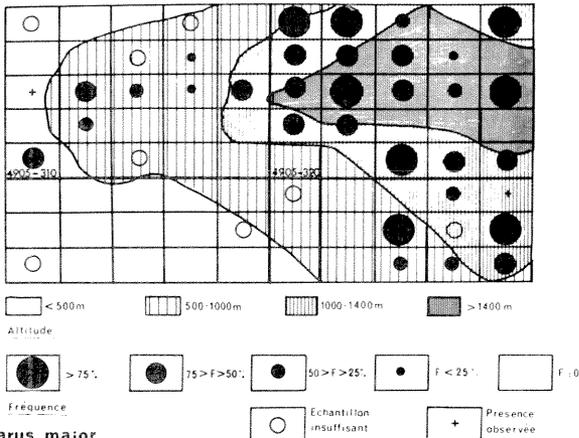
Figure 4.--EFP maps showing distribution of
Coal Tit (above) and Great Tit with relation
to elevation. Frequency, as shown by size
of the dots in the legend, is based on an
average of about four 20-minute IPA counts in
each of the small rectangles. From Blondel
(1975).

standardized and time-saving EFP method "seems
very well adapted to solve problems of
theoretical and applied ecology at the
community level, and can be used fruitfully
for environmental monitoring."

Comparison with spot-mapping

In comparing point counts (IPA) with
mapping census in Białowieża Forest in Poland,
Tomiałojć et al. (1978) found that point
counts overestimate the population when the
density is low and underestimate when density
is high. IPA counts also require better ob-
servers and encounter more problems separating
migrants or other non-breeding birds from
breeding individuals than do mapping censuses.

Combining transects and point counts

Bond (1957) used a method that was
essentially a combination of the transect and
point count methods to compare bird popula-
tions in 64 upland hardwood stands in Wiscon-

sin. After entering a woodland he walked
about 50 m along a transect line. At this
point he stopped for 5 minutes and counted all
birds seen and/or heard ahead of him. He then
walked ahead slowly for 5 minutes, averaging
150-175 m. He repeated this procedure until
he had 5 sample 10-minute counts from each
forest interior. Two early morning visits
were made to each woodlot and the highest
count for each species was used. These counts
detected 76%, 78%, and 70%, as many pairs as
were found by spot-mapping censuses in three
of the same woodlands. Palmgren (1930) and
Kendeigh (1944) found 81% and 63% of their
birds in spot-mapping censuses were detected
on the first two visits.

$$y = 0.0163x - 0.68$$
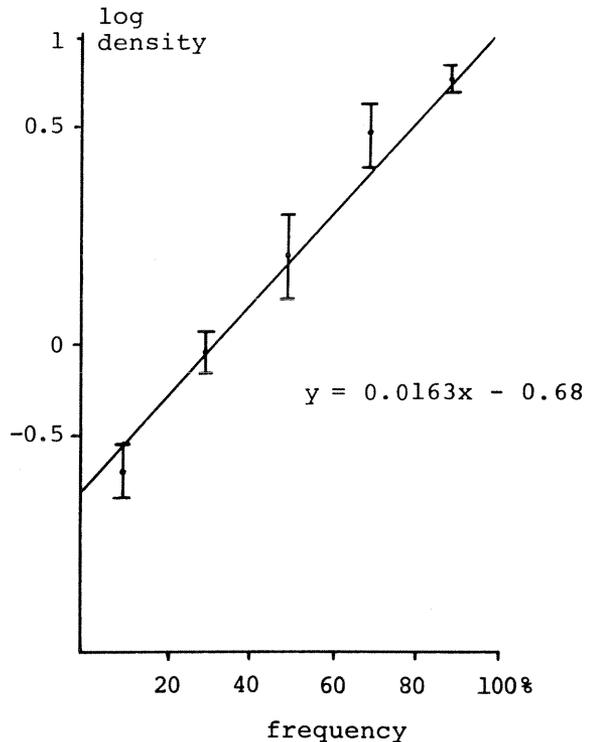
Figure 5.--Relation between frequency of
detection and logarithm of numbers of indi-
viduals detected for 239 pairs of 57
species. Confidence interval, p =.05. From
Blondel (1975).

Breeding Bird Survey

The North American Breeding Bird Survey
(BBS) was developed by the U. S. Fish and
Wildlife Service to monitor bird population
changes in North America over a period of
years (Robbins and Van Velzen 1967, 1969, 1974).
Each survey route is a series of 50 3-minute
point counts at 1/2-mile intervals along a 24
1/2-mile roadside transect that was selected
by a random procedure. Coverage extends from
one-half hour before sunrise to about 4 hours
after sunrise and thus embraces the period of

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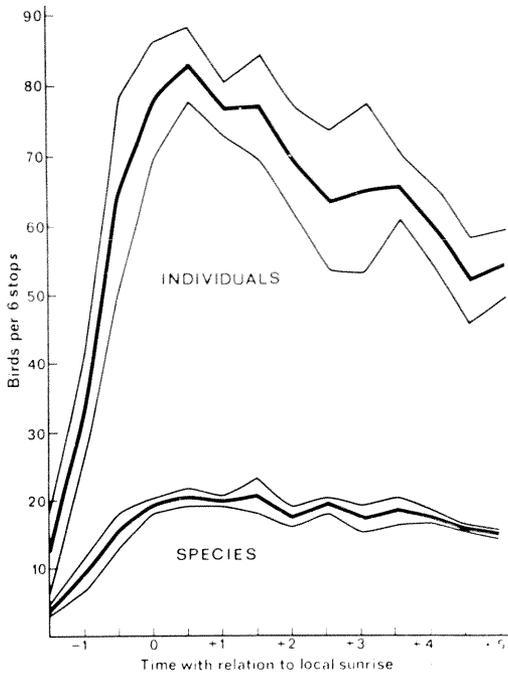
Figure 6.—Hourly variation in bird counts. The outer lines represent 95% confidence limits based on 4 days in June 1969. From Robbins and Van Velzen (1970).

greatest bird activity (fig. 6). At each of the 50 stops, all birds heard and all birds seen within one-quarter mile of the counting position are tallied. The BBS, which now embraces the populated areas of Canada and all of the United States except Hawaii, provides an annual sample from 1700 or more roadside transects. The results are widely used for documentary and research purposes, and are also available for comparison with intensive local population studies, such as Miniroutes that use the same method.

The BBS results are used primarily for statistical analysis of population changes over the years (fig.7) and for mapping of relative breeding densities throughout the North American range of a species (fig. 8). A ten-year summary of the BBS results is in preparation.

BBS Miniroutes

For intensive local studies, BBS routes can be laid out in a non-random way, so that all or most secondary roads within the area of interest are included in the sample (fig. 9). The term "Miniroute" results from a 25-stop instead of a 50-stop format. By using a shorter route, observers were able to complete
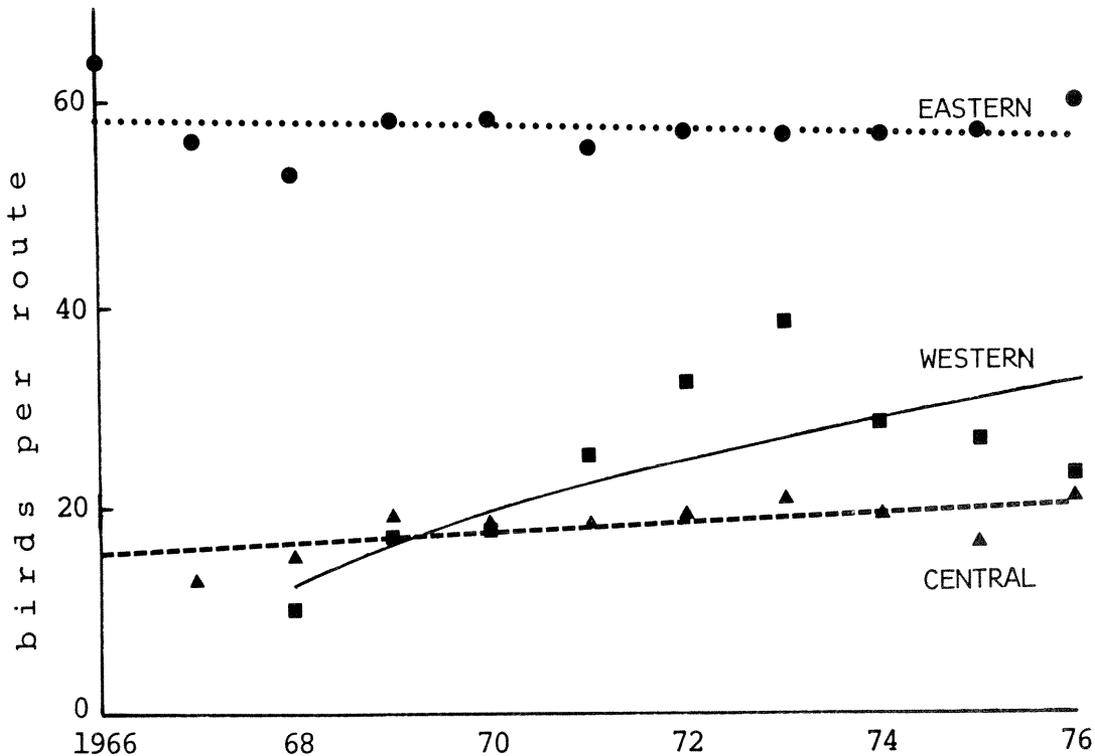
Figure 7.—Population trends in the Starling in the western, central, and eastern regions of North America. Data from Breeding Bird Survey.
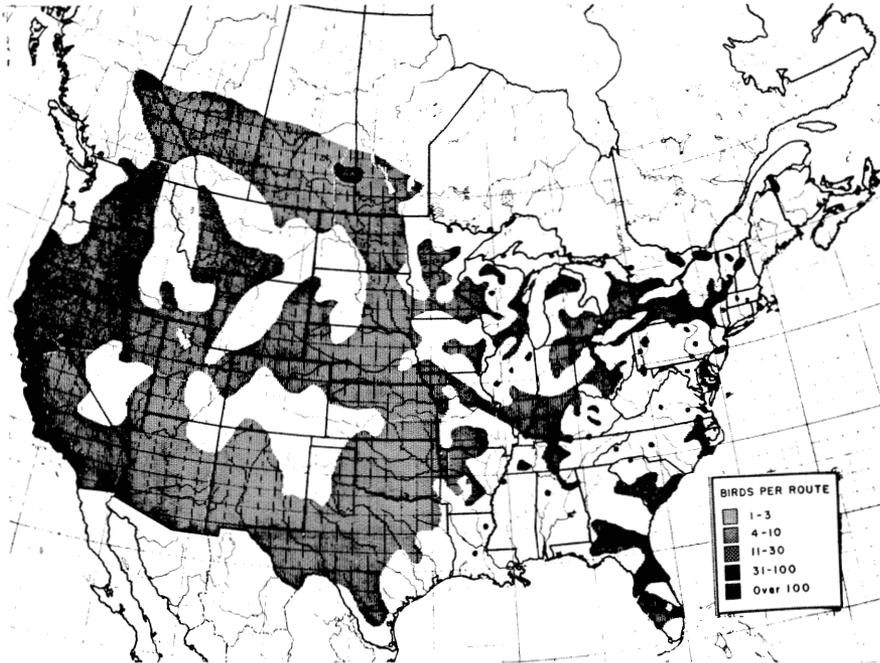
Figure 8.--Relative abundance of the Red-tailed Hawk in
the 1968-70 breeding seasons. Data from Breeding Bird
Survey.

