Tuesday Afternoon, January 23

NONGAME BIRD HABITAT MANAGEMENT

Moderator: Roger Holmes
Minnesota Department of
Natural Resources

THE EFFECTS OF CHANGES IN HABITAT ON NORTHERN HARDWOOD FOREST BIRD COMMUNITIES

Barry R. Noon[1], Verner P. Bingman[2], and J. Paige Noon[3]

Abstract.--The effects of habitat change on the avian communities of northern hardwood forests were examined from several perspectives. First, we critically reviewed published reports dealing specifically with the response of birds to habitat change. We then examined bird census data from communities representing varying degrees of habitat disturbance. Specifically, we analyzed census data according to the shape of their rank-abundance distributions and drew inferences about their community structure according to their fit to known distributions.

The consensus of the published accounts that we reviewed is that, over the long term, bird communities are very resilient to habitat change. We generally concur with these findings but with notable exceptions. Most importantly we found that the rare species of undisturbed forests are particularly sensitive to habitat changes. In many disturbed habitats the rare species group is either greatly reduced or completely eliminated. From a conservation perspective, we feel that the normally rare species of undisturbed forests should be of primary concern to forest managers in order to assure their persistence.

INTRODUCTION

It is generally accepted that habitat selection by passerine bird species is most strongly influenced by the structure of the vegetation (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). Further, niche separation by specific habitat selection appears to be the most common mechanism of achieving competitive coexistence in temperate bird communities (e.g., Shugart and Patten, 1972; James, 1971; Whitmore, 1977; Noon and Able, 1978; Noon, 1979). In light of the apparent integral connection between habitat structure and species composition, it becomes very important to assess the impact of habitat disturbance on avian communities.

From the studies references above one would predict that habitat alterations, such logging, would result in dramatic changes in bird species composition. However a search of the literature quickly reveals little quantitative information documenting the effects of habitat change on the populations of passerine birds. Hagar's (1960) studies of Douglas-fir forests revealed that logging altered the composition of the bird community and caused a short term decline in the density of breeding birds. Density rapidly returned to pre-cut levels, but the species composition remained changed for many years.

Kilgore (1971) studied the effect on bird species of a large scale reduction in the understory of a giant sequoia forest. He reported only slight changes in species composition, with ground-foraging and ground-nesting birds decreasing and flycatchers and robins increasing. Bird density increased on the disturbed site, however, total breeding bird biomass remained constant.

Hooper (1967, unpublished master's thesis; cited in Webb, et al., 1977) studied clearcut stands in Virginia 6 years after logging. He reported both an increase in species richness and density which he attributed to increased understory development. Conner et al. (1975) studied the effect of clear-cutting on the populations of 4 woodpecker species in Virginia. In the absence of snags

1/ Department of Biology, Siena College, Loudonville, NY 12211
2/ Department of Biology, State University of New York at Albany, Albany, NY 12222
3/ 25 Orlando Avenue, Albany, NY 12203

they found this level of logging benefited only one of the 4 species, with the other 3 restricted to less disturbed forests.

Recently, the results of a long-term investigation into the effects of logging on songbird populations in a northern hardwood forest have been reported (Webb et al., 1977). Due to the direct relevance of their research to this symposium, we will discuss the results of their monograph in some detail. In addition, we examine many breeding bird censuses collected from both mature and disturbed hardwood forest communities in order to gain further insights into the apparent correlation between habitat structure and species composition. We conclude by attempting to identify those species groups most negatively affected by habitat disturbance and thus in most immediate need of effective habitat management.

DESCRIPTION OF FOREST TYPE

Northern hardwood forest communities have an ecotonal character, lying south of the pure coniferous forest of the Canadian zone and north of the pure deciduous forest of more austral regions. However, they are not just transitional subclimax forests, but rather represent an extensive climax forest type. Their character alternates between pure deciduous, mixed, and coniferous regions. In the primary deciduous communities the dominant tree species are sugar maple, beech, basswood, yellow birch and red maple. In secondary deciduous communities, aspen, balsam poplar, paper birch, and gray birch are abundant species (Braun, 1950). In northern Michigan and Minnesota the aspen-birch association is the dominant secondary forest type.

The region contains four groups of species (Braun 1950; (after Nichols 1935)): 1) those with distinct southern affinities - beech, white ash, black cherry; 2) those whose northern limit occurs in the northern hardwood zone - sugar maple, basswood and northern red oak; 3) those species which reach their maximal abundance within the northern hardwood forest region - hemlock, white pine, yellow birch and red spruce; and 4) those whose centers of north-south distribution lie within the Canadian zone - white and black spruce, fir, larch, balsam poplar, and paper birch.

The primary mixed communities in north central and northeastern regions are mixtures of northern hardwoods and hemlock. In montane regions of the northeast the primary hardwoods, sugar maple, beech and yellow birch, are mixed with red spruce and in virgin areas with large white pines. In the northeastern zone of the hardwood forest belt the term hemlock-hardwood forest is most applicable. However, in western regions of this zone hemlock is absent and white pine becomes a regular climax dominant (Braun, 1950). In the extreme northern limits of this zone white spruce and balsam fir also achieve dominant status.

Along steep moisture gradients the composition of northern hardwood communities often change rapidly (Fig. 1) giving many areas a mosaic appearance. This pattern greatly increases local bird species diversity. The discrete forest types integrate abruptly into one another and are frequently large enough to maintain regular populations of habitat specialist bird species. This large scale patchiness, particularly pronounced in northeastern hardwood forests, contributes extensively to the high species richness characteristic of these latitudes.