Figure 9.--Map of Howard County, Maryland,
showing locations of the mid-points of each
5-stop section of the network of Miniroutes.

Figure 10.--Mean number of Red-eyed Vireos
recorded per half hour on Howard County
Miniroutes, 1973. The top line is the sum
of the two coverages of each route. Time in
hours is given with relation to local sunrise
(SR).

their coverage before working hours in the
morning. By covering each route twice (once
in each direction) and combining the results
of the two counts, most of the difference in
activity resulting from time of day could be
eliminated (fig. 10). Bystrak and others
(Klimkiewicz and Solem 1974) used Miniroutes
to map relative abundance of breeding birds
throughout two Maryland counties (fig. 11) as
part of a Breeding Bird Atlas program for
these counties. Although the Miniroute
technique was designed for roadside use, it
could be applied with slight modifications to

coverage of forested areas on horseback or by
off-road vehicles, making it possible to map
distribution of breeding birds over a wide
area with a minimum of expenditure of time.
Differences in bird populations could then be
correlated with differences in vegetation
obtained from aerial surveys or by ground

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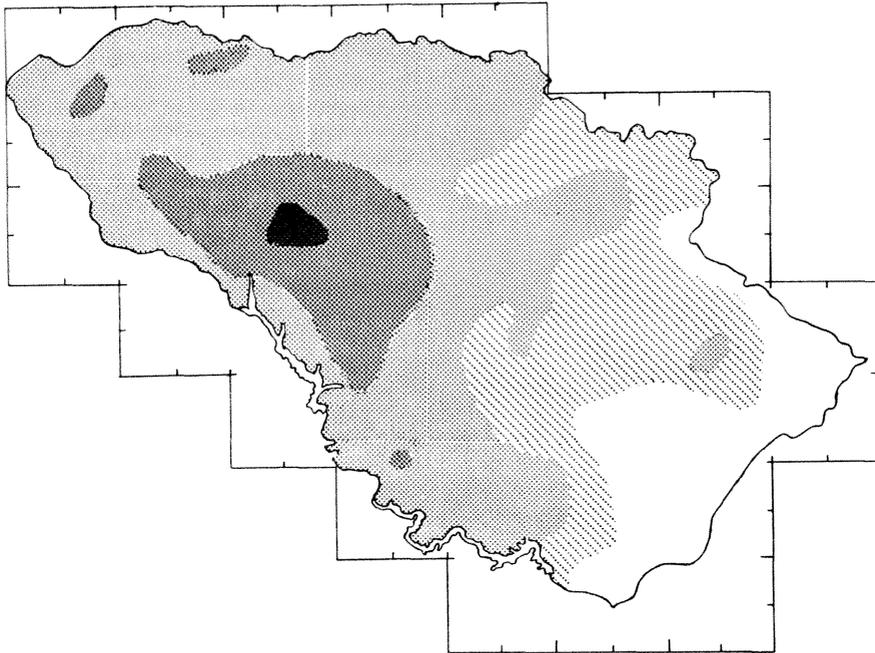
Figure 11.—Relative abundance of breeding Red-winged
Blackbirds in Howard County, Maryland, plotted from the
summation of two coverages of each of the five-stop
segments shown in figure 9.

survey methods.

Breeding Bird Atlas

Breeding Bird Atlasing has become a popu-
lar pastime among bird observers in Europe
during the past decade. Atlases showing
breeding distribution maps for each species
have recently been published for the British
Isles (fig. 12), France and Denmark; and
similar atlases are in progress in several
other European nations (Belgium, Czecho-
slovakia, Finland, Federal Republic of
Germany, Italy, Netherlands, Poland, Sweden,
Switzerland). A more comprehensive mapping
program involving all of Europe is planned
for 1985-1988 using 50-km grids.

The initial purpose of preparing a
Breeding Bird Atlas was to correlate bird
distribution with that of plants as shown in
the Atlas of British Flora (Perring and
Walters 1962). In a government-sponsored
program carried out through the British Trust
for Ornithology and the Irish Wildbird
Conservancy, observers visited every one of
the 3,862 10-kilometer squares (100 square
kilometers each) of land area throughout the
British Isles during a 5-year period and
reported presence or absence of each bird
species (Sharrock 1976). Twelve transparent
overlays, that must be ordered separately from
the book, facilitate correlation of bird
distribution with selected environmental

factors such as July temperature, elevation,
and distribution of moorland, sessile oakwoods
(fig. 13), and standing fresh water.

In other countries, the sampling blocks
have been of different sizes, depending upon
the size of the total area to be sampled and
the standard maps available. In France the
sampling unit was 20 by 27 km (Yeatman 1976)
while in Denmark it was a 5-km square (Dybbro
1976). In several countries (Belgium,
Czechoslovakia, Poland) the method has been
modified to include some indication of abun-
dance rather than merely noting presence
or absence.

No large-scale atlas has been attempted
in the United States because the BBS provides
an annual sample of changing abundance of each
species and also gives a density of coverage
roughly comparable with the projected European
atlas of the 1980's.

Nevertheless, atlas studies have been
initiated in several states (Illinois, Mary-
land, Massachusetts, Vermont, and parts of
California and Michigan), generally using
grids smaller than the 10-km British grid.
These American atlas studies will provide a
source of information on presence and absence
of the various species in many forested areas.

The majority of atlas studies in the
United States utilize a 5-km grid (6 blocks

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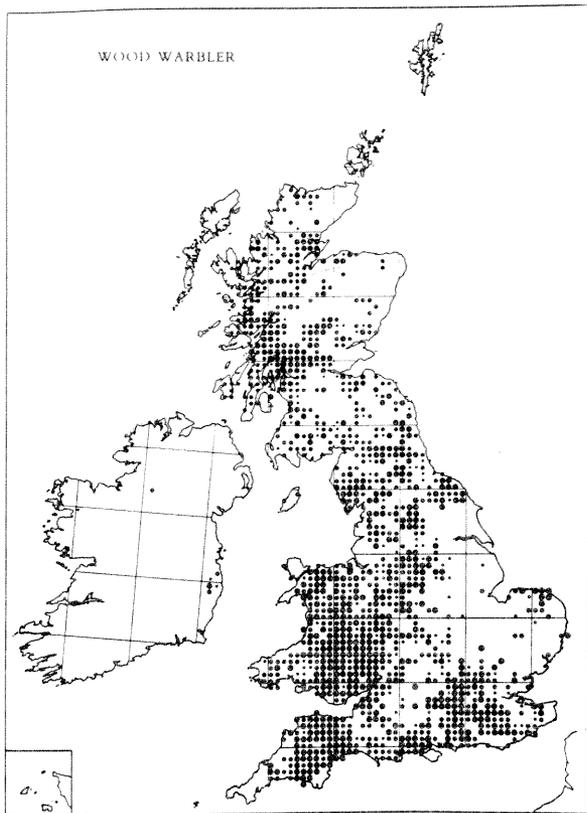
Figure 12.--Breeding distribution of the Wood Warbler in the British Isles. Size of dots indicates the three atlas categories of possible, probable, and confirmed (largest dot) breeding. Map from Sharrock (1976).
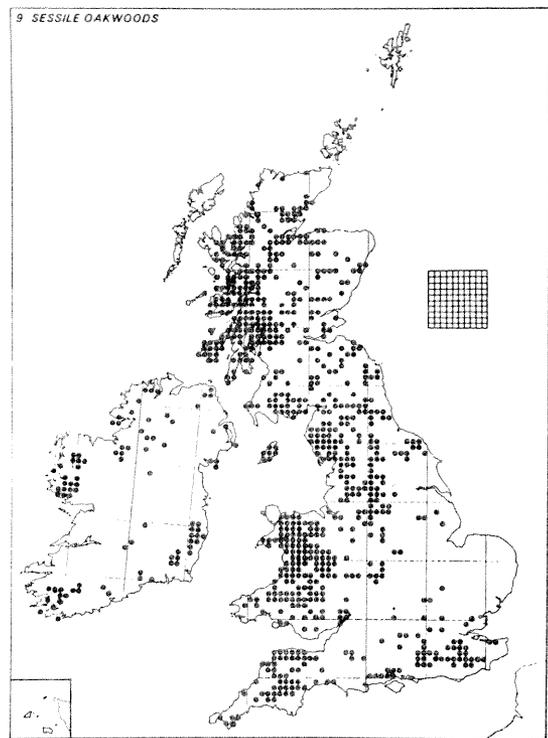
Figure 13.--Transparent overlay from Sharrock (1976) showing distribution of Sessile Oak Woodlands. Compare with figure 12.

per 7 1/2 minute topographic map), but the Maryland Ornithological Society has changed from 5 km to 2 1/2 km "quarter blocks" (about 600 hectares or 1500 acres). The quarter blocks not only make it possible to pinpoint the location of rare species and others of special interest, but they also are much better for outlining areas where a particular species is not present (fig. 14) (Klimkiewicz and Robbins 1974). This feature takes on special significance in areas where commercial or residential communities are expanding or where habitats are being lost through various types of development. And in areas where large forests are being destroyed by changes in land use, quarter-block atlas data have been of immense value in showing to what degree various breeding species disappear when forested areas become fragmented into smaller tracts (fig. 15).

In situations where insufficient personnel is available to visit all atlas blocks, intensive coverage of a random sample
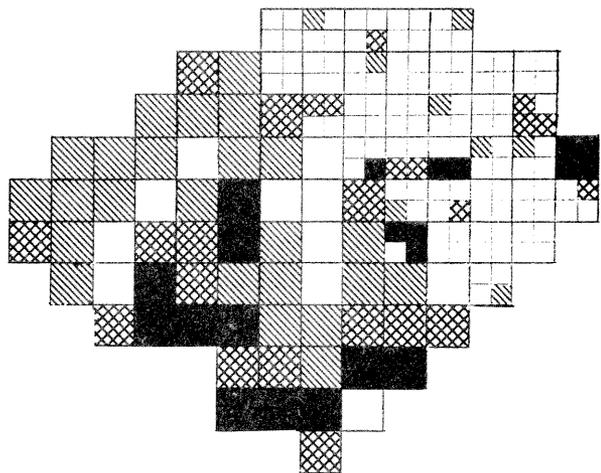
Figure 14.--Breeding distribution of Pileated Woodpecker in two Maryland counties in the Baltimore-Washington area showing the great improvement in precision when 5-km atlas blocks (Montgomery County) are replaced by 2 1/2-km quarter blocks (Howard County). The three atlas categories are indicated by darkness of shading.

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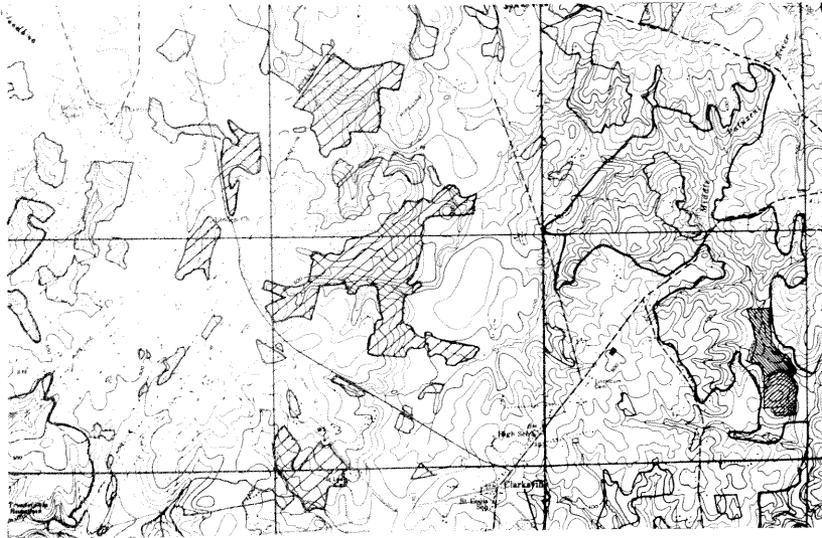
Figure 15.--Atlas quarter-blocks in Howard County, Maryland,
showing forest fragments from which breeding bird species
that require large tracts of forest interior are lacking.
The species missing from the fragments still nest in the
extensive woodlands along the Patuxent and Middle
Patuxent stream valleys at the left and right edges of
the map: Black-and-white, Worm-eating, Northern Parula,
Cerulean, Kentucky, and Hooded Warblers, and others.
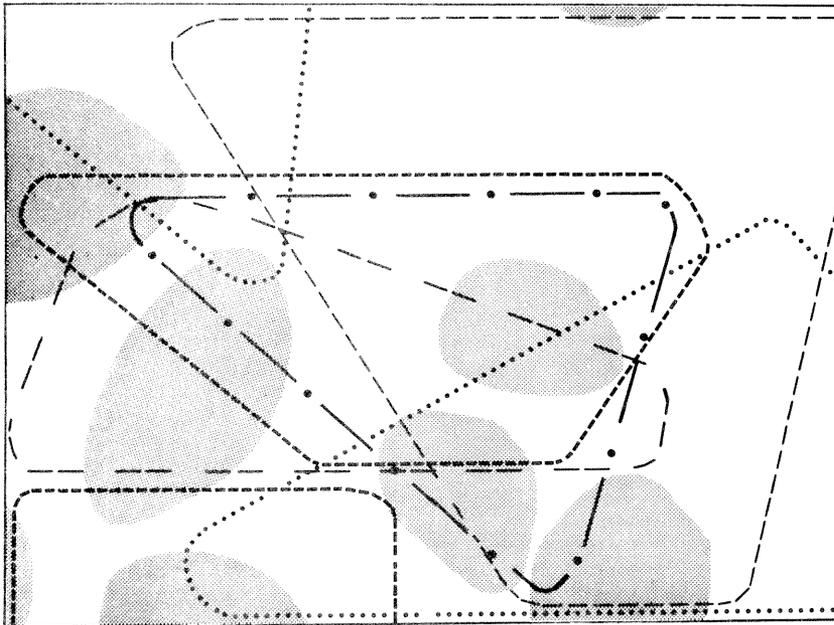
Figure 16.--Size comparison of Wood Thrush singing
territories at Patuxent Wildlife Research Center deter-
mined from spot-mapping (shaded ovals), and home ranges
of some of the same males determined by banding. Total
area of this map section is 22 ha.

of small blocks is greatly to be preferred
over casual coverage of much larger blocks.

The atlas technique yields high returns
in the first day of field work in a given
block. In 12 10-km blocks, each with 78 to 90

breeding species, an average of 72 species
were detected in the first 16-hour day
(Sharrock 1974); 40 of these species had been
found in the first hour and 60 by the end of 8
hours. It is the added effort of searching
for the important hard-to-find species and the
accumulation of nesting evidence that is very
time-consuming. Recent recognition that rare
and/or disappearing species are most likely to
be present in the largest forest tracts within
a given grid should greatly reduce the effort
required to locate such species.

Banding

Several investigators in the United
States, Sweden, and France have used the
marking and recapture of birds as a means of
studying the effectiveness of other census
methods (Stamm et al. 1960, Svensson pers.
comm., Frochot 1977).

Banding in itself is neither an efficient
nor a highly accurate way of measuring entire
breeding bird populations in forest habitats.
It is, however, a very effective way to
determine how many pairs of certain species
are present. It also makes it possible to
distinguish migrants from summer residents
and, to some degree, non-breeding from
breeding individuals. Color banding can be
used to define the ranges of individual birds
and also can point out errors in judgment that
occasionally occur when the observer relies
entirely upon the mapping method. Bear in
mind, however, that home ranges of many
species are much larger than their singing
territories (Fig. 16).

Frochot (1978) has compared mapping, IPA,
and banding techniques in the same oak forest
plot of 100 hectares. Comparing the results
for 12 common species, he determined a density
of 49.9 breeding pairs per 10 hectares by the
mapping method as compared with 47.0 by the
IPA method (with appropriate corrections for
conspicuousness). Banding data sufficient for
computation of population estimates were
available for only 4 of the 12 species, but
for 3 of these 4 species the estimate from
capture-recapture was higher than that
obtained by either of the other two methods.
Frochot reported that the IPA census required
nearly 10 hours of prime time in the early
morning, while the mapping census required 43
hours, and the banding study took 400 hours.
The chief advantages of the capture-recapture
method emphasized by Frochot are: 1) it
permits a census of females and young as well
as of singing males, 2) it can be used for
testing mapping and IPA methods, and 3) it
gives additional information about daily range
and habitat utilization of the individual
birds.

Nest Finding

To the uninitiated, nest finding appears
to be the obvious way to determine accurately
the breeding bird population of a forest plot.
In actual practice, however, it is seldom
possible to find enough active nests of a
species to use this method as a measure of the
breeding population--especially in forest
habitats. While a nest census is effective
for many colonial nesting species, such as
herons and ibis, there are very few forest-
nesting species that are colonial.

Nest censuses have been conducted
successfully for a few species such as the
Red-shouldered Hawk (Steward 1949, Henny et
al. 1973). They have also been successful in
a few habitats, especially in residential and
park areas, where a high percentage of the
nests are within 10 feet of the ground and
where nests tend to be clustered in suitable
strips of vegetation rather than scattered
more or less randomly throughout the entire
study plot. In a normal situation, nesting is
spread over a period of at least 4 to 6 months
and during this time nests are continually
being destroyed or deserted and additional
nesting attempts initiated. In the southern
United States there is probably no one time
when all members of a given species are
nesting, so that even if it were possible to
locate every nest during some particular week,
this still would not be a census of that
species in the plot. Tomiałojć (1974) studied
nesting behavior of 17 pairs of Woodpigeons
(Columba palumbus) near Wrocław in Poland and
found that no more than 6 of the 17 had active
nests at any one time (fig. 17).

A good example of a nesting study of a
single species is a Wood Thrush investigation
in a 14.4 ha Delaware woodlot by Longcore and
Jones (1969). Systematic nest searches were
conducted during a 3-month period in 1965 and
again in 1966. Grid lines located at 150-foot
intervals were traversed at least once every 3
days except for a 2-week period in July 1965.
A total of 142 Wood Thrush nesting attempts
were documented (fig. 18) of which 38% were
successful. This study was supplemented by an
intensive banding effort every 2 to 3 weeks
during the 1966 breeding season. This effort
resulted in 46 Wood Thrushes being banded.
This study was directed primarily toward
determining reproductive success rather than
measuring the population, but it gives an idea
of how much effort would be involved in
gathering enough information about a single
species to get an accurate measurement of the
breeding population.

In summary, I do not minimize the import-
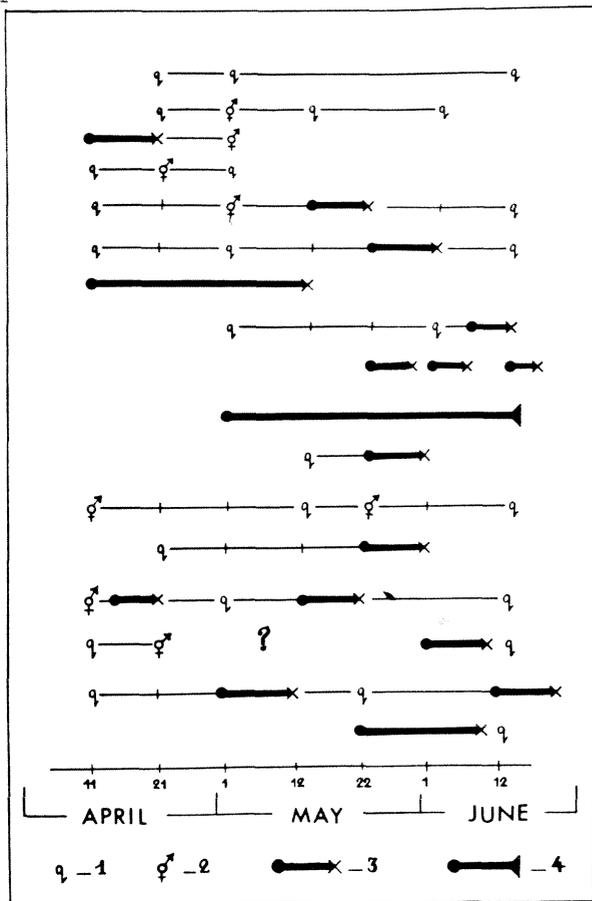ance of actual nest counts as a supplement to

Figure 17.—Nesting status of 17 pairs of Woodpigeons near Wrocław, Poland. Symbols mean: 1—cooing male, 2—pair showing breeding behavior, 3—date of discovery of nest and period it remained active, 4—successful nest. From Tomiałojć (1974).

other methods; I simply question their practicality as a census method under normal circumstances. There are, of course, exceptional cases where populations of an individual songbird species can be determined by a thorough search for nests—but this normally requires a prohibitive amount of field work. For many canopy species it would be nearly impossible to find all the nests even with a large crew of observers.