The northern hardwood forest region extends from northern Minnesota and southeastern Manitoba eastward through the upper Great Lake regions, across New England and north to southern Canada (Braun, 1950). It covers most of the Appalachian Plateau in New York and Pennsylvania and has an extensive finger-like projection down the

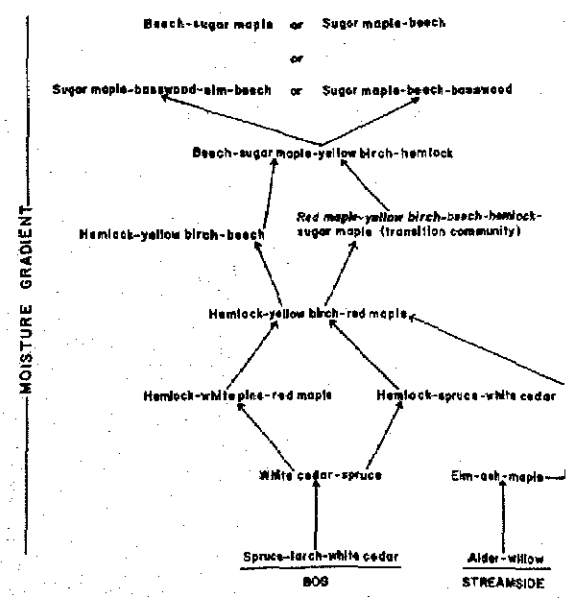

Figure 1.--Relationship of various forest communities of the northern hardwood region arrayed along a gradient of decreasing water requirements from bog to elevated ridge (after Braun, 1950).

Appalachian Mountain chain into western Maryland and West Virginia. The cross-hatched region of Figure 2, labeled coniferous-deciduous forest ecotone, indicates the extent of this forest type.

THE AVIFAUNA

The reader is referred to Table I for a listing of all the species we encountered in our survey of 70 breeding bird censuses. The species tabulated are found breeding in either mature and/or disturbed habitats. Of particular relevance to the topic of our paper are those species which reach their highest frequencies in mature forests, those restricted to these habitats, and those most often encountered as community dominants.

SYNOPSIS OF THE WEBB MONOGRAPH

Webb et al. (1977) studied the long term effects of different intensities of logging on breeding bird populations. Their study area was within a continuous 15,000 acre northern hardwood forest located in New York's Adirondack Mountains. The canopy of this forest was dominated by sugar maple, yellow birch, and beech with hemlock and red spruce comprising a small, but significant component of the forest.

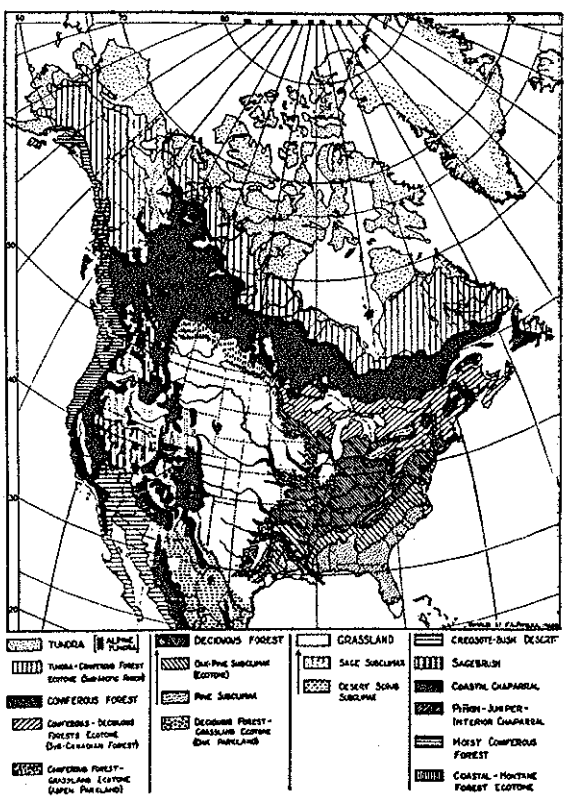

Figure 2.--The biomes of North America, with extensive ecotones and certain subregions indicated (after Pitelda, 1941).

Five extensive study sites were selected and subject to 5 levels of treatment. A natural area where no logging was done served as a control. Four areas were logged at 4 different intensities and were identified as the 25, 50, 75, and 100 percent areas. These percentages indicate the approximate amount of commercial timber volume removed when they were first logged. For softwoods the lower dbh limit was 12 inches while for hardwoods the lower limit varied from 14-16 inches dbh. Adirondack forests are particularly well stocked with trees greater than 12 inches dbh (Webb et al., 1977; Noon, unpublished data) and even selective logging results in significant changes in forest structure. The extensive disturbance of at least the 75 and 100 percents areas are still noticeable today (Richard Sage, Jr., personal communication).

Each study site contained 6 censusing stations where every bird seen or heard during a given period of time was tallied. The bird populations on each of the study sites were censused over a 10 year period. Neither the breeding status of individual birds nor the area sampled were determined; thus, only indices of relative abundance of presumed breeders were derived. The sum of the highest number of individuals recorded for a given species at each sampling station became the annual population index for that species for that particular stand. Each species' annual indices were then summer over the 10 annual censuses resulting in a total population index for each species for each stand.

During the 10 year interval a total of 56 species were recorded. However, only those species with a cumulative population index of 50 or above were studied for population trends. This reduced the number of species examined to 26 and excluded, for example, all the woodpeckers, except the yellow-bellied sapsucker, and all birds of prey.

The results of Webb et al. (1977) can be succinctly summarized by noting the effects of logging on:

a) Faunal composition: The fauna on the unlogged area was not supplanted by a different fauna on the logged area. Of the 26 "indicator species" only the veery was never observed on the unlogged control. By contrast, 6 species, ruffed grouse, pileated woodpecker, olive-sided flycatcher, veery, mourning warbler, and chipping sparrow were only recorded on logged sites. Using Spearman rank correlation as an index of shifts in importance value, no significant differences in rank order were observed when each of the treatment stands were compared to the control area. However, a trend of decreasing correlation from lightest to heaviest logging was apparent.

Table 1. Avifauna of the northern hardwood forest region.