Species Studies

When interest relates primarily to a single species or a small group of species, considerable time may be saved by a knowledge of the habits of the particular species. For the Scarlet Tanager, for instance, there is a very short period just at dawn when singing reaches a high peak. By scheduling trips to include this critical period and by moving
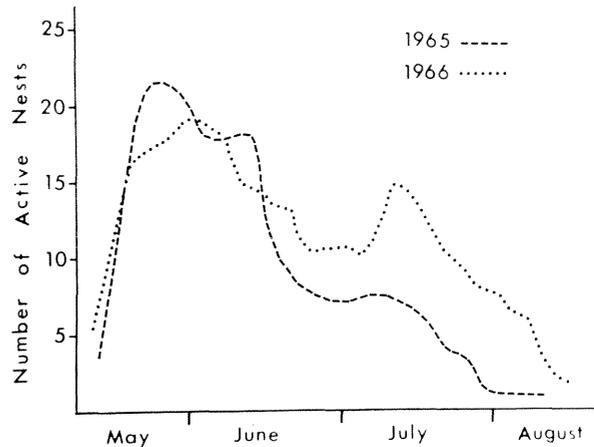
Figure 18.—Three point floating averages for the daily number of active Wood Thrush nests in a 14.4 ha woodlot in Delaware, 1965–1966. From Longcore and Jones (1969).

rapidly through the area while the birds are at their peak of song, the total amount of field time can be reduced.

Tape Recordings

For many species, playback of tape recordings can be used to induce song from silent territorial males. The technique may increase census accuracy, especially for species with low song activity, with a minimal expenditure of time. Also, the technique can be used to determine territorial boundaries. Indiscriminate use of tape recordings on repeated visits during the breeding season, however, can bias one's results because birds may alter their habits or their territorial boundaries if they believe a competing member of the same species is holding territory nearby.

WINTER SEASON TECHNIQUES

Winter Bird-Population Study

In 1948 the National Audubon Society inaugurated an annual Winter Bird-Population Study, which is published in American Birds. The purpose of this study is to obtain an estimate of the average number of birds using a particular habitat. Many observers use the same plot in which they have conducted a Breeding Bird Census by spot-mapping. Most plots range in size from 6 to 20 ha. The plots are visited from 6 to 10 times in mid-winter and the totals for each species are averaged. As in the Breeding Bird Census, the results are expressed in terms of birds per
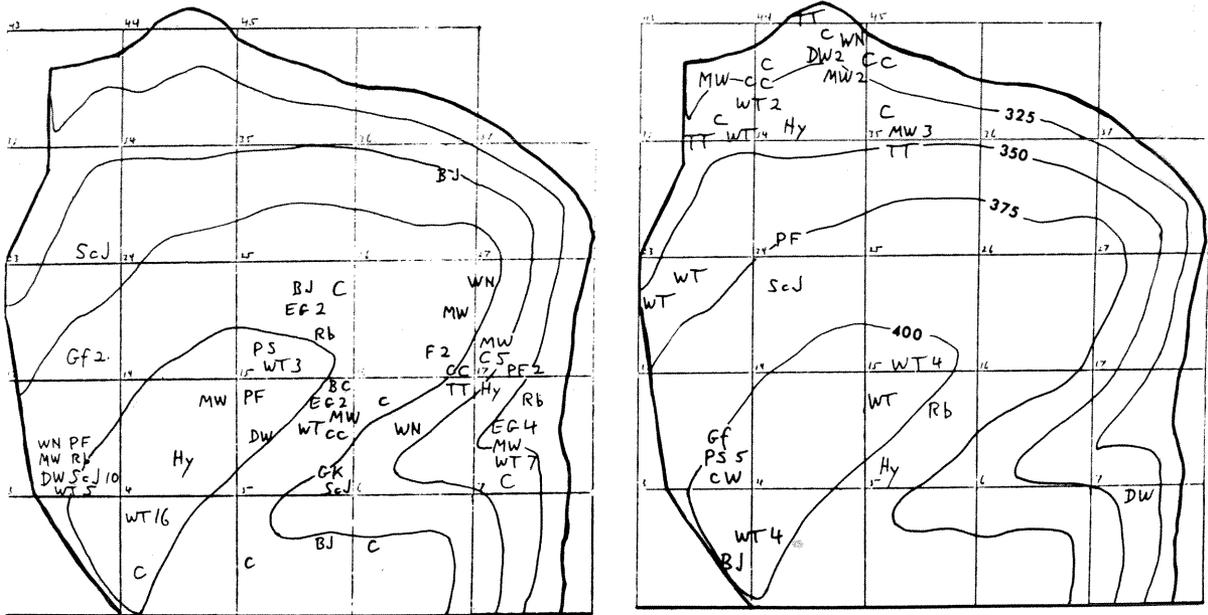
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Figure 19.--Comparison of morning (left) and afternoon distribution of birds in an upland deciduous forest in Howard County, Maryland, 22 January 1978. On cold days in winter, birds tend to be attracted to sunny exposures. Squares are 250 feet on each side; elevations are in feet.

square kilometer and birds per 100 acres. Several visits per winter are necessary because populations and even the species present in a given plot vary from day to day and from morning to afternoon. Finches, robins, and waxwings for example, often range over many square kilometers in the course of two or three days. Many other species are loosely attached to mixed flocks, which may range widely, in and out of a study plot. Such flocks tend, especially on cold days, to favor sunny exposures (fig. 19), to concentrate in the better feeding sites, and to avoid windy areas.

Even when plots are covered during the best weather conditions, results must still be considered as minimum population estimates because rarely is it possible to find all the birds that are present within the plot at any given time--especially in a forest habitat.

Difficulties not withstanding, the method does give an opportunity to compare populations of different habitats and, to a lesser degree, to follow population trends over a period of years. Webster (1966) analyzed the results of 248 winter studies in forest habitats and 25 studies in grasslands.

By plotting species richness against population density he found that southern pine forests mixed with oaks or gums tended to have a higher species richness than did other eastern forests.

This method can be used effectively to obtain indices of winter use. I should stress, however, that winter bird populations vary enormously from year to year at any one place, so it is highly desirable to conduct a winter population study for at least 2 years. A critique of this method (Robbins 1972) showed that in forest habitats 6 trips were sufficient to obtain a stable minimum estimate of the total wintering bird population, but that at least 8 or 10 trips were required to obtain such estimates for individual species.

Christmas Bird Count

The Christmas Bird Count (CBC), sponsored by the National Audubon Society since 1900 and published annually in American Birds, is the best known and probably the most used source of information on geographical distribution of nongame birds in winter.
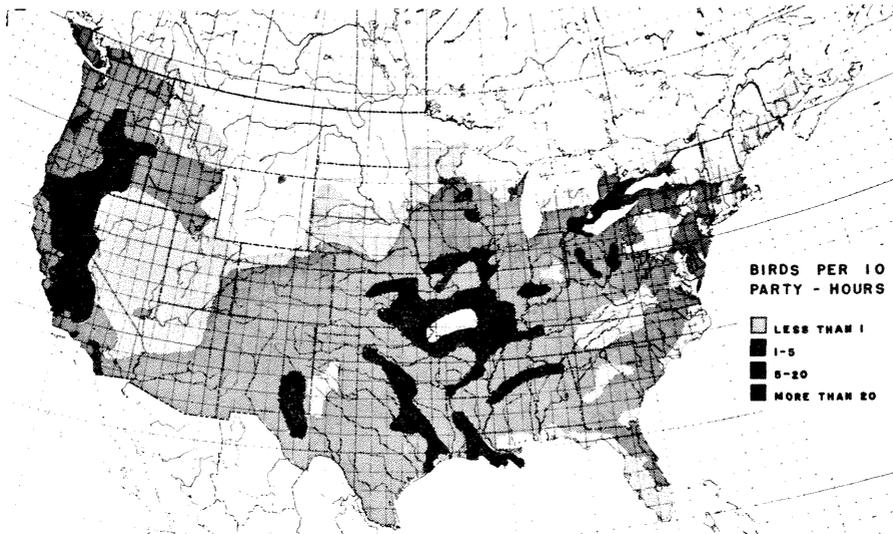
Figure 20.--Winter distribution and relative abundance of
Red-tailed Hawk in 1972. From Bystrak (1974). Compare
with figure 8, bearing in mind the difference in scales
of abundance.

As many as 1,275 circles, 15 miles in diameter, are covered annually in North America. Observers keep a record of party-hours and party-miles in the field, and estimate the time spent in each major habitat.

Maps showing the distribution and relative abundance of 143 species, based on Christmas Bird Counts (fig. 20), were compiled by Bystrak (1974) and similar maps for a few dozen other species have been published from time to time in American Birds. These maps are sufficiently detailed that likelihood of occurrence of these analyzed species in any particular forest area in the Southeast could be estimated on the basis of availability of suitable habitat.

Christmas Count data also can be used for comparison of winter bird populations of any particular forest area with those of published studies in the same or nearby counties.

Winter Bird Survey

In an effort to design a more standardized method of assessing bird populations in winter, the Maryland Ornithological Society undertook a Winter Bird Survey in central Maryland for 5 consecutive years, 1970-1974. Preliminary tests showed that the Breeding Bird Survey method would not be practical because of heavy traffic problems on many roads in the first few hours after sunrise in winter and because lack of singing made it difficult to detect birds that could not be seen from the roadside (Robbins 1970).