Species (by foraging guild)	Mature (undisturbed) habitats: Percent of censuses recorded	Mature (undisturbed) habitats: Percent of censuses dominant	Disturbed and successional habitats: Percent of censuses recorded	Disturbed and successional habitats: Percent of censuses dominant	Disturbed and successional habitats: Changes in species frequency
Foliage gleaners					
Yellow-billed Cuckoo	20		3		
Black-billed Cuckoo	5		20		
Blue Jay	53		43		
House Wren	13		17		
Winter Wren	15		7		
Carolina Wren	15		16		
Catbird	10		32		I[b]
Blue-gray Gnatcatcher	3		13		
Cedar Waxwing	3		27		I
Solitary Vireo	8		13		
White-eyed Vireo	-		7		
Yellow-throated Vireo	43		3		D
Red-eyed Vireo	100	67.5	90	20.0	
Philadelphia Vireo	5		-		
Warbling Vireo	-		13		
Worm-eating Warbler	3		3		
Golden-winged Warbler	-		10		
Nashville Warbler	3		30		I
Yellow Warbler	-		13	6.7	
Magnolia Warbler	5		37		I
Yellow-rumped Warbler	5		10		
Black-throated Green Warbler	55	5.0	40	3.3	
Black-throated Blue Warbler	15		40		I
Cerulean Warbler	48		-		
Chestnut-sided Warbler	10		67	16.7	I
Bay-breasted Warbler	5		-		
Pine Warbler	-		3		
Prairie Warbler	-		10		
Palm Warbler	-		3		
Yellowthroat	8		47	16.7	I
Yellow-breasted Chat	3		17		
Mourning Warbler	8		40		I
Hooded Warbler	40		13		D
Canada Warbler	3		27		I
Red-winged Blackbird	-		20		I
Common Grackle	15		17		
Northern Oriole	3		23		I
Scarlet Tanager	78		43		D
Cardinal	70		20		D
Rose-breasted Grosbeak	45		57		
Indigo Bunting	15		47	10.0	I
Purple Finch	3		10		
American Goldfinch	8		13		
Chipping Sparrow	-		23		I
Field Sparrow	20		17		
Swamp Sparrow	-		3		
Song Sparrow	20		43	6.7	I
Average importance of guild (mean and (standard deviation))	.426 (.088)		.528***[a] (.083)		

Table 1. Avifauna of the northern hardwood forest region. (continued)

Species (by foraging guild)	Mature (undisturbed) habitats: Percent of censuses recorded	Mature (undisturbed) habitats: Percent of censuses dominant	Disturbed and successional habitats: Percent of censuses recorded	Disturbed and successional habitats: Percent of censuses dominant	Disturbed and successional habitats: Changes in species frequency
Ground foragers					
Ruffed Grouse	28		27		
American Woodcock	-		7		
Mourning Dove	15		3		
Yellow-shafted Flicker	45		43		
Common Crow	30		7		D
Brown Thrasher	3		13		
Robin	58		50		
Wood Thrush	80		47		D
Hermit Thrush	13		23		
Swainson's Thrush	15		20		
Veery	18		77	10.0	I
Starling	18		10		
Ovenbird	88	7.5	77	10.0	
Northern Waterthrush	-		3		
Louisiana Waterthrush	35		3		D
Kentucky Warbler	10		10		
Brown-headed Cowbird	65		17		D
Rufous-sided Towhee	58		70	3.3	
Dark-eyed Junco	10		37		I
White-throated Sparrow	8		23		
Average importance of guild (mean and (standard deviation))	.287 (.052)		.352* (.088)		
Salliers					
Eastern Kingbird	5		17		
Great-crested Flycatcher	83		23		D
Eastern Phoebe	43		3		D
Acadian Flycatcher	63	10.0	3		D
Least Flycatcher	20	7.5	23		
Alder Flycatcher	-		13		
Eastern Wood Pewee	93		47		D
Olive-sided Flycatcher	-		7		
Eastern Bluebird	3		3		
American Redstart	60	2.5	20		D
Average importance of guild (mean and (standard deviation))	.155 (.098)		.056**** (.063)		
Bark gleaners					
Black-capped Chickadee	65		57		
Carolina Chickadee	25		3		D
Tufted Titmouse	75		3		D
White-breasted Nuthatch	90		17		D
Red-breasted Nuthatch	3		13		
Brown Creeper	5		7		
Black-and-white Warbler	15		57		I
Average importance of guild (mean and (standard deviation))	.054 (.039)		.039 (.029)		

Table 1. Avifauna of the northern hardwood forest region.

Species (by foraging guild)	Mature (undisturbed) habitats: Percent of censuses recorded	Mature (undisturbed) habitats: Percent of censuses dominant	Disturbed and successional habitats: Percent of censuses recorded	Disturbed and successional habitats: Percent of censuses dominant	Disturbed and successional habitats: Changes in species frequency
Predators					
Cooper's Hawk	8		-		
Marsh Hawk	3		-		
Red-tailed Hawk	15		-		
Red-shouldered Hawk	-		3		
Broad-winged Hawk	13		7		
Screech Owl	10		-		
Great Horned Owl	10		-		
Barred Owl	20		3		
Average importance of guild (mean and (standard deviation))	.006 (.006)		.002* (.005)		
Bark drillers					
Pileated Woodpecker	30		17		
Red-bellied Woodpecker	53		-		D
Red-headed Woodpecker	23		-		D
Yellow-bellied Sapsucker	13		17		
Hairy Woodpecker	95		43		D
Downy Woodpecker	83		27		D
Average importance of guild (mean and (standard deviation))	.052 (.041)		.012**** (.016)		
Hover gleaners					
Golden-crowned Kinglet	3		-		
Parula Warbler	10		3		
Blackburnian Warbler	15		13		
Average importance of guild (mean and (standard deviation))	.015 (.020)		.004* (.012)		
Hawkers					
Whip-poor-will	-		3		
Chimney Swift	-		10		
Tree Swallow	-		10		
Average importance of guild (mean and (standard deviation))	- -		.004 (.010)		
	N = 40		N = 30		

[a] *, $p<.05$; **, $.01<p<.05$; ***, $.005<p<.01$; ****, $p<.001$

[b] I - species frequency increased by at least 20%;
D - species frequency decreased by at least 20%.

b) Diversity: Species richness was lowest on the natural area and increased with logging intensity. However, only at the 2 highest logging intensities was the difference significant. Comparison of the logged stands to the control by their Shannon indices revealed a significant difference only for the 2 highest logging intensities. In both instances these stands had higher diversities, primarily a consequence of the difference in species richness and not evenness. Only the most heavily logged area had a significantly higher evenness.

c) Population trends: Five species showed a negative trend in population size with an increase in logging: ovenbird, black-throated-green warbler, blackburnian warbler, winter wren, and least flycatcher (Fig. 3). The wood thrush had a high population density on the control plot and appeared to be rather equally affected by all levels of logging (Fig. 3). In addition, the yellow-bellied sapsucker responded negatively only to the most intense level of logging. Six species showed a positive trend in population in response to logging: American redstart, chestnut-sided warbler, rose-breasted grosbeak, white-throated sparrow, black-and-white warbler and veery (Fig. 4). Many of the species

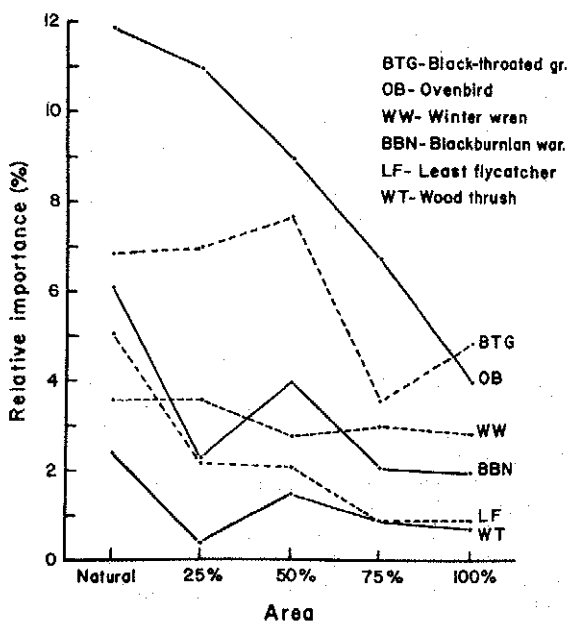

Figure 3.--Bird species showing decreasing trends in relative importance as a function of increasing habitat disturbance (modified from Webb et al., 1977).

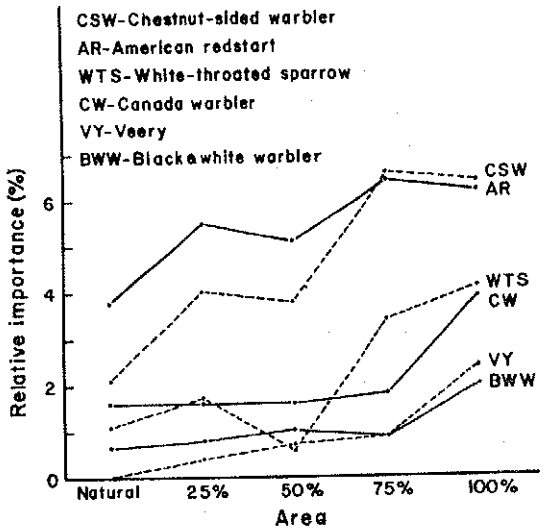

Figure 4.--Bird species showing increasing trends in relative importance as a function of increasing habitat disturbance (modified from Webb et al., 1977).

affected by logging showed trends back towards their pre-treatment levels. Most notable were positive trends for the ovenbird, winter wren and wood thrush and negative trends for the chestnut-sided warbler and white-throated sparrow.

Webb, et al. (1977) conclude that logging in northern hardwood forests does not completely eliminate any breeding bird species. In addition, their results suggests that over the long term these avian communities are resilient to even severe habitat disturbance. However, we feel that the study of Webb et al. (1977) may suffer from some methodological inadequacies which lead us to question some of their conclusions.

The inadequacies we perceived are outlined below:

a) Population censusing techniques: Their method of calculating a population index not weighted by sampling area undoubtedly over-estimates true abundances. Their method is most problematic in the extensively logged habitats where increased visibility and decreased sound interference would likely result in the observer recording species over a much larger area. As a result, decreases in abundance may go unrecorded.

b) Breeding status unknown: The breeding status of individual birds was not determined and, like the population index, may be most problematic for the disturbed habitats. The logged stands were enclosed within an extensive undisturbed tract of forest which may have resulted in there being more rapid recolonization than would occur in more isolated forest plots. Also, recolonization, especially during the first few years following disturbance, may have been largely by non-territorial individuals excluded from surrounding undisturbed habitats. Stewart and Aldrich (1957) and Hensley and Cope (1951) have supplied evidence that a portion of the population of some species of these forests are composed of a floating population of unmated males. Disturbed, sub-optimal habitats may "collect" these unmated indivuduals.

c) Pooling of data: The only data available to the reader are the pooled population indices. Of most interest are the immediate effects of logging which would only be apparent from individual year censuses. As will become apparent later in our discussion, pooling may mask dramatic year-to-year fluctuations in species composition and relative abundance.

d) Exclusion of rare species: Most of the rare species were excluded from detailed analysis. Threatened or endangered species are most likely part of the rare component of any community. From a conservation perspective these are the species most in need of accurate censusing to determine the effect of various management practices on their populations.

e) Lack of quantitative vegetation data: Only a qualitative description of the forest type was given. As a result it was impossible to unambiguously assess the degree of habitat disturbance. Most lacking was a frequency distribution of trees by dbh size-class before and after logging.

COMMUNITY-LEVEL ANALYSIS

In order to resolve the direct effects of logging on community structure per se, we have analyzed the Webb data (Webb *et al.*, and numerous other censuses in terms of their rank-abundance distributions (MacArthur, 1957, 1960; Whittaker, 1972). In addition to identifying changes in species composition, we analyze the rank-abundance distribution of each of the censuses according to their fit to various theoretical distributions. We then discuss the underlying biological assumptions of these theoretical rank-abundance distributions with regard to specific censuses. Specifically, we are interested in determining the effects on community structure of various intensities of disturbance. In addition, we divided the individual censuses into 1 of 2 groups, mature or disturbed (successional), and examined these data according to changes in the relative importance of various feeding guilds (Table 1).