The method adopted, therefore, involved

transects of 8 km (5 miles) that were covered on foot in the first 4 hours after sunrise. One route was established at the center of each 7 1/2-minute Geological Survey map in central Maryland, giving an 11 x 14 km grid. An effort was made to lay out each route in the form of a square, 2 km on each side. Many routes were forced to depart from the square shape because of streams, ponds, buildings, high fences, and other obstacles; but despite changes in shape, the total length of 8 km was maintained. By timing their walking speed for the first quarter of the route, observers were able to arrive back at the starting point within a very few minutes of the prescribed 4-hour period. A separate count was kept for each hour, and birds identified at a distance greater than one-quarter mile were recorded in a separate column on the form.

Most of the 46 routes were covered each year, and because coverage was standardized, the population changes from year to year could be analyzed statistically. Significant changes were found for many species. The Winter Bird Survey data also were used to map the relative abundance of various species throughout central Maryland (Bystrak and Robbins 1972, Robbins and Bystrak 1974).

Comparison with Christmas Bird Count Data

There were four CBC circles within the area covered by the Winter Bird Survey. This permitted direct comparison of the results of the two methods. Although published CBC's, from their inception in 1900, have included the number of hours of field coverage, this coverage varies enormously among areas and
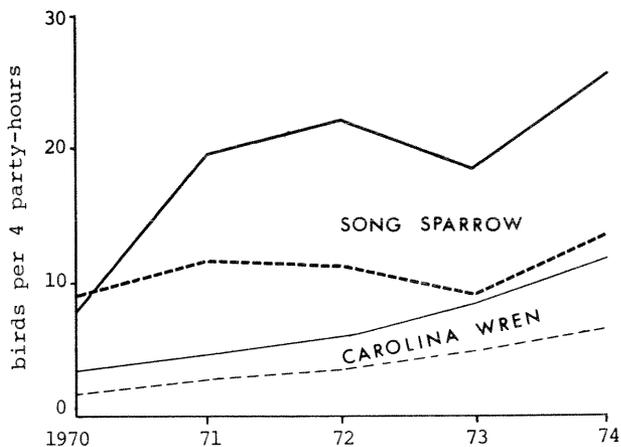
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Figure 21.--Comparison of bird population
  trends as shown by Winter Bird Survey (solid
  lines) and Christmas Bird Count (dashed
  lines).

from year to year. Because of the changes in
coverage, changes in observers, and lack of
control over weather conditions, the CBC data
have been believed too crude for application
of statistical analysis. Comparison with the
Winter Bird Survey data, however, revealed
that the CBC's show year-to-year trends very
similar to those detected in the same geo-
graphic area by the Winter Bird Survey (fig.
21). Species commonly seen along roadsides
and at feeding stations were recorded in
larger numbers (per 4 hours of field work) on
the CBC, while species typical of fields and
forests were found in larger numbers on the
Winter Bird Survey. Nevertheless, the
year-to-year trends were similar, suggesting
that, despite the disadvantage of uncontrolled
variables, CBC's can be used in a general way
to show population changes. The advantages of
the CBC data are the large number of years
represented and the large sample of
observations each year: as many as 200-300
party-hours concentrated in a small area.

European Winter Transects

     The Winter Bird Survey method was tested
simultaneously in the British Isles and in
Maryland. The British had some reservations
about the success of their program, largely
because of high variability caused by wander-
ing Lapwings, a plover that occurs in large
flocks and moves gradually from east to west
across the British Isles as the winter
progresses. Hence, the British study was
discontinued and the results were not
published.

     A series of walking transects, varying
from 2 to 30 km in length, was initiated in
Finland in 1956. About 6500 km of Finnish

landscape are now hiked each winter
(Sammalisto 1974).

     In Sweden the winter transects consist of
twenty 5-minute stops (Källander 1978). Each
transect is covered monthly from November
through March with the same stops, same time,
and same observer each year. The data from
both Finland and Sweden are entered on punch
cards and analyzed statistically to show
national trends in winter populations.

TECHNIQUES FOR OTHER SEASONS

Transects

     The transect method has been the one most
frequently used to monitor year-around changes
in bird populations. Admittedly, its accuracy
varies with season of the year depending upon
activity of the birds and visibility across
the various habitats. Width of the transect
strips has varied with the several authors,
and no attempt has been made so far to
standardize strip width among investigators
in different countries.

     Most transect workers have walked alone,
but Stewart et al. (1952) in a 2-year study at
the Patuxent Research Refuge in Maryland, used
3 observers walking parallel lines 100 m apart
to sample a strip 300 m wide and 4.2 km long
(about 123 ha). During the breeding season
the observers worked strictly from the census
lines, but at other seasons they departed as
far as 50 m from the census lines whenever
necessary to get better counts of flocking
birds. Two observers often worked together on
the same flock to obtain the best estimate of
flock size and composition. It was believed
that by having three observers the errors in
estimating lateral distances were minimized as
was the likelihood of obtaining poor estimates
of flocking species.

Transect Sampling in North Wales

     To determine bird use on nine national
nature reserves in the county of Merioneth,
North Wales, the Nature Conservancy estab-
lished a program under which 50 km of heather
and 50 km of grassland would be censused by
transects during each month of the year
(Jones, 1974). Each transect belt was 200 m
wide and the right angle distance to each bird
from the transect line was estimated. This
long-term study began in 1968 and was to
continue until the sample for each month in
each major habitat reached 50 km. Jones used
the method of Gates et al. (1968) and Emlen
(1971) to convert transect data into an
estimate of the total population, using a
coefficient of detectability. This method is

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birds per
80  1000 net-hours




70



60



50



40



30



20



10



 0
         10        20        30        10        20        30
        September                    October
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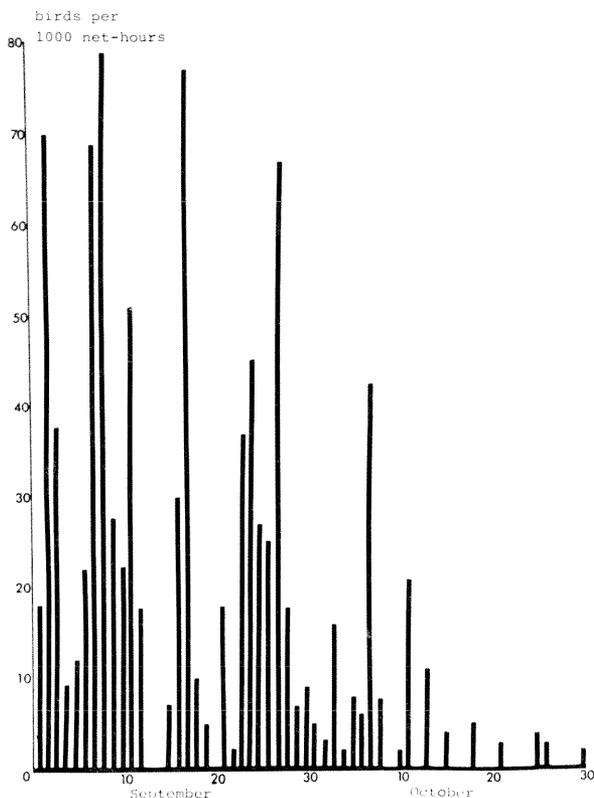
Figure 22.--Daily bandings (birds per 1000 net-hours) of American Redstart at Ocean City, Maryland, September and October 1966.

more likely to be successful in open habitats such as those used by Jones than in heavily forested habitats where many birds at close range can escape detection.

Bird Banding

When banding is done consistently throughout a migration season, it provides quantitative data on populations of those species that are readily trapped under the conditions that prevail at the particular banding site. The records of the major bird observatories in North America (and also of those in Europe) provide an excellent sampling of a wide variety of species and have an additional advantage in that reliable age ratios for each species for the particular locality are obtained. As in any study during the migration periods, weather has a major effect on daily counts of migrating birds (fig. 22) and also causes problems such as local concentrations or overflights, any of which may reach major proportions and make it frustrating to attempt statistical analysis of data from a single year. Over a period of years, however, a good statistical sample can

be obtained. Attempts to monitor migratory populations by banding are most successful where shorelines, mountain ridges, river valleys, oases, or other topographic or vegetational features help to concentrate the migrating birds.

One important advantage of monitoring migrants by trapping and banding is that mist nets are especially effective for birds of heavy underbrush and dense thickets; such birds are rarely seen and are almost impossible to detect when they are not singing. While mist nets are highly effective for capturing migrants, it must be born in mind that they cannot be used effectively on a daily basis during breeding or winter seasons because the birds rapidly become familiar with the placement of the nets and learn to avoid them. It should also be emphasized that use of mist nets is a specialized technique that requires special Federal and State permits, which are granted only to workers with considerable training and experience.

DISCUSSION

The above commentary gives the research biologist a considerable selection of methods from which to choose. Each method has severe limitations if one's objective is to achieve an accurate measurement of the absolute size of bird populations, especially if abundance of one species must be compared directly with abundance of other species.

Attempts to measure statistical error of bird census results will be frustrated by almost insurmountable biases associated with: (1) daily or even hourly changes in the populations being sampled; (2) daily changes in behavior such as nesting activities and singing (Weber and Theberge 1977); (3) effects of different weather conditions on audibility, visibility, and behavior of the birds and of the observers; (4) differences, even slight ones, in time of day as it affects bird activity (Robbins and Van Velzen 1970); (5) differences among observers; (6) differences in attentiveness of even a single observer; (7) differences such as walking speed (Colquhoun 1940) or the exact route the observer follows from day to day; and (8) lack of information on the absolute numbers being estimated.

Design of the procedures and selection of experienced personnel to conduct the field work and analyze the results are no less important than the selection of census methods. The objectives of the study and the time frame in which it must be completed will dictate

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which method, or more likely, which combination of methods, will be most efficient. Attempts should be made to minimize effects of as many as possible of the inherent variables. The bulk of the field work should be concentrated in the early morning when activity is greatest and most consistent. Except for studies of migration itself, the migration periods should be avoided and work should center on the peak of the nesting period or the middle of winter. Census work should be standardized with relation to sunrise (or sunset). Minimum weather standards for field work should be established. Observers with considerable experience in census work should be chosen, bearing in mind that most of the censusing of forest birds is done by ear. Most biologists, whatever their level of general knowledge, lack the specialized skills required. Observers should be calibrated, rotated among the various tracts being compared, and for studies lasting more than 1 year, enlisted for the duration of the study.

It is desirable to assess the accuracy of the method or methods being used. This is frequently best accomplished by a more intensive study of two or more of the sample plots.