Over the years avian ecologists have accumulated much information on the relative abundance of species occupying specific habitat types. Many researchers noted that the distribution of relative abundance in communities assumed a few characteristic patterns. Subsequently, models based on the interactions among populations within communities were proposed to account for the observed patterns of relative abundance. Specifically, MacArthur (1957, 1960) proposed several models of relative abundances based on different assumptions about the biological organization of the community.

For 2 of these models a stick, symbolic of a finite resource dimension, was broken into N segments, where N was equal to the number of species. In the first model N-1 points were picked at random along the stick, then the stick was broken at these points. The lengths of the resulting segments were proportional to the relative abundance of the species. In the second model, N independent pairs of points are successively chosen at random locations along the length of the stick. The length of the segment between a given pair of points is proportional to the species abundance. Both broken-stick distributions are specified by a single parameter, the number of species.

The biological assumptions of the first model are that the critical resources are continuously distributed along a single dimension, all resources are utilized, but the species do not overlap in their utilization of the resources (Ricklefs, 1973). The model is restricted to communities comprising a relatively limited number of related species competitively interacting in a structurally homogeneous habitat. This model is often referred to as the non-overlapping niche model (Fig. 5).

The second model assumes a much more even distribution of species abundances. The model rests on the assumption that the abundances of species are independent of each other; that

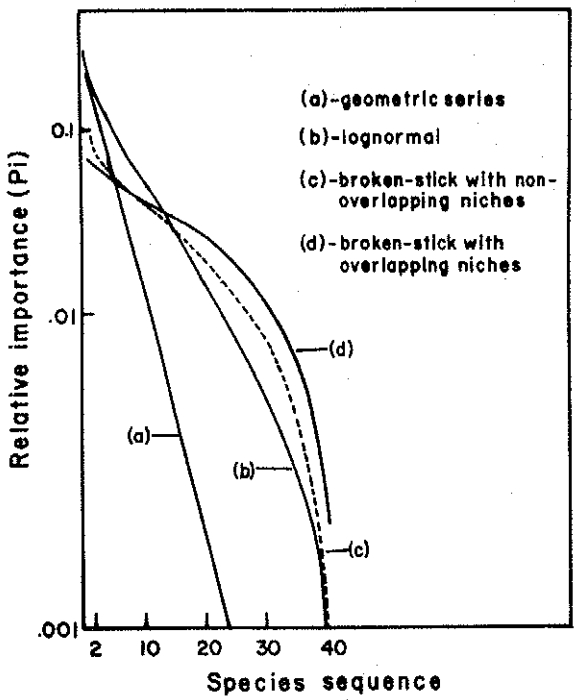

Figure 5.--Theoretical rank-abundance curves fit to 4 major hypotheses: a) geometric series (c = .750); b) lognormal distribution (a = .25, S_0 = 6); c) non-overlapping niche hypothesis; d) overlapping niche hypothesis. All curves were calculated on the basis of 40 species.

is, species do not compete and resources are not fully utilized (Ricklefs, 1973). This model is referred to as the overlapping niche model (Fig. 5).

Observed bird species-abundance distributions show their best fit to the non-overlapping niche model (MacArthur, 1957, 1960; King, 1964; Longuet-Higgins, 1971). Deviations from this distribution most frequently result from too many common species and too few rare species. However, as pointed out by Cohen (1966, 1968) and others, the specific biological assumptions of the non-overlapping niche model are not always supported. Cohen (1968) was able to derive this same model by a completely different set of hypotheses. Even though the strict biological assumptions of this model are not validated, good fits to this distribution do indicate that some major factor is being roughly evenly apportioned among the constituent species of the community (May, 1975).

If the distribution of species relative abundance proceeds in a strictly hierarchial fashion we arrive at a geometric series distribution. In this model one assumes that the community is dominated by a single factor with a species success determined by its ability to preempt some fraction of the unutilized resources. The most successful species will preempt a fraction k of the resource and the second species a fraction k of the remainder, and so on resulting in a geometric distribution (Fig. 5). This distribution, referred to as the niche preemption model, is usually best fit by data from communities with few species characteristic of an early successional stage or occupying harsh environments (e.g., Whittaker, 1972). The phenomenon of strong dominance usually characterizes such circumstances.

If a variable such as relative abundance is determined by a large number of factors the distribution of that variable will be normal. In communities with many species and large numbers of individuals the distribution of relative abundances is often best described by the log normal (Fig. 5). Communities characterized by this distribution have many moderately abundant species and few common or rare species (Preston, 1948). The biological assumptions underlying this model are obscure and little can be deduced about the structure of communities fit by this distribution. The most consistent condition is the absence of any single, obvious controlling influence on the species' relative abundances.

RANK-ABUNDANCE ANALYSES

Figure 6 presents the rank-abundance results for the data from Webb et al. (1977). It is immediately apparent that there is very little difference in the general shape of the distributions. All curves are best fit by MacArthur's non-overlapping niche distribution (hereafter referred to as the broken-stick). The 100% curve also gives a moderately good fit to a lognormal distribution, probably because of this area's extreme heterogeneity represented by 10 years of pooled data. In general, polling of data over many years improved the fit to a broken-stick distribution for all types of forest stands we examined (see below). As mentioned previously, pooled data likely masks any of the immediate effects of logging on community structure. It would be of great interest to look at rank-abundance distributions for each of the stands on a yearly basis. Unfortunately, the annual data is not available.

These curves deviate from the theoretical broken-stick distributions by having too many common species and too few rare species. However, if broken-stick distributions are calculated on the basis of the number of observed ranks, and not on the number of observed species, all these curves are fit very accurately. Calculations of goodness of fit on

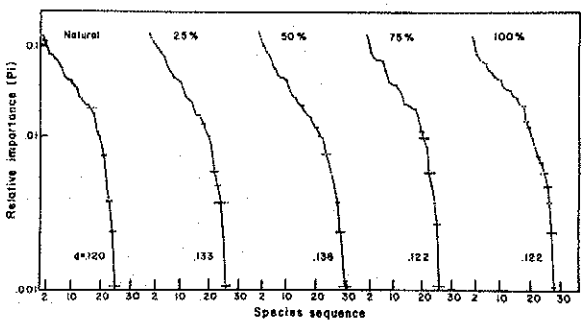

Figure 6.--Rank-abundance curves for the bird communities from the 5 areas of Webb et al., (1977). The d - values indicate the relative importance of the most common bird species, i ($d = n_i/N$total).

this basis seems reasonable: if the populations were perfectly sampled the probability of having 2 species with exactly the same number of individuals would be very small. Perfect sampling increases the number of ranks and usually decreases the dominance resulting in improved fits to the broken-stick distribution.

Rank abundance distributions well fit by a broken-stick model are characteristic of ecologically homogeneous groups of species which randomly apportion amongst themselves a fixed amount of some key resource (May, 1975). The implication from a comparison of these distributions (Fig. 6) is that this apparent mechanism of allocation of a major resource is not disrupted by logging. Our conclusion from this type of community-level analysis corroborates those reached by Webb et al. (1977). Northern hardwood bird communities appear to recover rapidly from habitat disturbance and, despite changes in species composition, community structure remains relatively stable.

Some questions remain, however, about the generality of this conclusion. We have already elucidated what we consider to be methodological difficulties with the Webb data. To unravel the effects of pooled data and to determine whether the conclusions reached by Webb et al. (1977) are consistent with other published data, we examined censuses from several disturbed northern hardwood forest communities. Most of the data were taken from breeding bird censuses published in American Birds (Audubon Field Notes).

When we examined other bird census data to test the generality of Webb's results we found that data directly comparable to their study were scarce. However, bird census data were available from a mature northern hardwood community both before, and after, logging (Fig. 7) (DeGarmo, 1948, 1953; Chandler, 1958; Harrison et al., 1964; Leitsch, 1968; Smith, 1973). This 15 acre plot, located in West Virginia, was selectively logged of most of its marketable timber in 1955, and we feel closely approximates the 75-100 percent logged areas of Webb et al. (1977) in degree of habitat disturbance.

The shape of the rank-abundance curves both before and after logging are very similar (Fig. 7). Therefore, logging appeared to have little effect on the overall community organization. All the single year censuses are best fit by geometric series and contrast sharply with the pooled distributions of Webb et al. (1977) (Fig. 6). These communities have low species diversity, high dominance, and

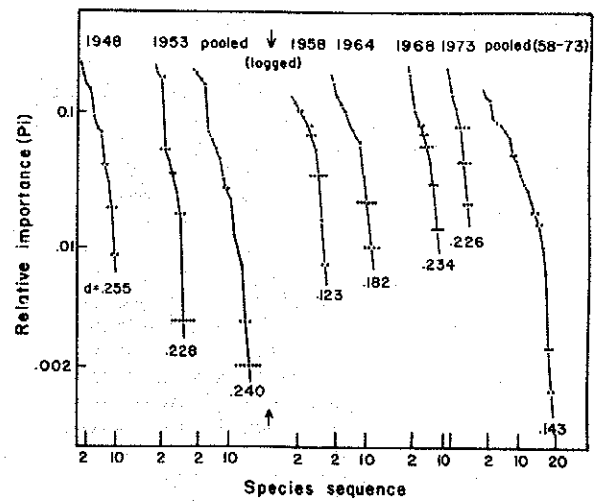

Figure 7.-- Rank-abundance curves for the bird communities of a hardwood forest plot before and after selective logging. Numbers above the curves indicate the year of the census. Pooled curves represent data combined over 2 or more years. d-values as in Fig. 6.

according to the biological assumptions underlying this model, should be characterized by a pattern of niche preemption.

Individual year censuses on this plot recorded few species and were marked by extensive year to year variability in the relative abundance and presence of the less common species. Only by pooling data over years do the rank-abundance curves approach the broken-stick distribution proposed by MacArthur (1957, 1960) as characteristic of temperate bird communities. Turnover of some portion of the rare species each year results in a much higher apparent species richness when the data are pooled. Up to some asymptotic limit, total species richness of a small plot may be a function of the number of years of study, a consequence of a great deal of variability in yearly species composition.

Our initial conclusions from these comparisons (Fig. 7) indicate that the avian community structure of this site was little affected by selective logging. However, unlike the Webb results, there was extensive turnover in species composition. Rufous-sided towhee, mourning dove, and chestnut-sided warbler appeared for the first time as the second, fourth, and fifth most dominant species, respectively.

In addition, there is a suggestion of a greater number of rare species in the undisturbed habitat relative to the logged habitat (Fig. 7). This is apparent from the number of ranks falling in the third log cycle. In this regard it may be significant that the 1948 census comprised only 7 man-hours and likely underestimated richness, particularly for the rare species.

To further test the sensitivity of rare species to logging, and the effects of habitat disturbance on northern hardwood forests in general, we contrasted rank-abundance curves representing the avian communities of mature (undisturbed) forests to those from successional and disturbed forests (Figs. 8-10).