CONCLUSIONS AND RECOMMENDATIONS

1. Although bird censuses are imprecise, they have considerable value in a relative sense.
2. If the techniques are designed so as to minimize effects of variables that can be controlled, valid comparisons may be made among bird populations of two or more plots.
3. The spot-mapping method is recommended for greatest precision, and when a study is to be repeated over a period of years. Carefully standardized transects or point counts are most effective when many plots are being compared, and relative rather than absolute numbers will suffice.
4. Any method selected may be calibrated by a more thorough coverage of sample plots by the same or another method.
5. Demand for data on bird populations and species composition in specific habitats is increasing rapidly. Therefore, the results of census work should be published or at least made available through data banks or other means.

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Research Plans

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A Representative Sample of Ongoing and Planned Nongame Bird Research in the Southeastern Region United States

Robert L. Curtis, Jr.[1]

Abstract.--This paper highlights the ongoing and planned nongame bird research efforts in the Southeastern Region of the United States. Over 40 percent of all sampled ongoing research is directed toward threatened and endangered species. The U.S. Forest Service and various southern universities are the agencies most heavily involved in nongame bird research. A comparison of ongoing research with previously defined nongame bird information needs is presented.

INTRODUCTION

Two and one-half years have passed since many of us met at the Symposium on Management of Forest and Range Habitats for Nongame Birds in Tucson, Arizona.

If a consensus of opinion regarding information needs was reached at that symposium it was perhaps that management of nongame birds and their habitats is a relatively new resource issue and that there is a serious scarcity of information available to land managers and resource decision makers for formulating and assessing management programs.

Michael Lennartz and Ardell Bjugstad, who highlighted information and research needs for nongame bird habitat management, stressed that any discussion of management information on research needs must follow some understanding of what management is or what management should attempt to achieve.

I doubt that we were able then, or could now, agree on this point. However, two philosophies for management and research for nongame birds tended to recur throughout that symposium. These are:

1. Native vegetative communities or habitat types must be protected and enhanced in order to protect and perpetuate all representative native avian communities, and

2. Endangered and threatened species and their habitats must be protected and perpetuated.

If we accept these as broad management guidelines, then the question becomes, what information do land managers need to meet them? Is this information being procured through our ongoing research programs?

The first portion of this question has been answered in a large part by Lennartz and Bjugstad (1975) with help from their fellow professionals at Tucson.

The focus of this presentation will hopefully shed some light on the second portion of the question. Just how far have we come since that first nongame bird symposium in 1975? Have we as a professional working group been successful in establishing a nongame bird research direction, and are we addressing the priority information needs which were identified two and one-half years ago?

METHODS

In this presentation, I have attempted to assemble a representative sample of ongoing nongame bird research efforts in the southeastern states. Attempts were made to sample a diverse selection of both Federal and state agencies having different research and management mandates. Colleges and universities, as well as private conservation organizations, were also queried. The entire geographic range of the southeastern region was covered, extending from the Atlantic coast to Texas, Oklahoma, Missouri, and Arkansas.

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A total of 35 questionnaires was distributed to nongame bird researchers in this region. Twenty-six investigators responded to my inquiry and provided me with a listing and description of 84 ongoing nongame bird research projects which form the substance of my presentation. A summary of vital information regarding each project is included in the Appendix.

To facilitate discussion and presentation, I have sorted the research projects into eight categories based upon the title, objectives, species or group of species, and, in some cases, study methodology. Although some projects could, of course, fit into more than one category, my sorting approach does provide an organized framework for discussion, presentation, and comparison.

The research categories include:

1. Threatened and Endangered Species Ecology

2. Effects of Forest Management Practices

3. Species Ecology

4. Avian-Forest Habitat Associations

5. Structural Niche Determinations

6. Surface Mining Impacts on Avifauna

7. Electric Transmission Line Impacts on Avifauna

8. Raptor Investigations

PREVIOUSLY DEFINED INFORMATION NEEDS

Before discussing each of the research categories and the current research programs I will quickly summarize the priority information needs identified by Lennartz and Bjugstad (Ibid.). These were:

Information Needs

1. Information allowing managers to assess the impacts of management systems on nongame birds and their habitats.

2. Greater quantitative explanations of the distributive niche selection of avian species and communities through accelerated use of multivariate analysis techniques.

3. A characterization of the extent, distribution, and condition of the avian resource base for use in avian management

planning in conjunction with other resource outputs--e.g., timber, forage, and water.

4. Information on avian community/forest community associations.

5. Accelerated research emphasis on climax or mature vegetative communities and microhabitat components--e.g., snags and cavity trees.

6. Information concerning habitat requirements and management for endangered and threatened species. This latter need was ranked, almost without exception, as the highest priority of both managers and researchers.

ONGOING NONGAME BIRD RESEARCH - AN OVERVIEW

With the above information needs in mind let me now provide an overview of the ongoing nongame bird research program.

Figure 1 presents the results of my regionwide inquiries and discussions with nongame bird investigators. The figure provides a category breakdown of all 84 research projects, and the percentage contribution of each category to overall regional research activities.

Two categories of research, threatened and endangered species investigations, and studies into the effects of forest management practices on avifauna, account for 49 of the 84 projects or 58 percent of the sampled research activity. The lion's share of this research effort belongs to threatened and endangered species, which account for 37 of the 84 studies for an impressive 44 percent of the sampled ongoing research.

The third most active research category, investigations of species ecology, is represented by 11 projects accounting for 13 percent of all research activity. Studies on avian-forest habitat associations account for 11 percent. The other five categories each account for less than 10 percent of all research.

RESEARCH CATEGORIES

Threatened and Endangered Species

Clearly, an impressive impetus has rapidly developed for the endangered species research program. The high level of support which this program now enjoys is a result of an awakened public concern and interest as well as a better understanding of man's role and moral responsibility regarding species extinction.
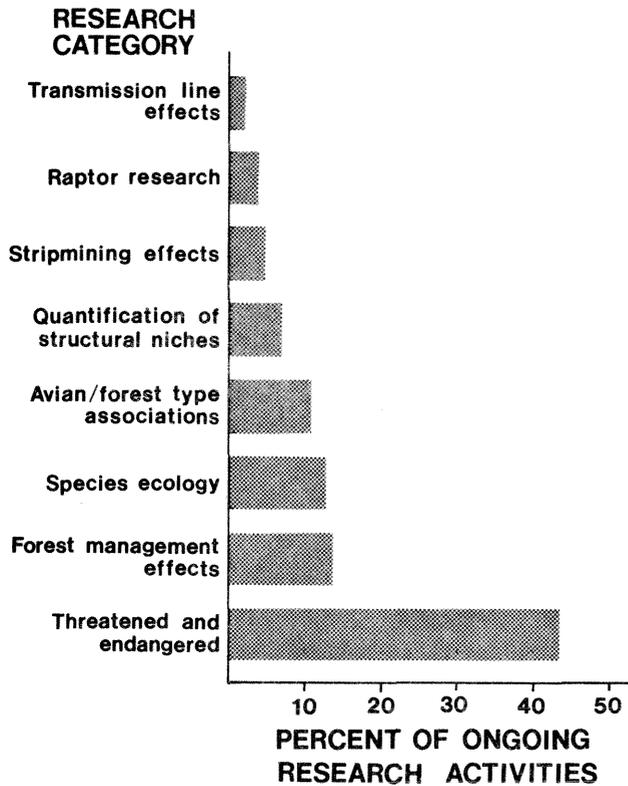
RESEARCH CATEGORY

Figure 1.--Percent composition by category for sampled ongoing nongame avian research in the Southeastern Region as determined by a survey conducted in October 1977.

Conceptually the information needs for endangered species are no different than for any other avian species. We need the same information regarding population, distribution, resource utilization, and habitat selection. But the needs are urgent; the time frame is critical.

The endangered species experience graphically illustrates that the future of wildlife in America is dependent upon much more than just our understanding of wildlife ecology. Law, economics, and politics will have increasing impact on wildlife populations and programs. For example, as Lennartz and Bjugstad (Ibid.) point out, the plight of species headed for extinction has become one of our most publicized and emotional contemporary wildlife problems. This interest, whether emotional or pragmatic, has been translated into active programs through Federal legislation (Endangered Species Act of 1973). Admittedly, not all of the support intended in the Act has materialized, but a firm foundation has been established.

The Endangered Species Act also requires that all Federal or Federally funded land management programs protect endangered species and their habitat (Ibid.). To do so requires a quantum jump in available information. In response to Endangered Species Act requirements for increased protection and management, we find a substantial portion (44 percent) of southeastern nongame bird research centered about endangered species problems.

From figure 2, it is readily apparent that the Red-cockaded Woodpecker is the endangered species receiving most of our research attention. Approximately one-third of the research projects directed toward the Red-cockaded Woodpecker are being sponsored by the U.S. Forest Service, Southeastern Forest Experiment Station (Lennartz and Hooper, 1976). The objective of their research is to determine the essential habitat elements selected by Red-cockaded Woodpeckers throughout their home range, so that forest managers can assess, or predict, the effects of alternative forest management strategies on woodpecker populations.
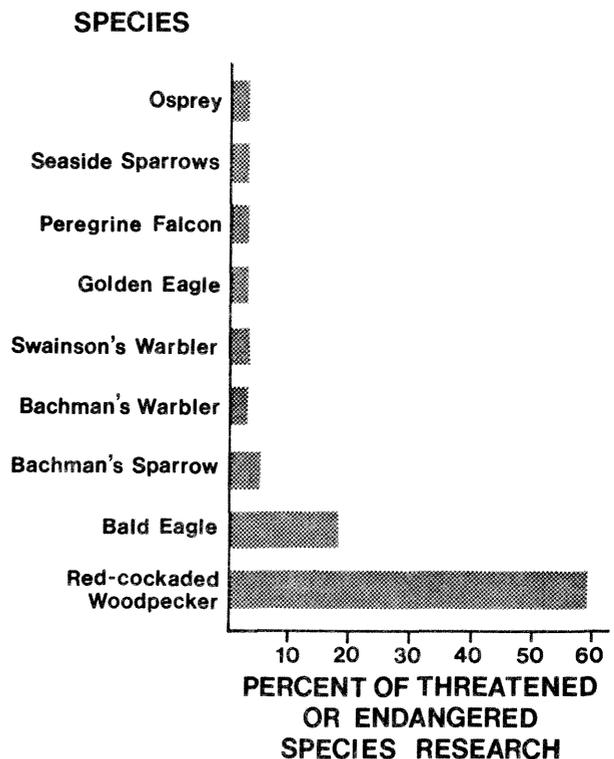
SPECIES

Figure 2.--Percent composition by species for sampled ongoing threatened and endangered species research in the Southeastern Region as determined by a survey conducted in October 1977.