Figure 8 represents a successional sequence of an initially disturbed northern hardwood forest in West Virginia. Censusing of this 15 acre plot began in 1948 and was continued intermittently until 1973 (DeGarmo, 1948; Brooks Bird Club, 1953; Baker et al., 1958; Hutton et al., 1968; Eddy et al., 1973). In 1948 the plot was a thicket with young trees 15-25 feet tall; by 1968 the plot was a young forest with most trees 4-8 inches dbh. Especially striking from this figure is that the rank-abundance curves showed no significant change in

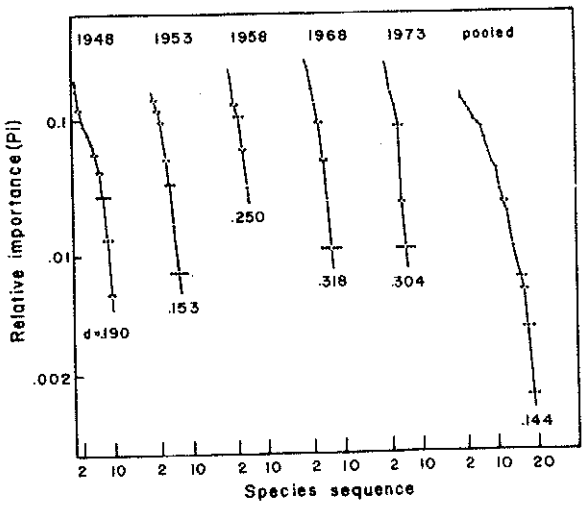

Figure 8.--Rank-abundance for the bird communities of a hardwood forest plot experiencing secondary succession. Labels as in Figs. 6 and 7.

shape over the 25 year period. As with other censuses, a broken-stick distribution is approximated only by pooling data. In terms of nutrient pools and vegetation structure it may take a northern hardwood forest 60-80 years to recover from severe disturbance (Likens et al., 1978). What remains unclear is whether the avian communities of these forests show the same long-term recovery time. Data presented below (Fig. 10) indicates that these bird communities may still be showing the effects of past habitat alteration.

Annual rank-abundance curves are best fit but geometric series, have low species diversities and, in some years, high dominance. All the rank-abundance curves reveal a lack of rare species; i.e., those with relative abundances less than .01. Thus, our suggestion of a sensitivity to disturbance on the part of rare species is further substantiated.

The changes in species composition during succession closely correspond with those reported by Webb et al. (1977) for Adirondack forests. Species showing negative trends through succession were the veery, chestnut-sided warbler, mourning warbler, and rufous-sided towhee. Species with consistent positive trends were the wood thrush and black-throated green warbler.

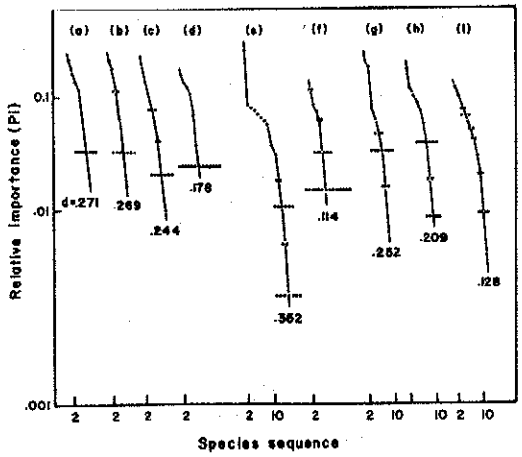

Figure 9.--Rank-abundance curves for the bird communities of successional and disturbed habitats: a-c) deciduous clearcuts 1, 3, and 4 years, respectively, after cutting; d-e) aspen-birch clearcuts 2 and 4 years, respectively, after cutting; f) an early successional hardwood forest; g) mature beech-maple-hemlock forest after an extensive natural disturbance; h) selectively cut-over forest; i) young red maple-gray birch forest. d-values as in Fig. 6.

Figure 9 presents rank-abundance curves for early successional and disturbed habitats. With the exception of Fig. 9e, all these single year curves are best fit by geometric series. Dominance varied appreciably, with some disturbed communities having surprising high equitability. The majority of these communities have few rare species, apparent from the figure as a lack of ranks in the third log cycle. A scarcity of rare species seems to be a relatively consistent trend in the disturbed communities that we examined. Figure 9e represents an exceptional case in terms of the extensively disturbed habitats we reviewed. However, it does indicate that a lack of rare species is not a universal response to habitat disturbance.

Admittedly, several of the curves in Fig. 9 illustrate severe habitat disturbance. However, to the extent that these curves convey actual community attributes, they illustrate that the species importance values of the community dominants are relatively immune to changes in habitat structure while the rare species previously occupying these habitats are often eliminated. Even though rare species are well represented in Fig. 9e, these species are not those characteristic of mature forests of this region and represent a turnover in the species composition of this group.

Relative to undisturbed forest communities these individual curves indicate little change in community structure (cp. Fig. 10). However, the species composition of many of these communities has changed dramatically. They are dominated almost exclusively by edge-species; most notably the chestnut-sided warbler, mourning warbler, rufous-sided towhee, veery, indigo bunting, and song sparrow. Forest interior birds have been completely eliminated from the heavily disturbed plots. The less severely disturbed forest habitats (Figs. 9g, h, i) remain dominated for the most part by birds characteristic of mature forests, but, significantly, these communities also show a loss of their rare species.

To substantiate the apparent trend in loss of rare species in early successional or disturbed hardwood forests, we have plotted for comparison a representative sample from bird communities occupying mature, undisturbed northern hardwood forests (Fig. 10). These rank-abundance curves contrast most obviously with the disturbed and successional habitats by the greater number of species whose relative abundances fall in the third log cycle. Thus, rare species appear to contribute substantially more to the species complement of communities of undisturbed forests than they do in disturbed areas. We feel this comparison clearly indicates a sensitivity on the part of the rare species component of undisturbed forests to habitat perturbations (cp. Figs. 7-9).

In agreement with the data from disturbed habitats, these rank-abundance curves are best fit by geometric series and do not approach broken-stick distributions unless censuses are pooled over years (Fig. 10e). In addition, even these unperturbed forests show considerable year to year variability in species composition, particularly pronounced as turnover in the identity of rare species. The variance in composition of the rare species group and relative abundances of even the community dominants, appears to be a common feature of the avian communities of north temperate forests.