The U.S. Forest Service's interest is understandable in light of Chamberlain's (1974) report that ". . . the National Forests of the Southern Region are extremely important to the Red-cockaded Woodpecker. In several states it is likely that a major portion of the state population occurs on National Forest lands."

The states of Florida, Arkansas, and South Carolina also have active projects on the Red-cockaded Woodpecker. These efforts are being funded primarily through the U.S. Fish and Wildlife Service, Endangered Species Act Federal Aid Program.

Other species currently subjects of research include Bachman's Sparrow, Swainson's Warbler, Bachman's Warbler, Southern Bald Eagle, Seaside Sparrow, and the Peregrine Falcon (fig. 2).

Forest Management Practices

It is probably true, as Hamilton and Noble (1975) point out, that most avian management on our forest lands will be in conjunction with other management objectives such as timber, recreation, forage, or water. The demands for timber will have increased greatly by the year 2000, yet, if current trends continue, there will likely be less acreage available for commercial timber production. Obviously to produce enough wood and wood byproducts to satisfy demands requires more intensive management effort on those lands which will remain in forest production.

Consequently, in managing for, and in consideration of, the avifaunal resources on forest lands, especially public lands, the ability of the manager to attain true multiple use will be strained to the utmost (Hamilton and Noble, 1975).

Probably one of the most difficult tasks facing the manager will be to determine the avian management objectives for an area. This will be even more difficult as other resource objectives enter into the planning process.

To ensure that avian management planning is no less sophisticated than planning for the primary resource outputs, managers must have information regarding the effects of the many silvicultural alternatives and various cultural techniques possible. Understandably, Lennartz and Bjugstad (1975) point to this as one of the most pressing information needs of managers.

My inquiries revealed that research efforts into the effects of forest management practices on avifaunal resources is the second most active category of investigation (fig. 1). Twelve of the 84 projects reported were within this category which represents 14 percent of sampled regional research.

A variety of forest cutting techniques, cultural systems, and forest management practices are currently being investigated (Appendix). Specifically, among them are:

1. The benefit of woodland openings to avifauna.

2. Effects of various type conversions and monoculture forest systems.

3. Effects of clearcutting, herbicide treatments, selection cutting, and various combinations of the three on avifauna.

4. Effects of cable logging and whole tree chipping.

5. The role of various microhabitat elements such as snags and nesting cavities in avifaunal habitat.

Of the five primary areas listed above, the greatest amount of research is being directed toward the effects on avifaunal resources of various cutting systems, i.e., clearcutting, clearcut/herbicide, selection cutting, and whole-tree chipping.

The general pattern of impacts directed on avian habitats and communities by these intensive timber management activities have been described by several authors (Thomas et al., 1975; Hamilton and Noble, 1975; Conner et al., 1975). Unfortunately, quantitative investigation of a more precise nature is almost totally lacking. Research which could provide indices of quantitative avian use of forest habitats under various management systems with special reference to habitat selection and resource is definitely needed. Many of the projects listed in the forest management practices category will provide this information.

The U.S. Forest Service is the leader in this research effort by being either directly involved or lending support services to 10 of the 12 projects listed under this category of research.

Species Ecology

Excluding threatened and endangered species work, much of the current research can be loosely described as avian community

ecology. I have included the species ecology category of research to capture those projects relating to the life history of a species or closely related groups of species.

Good quantitative field data on many facets of avian life cycles are either lacking, fragmentary, or comprised of small sample sizes. I would stress that information on both the individual species and the avian community is essential. As Balda (1975) has pointed out, neither autecological nor synecological studies alone can adequately describe the patterns of habitat selection and resource utilization.

Of the 84 projects, 11 were included in the species ecology category. This represents 13 percent of all research activities sampled (fig. 1). Included in this category are projects relating to nesting ecology, foraging ecology, range extensions, cavity nest predation, and parasite ecology (Appendix).

Avian-Forest Habitat Associations

Zeedyk and Evans (1975) suggest that more emphasis should be directed toward developing, with the necessary supporting research, silviculturally oriented avian management alternatives and guidelines. Among other things, coordinated monitoring of breeding bird populations would be an integral part of the forest inventory. Thus bird population trends could be correlated with shifting forest land-use trends. Lennartz and Bjugstad (1975) point out that foresters utilize various continuing inventory systems to assess the timber crop, and that as we become more knowledgeable about which birds are associated with which forest types, it may be possible to incorporate avian habitat assessments into existing forest inventory systems.

Nine of the 84 projects reported were classified under the category of avian-forest habitat associations studies. This represents 11 percent of the current research work (fig. 1). Although projects under this category differ greatly in their regional scope, study methodology, and specific objectives, they all attempt to identify bird communities associated with primary forest types and successional stages in either a portion of or the entire Southeast.

The U.S. Forest Service cooperative study with Clemson University (Gathreaux, 1977) plans a rather broad regional attempt at quantifying avian communities with forest

associations. These associations and the resulting avian habitat assessment system will be developed primarily from existing literature sources with some field validation (Lennartz, personal communication). The feasibility of such habitat assessment systems is in direct proportion to the amount of information available regarding avian community/plant community associations and quantified parameters of habitat suitability (Lennartz and Bjugstad, 1975). Fulfilling this need is one of the tasks being done by the Southern Forest Experiment Station in Nacogdoches, Texas, with the objective of elucidating the effects of stand structure on bird population in two limited but specific forest types, in this case the pine and pine-hardwood forests of east Texas (Dicksen, 1977).

Studies such as these, as well as the others in this category (Appendix), may provide us with the basis for characterizing, on a regional basis, the distribution and extent of our avian resource. This type of information is basic, indeed essential, to intelligent land management planning.

Quantification of Structural Niches

In my sample, this category accounts for 6 percent of the current research activity (fig. 1). Five research projects were placed in this category. I should point out that the title of this category stresses quantitative efforts, particularly those utilizing multivariate analysis, as these methods provide the means to most efficiently analyze vast amounts of acquired information.

Originally, the niche concept was used to summarize the general characteristics of a species' natural history. This broad definition has since been redefined to describe functional relationships (Elton, 1927), interspecific interactions, and feeding and nesting preferences (Conner and Adkisson, 1976). Several studies have illustrated that both the structural and functional aspects of vegetation are important in avian habitat selection (Wiens, 1969; Anderson and Shugart, 1974). McArthur et al. (1962) by correlating bird species diversity with foliage height diversity predicted the presence of a bird species from measurements of the amounts of foliage in three horizontal layers. More recently, researchers have used both univariate and multivariate analysis in approaching the determination of a species niche (Cody, 1968; James, 1971; Shugart and Patten, 1972).

Ideally, niche information can be used by wildlife managers as a tool for the

preservation of wildlife habitat. A good understanding of species niche requirements is especially important where timber production and wildlife must coexist (Bunnell et al., 1977). An analysis of habitat characteristics comprising a niche is a prerequisite to rational application of land management systems.

Surface Mining and Reclamation Effects on Avifauna

Approximately 5 percent of ongoing avifaunal research is in the area of strip mine and reclamation impacts on avifauna (fig. 1). This category accounts for four of the 84 projects reported. There is a paucity of information regarding both the initial impacts of surface mining and the effects of various reclamation techniques on avifaunal resources. To date only two breeding bird studies have been completed on contour surface mines (Yahner, 1973; Garton, 1974). Information regarding the avifaunal resources on area surface mines is almost as sparse, with only three studies having been located (Brewer, 1958; Karr, 1968; Terrel and French, 1975). A further complication is that most previous research has been conducted on either orphan mine lands or on recently reclaimed conventionally mined areas.

With the increased emphasis on coal as a primary energy resource of the future, both contour and area surface mining activities will be accelerated in our southern coal production states of Virginia, Maryland, Kentucky, West Virginia, Tennessee, and Alabama. In all of these, surface mining has been a major source of habitat disruption.

Prior to reclamation laws, thousands of acres were simply stripped and abandoned. The best methodologies for reclaiming these abandoned lands for the benefit of avifaunal resources as well as other types of wildlife are poorly understood at this time. We know which birds live in each general habitat type, but quantifying the relationships so that specific reclamation models can be constructed has not been adequately achieved (Samuel and Whitmore, 1976). Recent passage of the new Federal strip mine legislation, with its back-to-contour provision, adds a new unexplored dimension to the reclamation problem.

A knowledge of the avifaunal utilization of surface mined areas is an important element in evaluating the management of reclaimed areas. Breeding bird population parameters may be the best indicators of

the relative health or degree of recovery of a mined area and are important factors in determining the degree of success of a reclamation plan.

Expanded quantitative studies on avian use of surface mine habitats are a basic prerequisite to sophisticated surface mine reclamation planning. Until this information is available, only rudimentary management will be possible.

Raptor Research

To date, few studies have been addressed specifically to the subject of raptor management or conservation. While information of importance to raptor conservation has been gained through studies aimed at other goals, progress toward comprehensive understanding of what is needed to sustain raptor populations is still in the formative stages. As yet, most comprehensive management efforts on raptors have been limited to threatened or endangered species (Snyder and Snyder, 1975).

My sample indicates that this situation has not changed a great deal within the last several years. Excluding threatened or endangered species, I have listed three of the 84 projects in the raptor research category. These three projects account for 4 percent of the ongoing research reported (fig. 1).

Additionally, there are 10 projects dealing with threatened and endangered raptors listed under the endangered species category. Much of this work, particularly on the Bald Eagle, is directed toward nesting surveys, determination of population status, and distribution patterns.

While the current emphasis on methods to save the threatened or endangered raptors is probably appropriate, in the long run we should hope for a broader program--one which strives to ensure that those species still in relatively good shape do not end up on the endangered list.

Electric Transmission Line Effects on Avifauna

This final category includes two projects accounting for slightly more than 2 percent of the ongoing research. Clearly, transmission line impacts have not been considered a priority research area within the last several years.

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There are two distinct types of impacts associated with electric transmission lines. The first type of impact is that associated with the actual transmission line clearing, construction, and subsequent maintenance of vegetation. These impacts are most predominant where previously forested habitats are converted to relatively narrow corridors of periodically maintained shrub vegetation. The second type of impact occurs as birds strike the electric transmission conductors and support towers.

Currently the U.S. Fish and Wildlife Service and the Tennessee Valley Authority are the only agencies reporting research on transmission line impacts. The Tennessee Valley Authority research contract with the University of Georgia addresses the first type of impact, i.e., habitat loss or vegetative type conversions through construction and maintenance operations.

Currently very little is understood regarding the second problem--birds striking transmission conductors and support towers. As evidence of increasing concern for this problem, a workshop is being organized by the Oak Ridge (Tennessee) Associated Universities in cooperation with the U.S. Fish and Wildlife Service to address this very question. Workshop objectives are to determine the scope of the problem of birds striking transmission lines and to produce guidelines for management and research on this subject.

PROGRESS TOWARD PREVIOUSLY DEFINED

INFORMATION NEEDS

Having presented an overview of ongoing and planned avian research, I would like to compare the ongoing programs and the previously defined information needs (Table 1).

The information needs listed are the six most critical areas requiring attention as defined by Lennartz and Bjugstad (1975) and listed earlier in the presentation. By reviewing each of the 84 project titles and objectives I have made an admittedly subjective determination regarding the information needs they fulfill. Several projects were judged to satisfy more than one information need. Therefore, the Number of Projects and Percent columns will total more than 84 projects and 100 percent, respectively.

The information needs in Table 1 are not ranked in any order of urgency with the exception that endangered species research was given the highest priority (Lennartz and Bjugstad, 1975).

It is apparent that endangered species research is receiving a great deal of attention. Some may argue that endangered species are demanding too much attention at the expense of other wildlife problems. The fact remains that it has been ranked as our number one research priority and the degree of emphasis that it is receiving is probably justified. The current emphasis on endangered species research is, however, heavily weighted toward the Red-cockaded Woodpecker (fig. 2).

Table 1 also indicates that emphasis is being given to the areas of (1) avian resource distribution, (2) impacts of forest management, and (3) climax communities and associated microhabitat elements. The survey revealed a lesser degree of activity toward the final two information needs: avian/ forest habitat association and avian niche selection.

Eleven percent of the current research activity is directed toward identification of avian/forest habitat associations (Table 1). The concept of incorporating avian habitat assessments into existing

Table 1.--Previously defined nongame avian information needs and the number and percent of sampled ongoing projects which contribute to each as determined by a survey conducted in October 1977.

Information Needs [1]	Ongoing or Planned Research	
	Number of Projects	Percent
Endangered Species	37	44
Impacts of Forest Management	12	14
Niche Selection	6	7
Distribution of Avian Resources	22	26
Avian/Forest Habitat Associations	9	11
Climax Communities and Associated Microhabitat Elements	17	20

[1] Lennartz and Bjugstad, 1975

forest inventory systems is fairly new. As greater precision is required in assessing trends and conditions of the avian resource, development of a practical habitat assessment system for all forest types and successional stages should receive accelerated emphasis.

Seven percent of the research activity is being directed to use of multivariate analysis for quantitative explanation of the vegetative structure of the avian habitat niche. Cody (1968), James (1971), and Shugart and Patten (1972), utilizing multivariate techniques, have identified important habitat factors of different avian species. Nevertheless, the application of multivariate statistical techniques to nongame bird habitat and its management remains at a minimum (Mann, 1977).

Multivariate statistical techniques can be exceptionally useful in optimizing management strategies for avian resources and for identifying potential impacts of change in management policies (Shugart et al., 1975). Both new and experienced researchers should be encouraged to become familiar with the descriptive power and utility of these techniques.

AGENCY INVOLVEMENT IN RESEARCH

As evidenced by Figure 3, almost one-half (48 percent) of the ongoing research is being conducted by university researchers, frequently masters' degree or doctoral candidates. Universities were found to be actively involved in all eight categories of avian nongame research.

The U.S. Forest Service is involved in 26 percent of all sampled research activities; over half of this 26 percent is being handled by the Service's own biologists at various forest experiment stations in the southern, southeastern, and north central regions. The remainder are cooperative projects between the U.S. Forest Service and various universities.

The survey indicates that the U.S. Forest Service is heavily involved in two of the eight research categories: threatened and endangered species, and effects of forest management practices on avifauna.

Our National Forest wildlife habitat programs in the past have sought to maximize the production of game species and research has been directed toward these ends. However, one of the greatest influences stimulating the U.S. Forest Service's new accelerated research in the area of endangered avian species has been

RESEARCH AGENCY
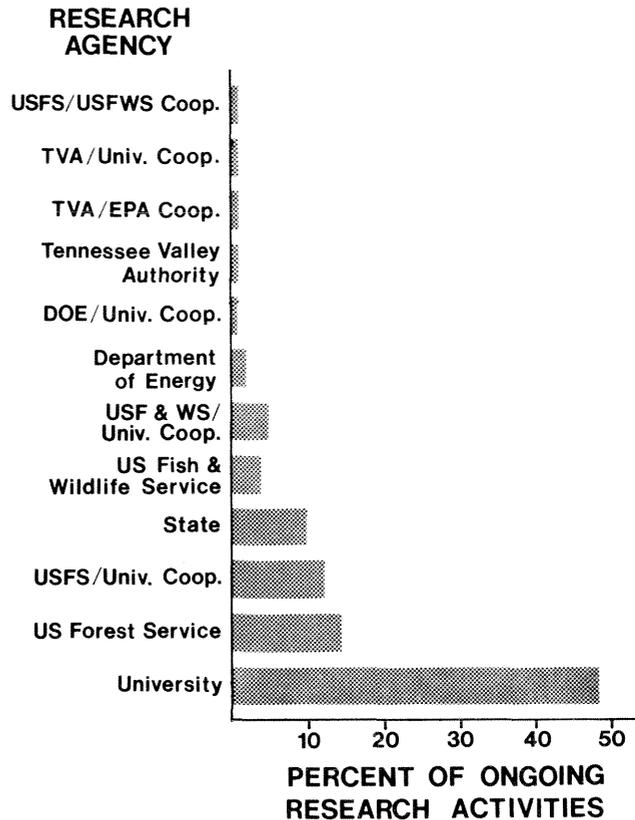

PERCENT OF ONGOING
RESEARCH ACTIVITIES

Figure 3.--Percent composition of agencies active in sampled ongoing nongame avian research in the Southeastern Region as determined by a survey conducted in October 1977.

the responsibility placed upon Federal agencies by the Endangered Species Act of 1973. In addition, the Service's mandate and policy to consider multiple resource management and use of all wildlife species, coupled with exploding public interest in nongame wildlife, have encouraged greater research emphasis on the unknowns of avian nongame management.

State agencies are engaged in approximately 10 percent of the sampled research activity. Their involvement is primarily with threatened and endangered species, with funds being provided by the Endangered Species Act of 1973 and administered through the U.S. Fish and Wildlife Service.

The U.S. Fish and Wildlife Service alone, and in cooperation with several southern universities, accounts for 9 percent of the ongoing research. They are involved in a diverse mix of research activities including surface mine studies, electric transmission line impacts, avian-forest

habitat type associations, raptor research, and endangered species research. The U.S. Fish and Wildlife Service also conducts and maintains data files on the National Breeding Bird Survey. This survey was started in 1965 and was designed to help monitor environmental quality by measuring changes in abundance in North American breeding birds.

Research activities of the Department of Energy and university cooperators accounted for 3 percent of the sample. These research projects are administered through and directed by the Environmental Sciences Division of the Oak Ridge National Laboratory.

Tennessee Valley Authority and TVA/ cooperative projects make up approximately 4 percent of ongoing research. The TVA projects relate primarily to energy production impacts on the avian resource and include research projects on surface mining impacts and effects of electric transmission lines on avian communities.

SUMMARY

Clearly, both wildlife management and research programs are having to respond to a new wildlife consitituency. This response has been a long time in coming but now seems to have gained a firm hold in what may be described as a new direction for the wildlife management profession.

While hunters still comprise 10 percent of the population, present estimates indicate that a great majority of Americans have an active interest in a broad spectrum of wildlife values other than the production of a shootable surplus. The diversity of our nongame birds provides an especially unique and challenging opportunity for resource professionals to coordinate the management of these species with other forest resource outputs. Yet, for most wildlife professionals, management of nongame birds and their habitats is a new resource issue, and a sound information base for a management program is lacking for many species. Consequently, as evidence and encouragement to you, the managers, that substantial progress is being made toward filling these information voids, I have attempted in this presentation to provide a capsule summary of our ongoing avian nongame research program in the southeastern region. I have also compared the ongoing research projects with the critical nongame bird information needs defined by Lennartz and Bjugstad (1975).

A summary of the salient points of the presentation is as follows:

1. Endangered species research accounts for 41 percent of all reported nongame avian research in the southeastern region.

2. Research on the Red-cockaded Woodpecker comprises almost 60 percent of all reported threatened or endangered species research. Approximately one-third of all Red-cockaded Woodpecker research is being sponsored by the U.S. Forest Service.

3. Research effort devoted to the effects of forest management practices on avifauna is the second most active research category, accounting for 16 percent of sampled research. The U.S. Forest Service is also the leader in this research effort, being either directly involved in or lending support services to 83 percent of the projects.

4. The development of avian-forest habitat associations constituted 11 percent of the sampled ongoing or planned research. Once knowledge of these associations is developed, monitoring of breeding birds populations can be made an integral aspect of continuing forest inventory. It may become possible to predict bird population trends associated with shifting forest land use patterns.

5. Effects of surface mining and reclamation on avifauna constitute a fairly small (5 percent) portion of ongoing research. With increased emphasis on coal as a primary energy resource of the future, surface mining activities will be vastly expanded. Habitat in six of our southeastern states (Virginia, Maryland, Kentucky, West Virginia, Tennessee, and Alabama) will be heavily impacted. Consequently, this area of avian research bears greater emphasis.

6. Aside from research on threatened and endangered species, the survey indicates that very few raptor studies (4 percent) have been initiated dealing specifically with the subject of raptor management on conservation.

7. The comparison of sampled ongoing research with information needs as defined by Lennartz and Bjugstad (1975) indicates that all six critical information voids are currently receiving research emphasis.

8. Approximately one-half (48 percent) of all ongoing avian research is being conducted by universities. The U.S. Forest Service is the second most heavily involved agency being either wholly or partially responsible for 26 percent of all sampled research activity.

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This symposium was held to familiarize land managers in the
South with the latest research information useful in manage-
ment of nongame birds on forested lands. Fourteen papers are
reproduced in the Proceedings.

Keywords: Avian ecology, wild-land management, nongame birds.

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