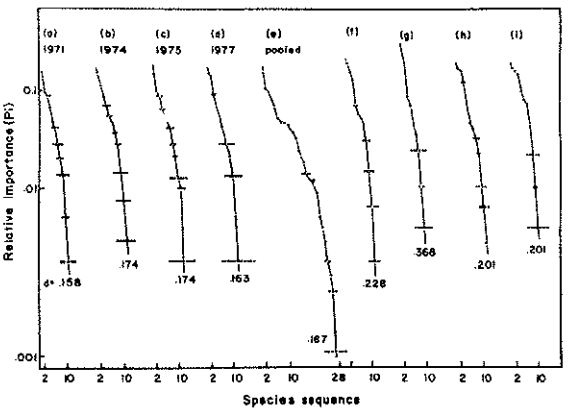

Figure 10.--Rank-abundance curves for the bird communities of mature, undisturbed northern hardwood forests: a-d) a forest plot censused over 4 intermittent years; e) pooled curve for the collective data of curves a-d; f) mature poplar forest; g) mature aspen-northern hardwoods forest; h) northern hardwoods forest; i) aspen-birch forest. Labels as in Figs. 6 and 7.

DISCUSSION

Our examination of the few published studies assessing the effect of forest management on avian communities revealed a lack of rigorous documentation of the response of birds to habitat change. From available data (e.g., Webb *et al.*, 1977 and Kilgore, 1971) the implication is that even extensive logging results in few long term changes in bird community composition. This conclusion appears to be in contrast to recent theoretical work establishing a strong relationship between habitat structure and species composition. Furthermore, in species rich, equilibrium communities the habitat differences permitting competitive coexistence of similar species are often very subtle and perhaps essential to maintain high species richness (Noon 1977; Noon and Able, 1978).

Our comparison of rank-abundance curves, contrasting mature and disturbed forests in terms of the distribution of species abundances, largely supports the resilience of community structure. In terms of the fit of these curves to theoretical distributions we found little evidence of change in community structure as a consequence of disturbance. However, large scale changes in species composition occurred after disturbance in many communities. These changes were noted in 2 ways: as a change in community dominants and as a loss of rare species.

In addition, we uncovered some interesting facts pertaining to theoretical concepts of avian community structure. Specifically, we found few annual censuses whose rank-abundance curves conformed to broken-stick (non-overlapping, contiguous niches) distributions. Good fits have commonly been reported for temperate forest bird communities at equilibrium and occupying relatively homogeneous habitats (MacArthur, 1957, 1960; King, 1964). We feel that our selection of censuses meet the criteria of the broken-stick model and the lack of fit represents a real discrepancy.

The data we examined differed most apparently from the broken-stick distributions by having higher dominance, too many common species and too few rare species. As a consequence they were best fit by geometric series. Only by pooling censuses over several years did these curves approach a broken-stock distribution (i.e., Fig. 7). We believe this occurred because of the extensive variability in the composition of the rare species group. By pooling censuses over time additional rare species are accumulated, dominance decreases, and the fit to the broken-stick distribution improves greatly (i.e., Fig. 10e).

The most striking difference we noted in our comparison of mature, undisturbed habitats to disturbed or early successional habitats was a lack of rare species in the latter habitats. This was graphically portraited by there being few, or no, species falling in the third log cycle of rank-abundance curves from disturbed habitats. However, it is important to determine whether this observed difference in rare species is simply a statistical artifact of the data. If mature habitats had significantly higher species richness values or higher breeding densities, or both, these differences could account for the lack of rare species in disturbed habitats. To examine this possibility we have analyzed these (and others) community attributes from both mature and disturbed habitats (Table 2). First note that there is a significant difference in the mean number of species per third log cycle (Table 2). This difference is clearly independent of breeding density, but is complicated by a significant difference in species richness in favor of mature plots (Table 2).

To normalize for the difference in species richness we have independently calculated the percent of species in each census falling in the third log cycle. When we compare these 2 means we find that there is still a signifi-

Table 2. Comparison of avian community attributes of rank-abundance curves (Fig. 7-10) representing mature and disturbed, or early successional, hardwood forest areas. Given are means (standard deviations) and the significance of mean difference where applicable.

Attribute	Mature	Disturbed and Successional
Species diversity	2.567 (.288)	2.464 (.262)
Evenness	0.755 (.028)	0.780 (.064)
Species richness	24.6 (6.6)	17.6 (4.4)**[a]
Density (males per 100 acres)	228.3 (106.6)	198.4 (116.9)
Dominance (n_{max}/N)	0.215 (.062)	0.222 (.068)
No. of species per third log cycle	8.50 (3.75)	1.94 (2.80)***
Percent of species per third log cycle	32.8 (9.0)	9.5 (12.2)****[b]

[a]**, .005<p<.01; ***, .001<p<.005; ****p<.001

[b]arcsin transformation

cant difference in the proportion of rare species (Table 2). Thus, undisturbed plots have both a significantly higher absolute number, and proportion, of rare species.

It is difficult to specifically identify the rare species because of the great variability from site to site in the species composition of this group. However, there do appear to be consistently rare foraging guilds (Table 1). Examining the species composition of these guilds may give us insights into what species are most threatened by habitat disturbance.

The most obvious, and the most readily understood, are the birds of prey. These species are rare even in their preferred habitat, but they seem to be particularly rare in disturbed habitats (Table 1). A second rare foraging guild showing significant decrease as a result of disturbance were the bark drillers (Table 1). Woodpeckers seem to be adversely affected at all but the lightest levels of disturbance. The only woodpecker maintaining a high frequency in logged plots was the ground-foraging flicker. Conner et al. (1975) reported similar results from logged habitats in Virginia.

Both the bark gleaner and hover gleaner guilds were consistently rare. Both guilds show decreased frequency in disturbed habitats, but only the hoven gleaner is significant (Table 1). A common factor links many of the species composing the bark gleaner, bark driller, and predator guilds; that is, many of these species are hole nesters. The hole nesters also include a sallier, the great-crested flycatcher, which also showed a large decrease in frequency in disturbed habitats. Hole nesters were also seen to decrease as a result of logging in Finnish forests (Haapenen, 1965). There is a likely correlation between decreases in the woodpeckers, which are primary hole nesters, and secondary hole nesters such as chickadees and titmice which are indirectly dependent upon the presence of primary hole nesters.

Although not a rare guild, the salliers also showed a significant decrease in frequency in disturbed plots (Table 1). The decrease was most pronounced for the great-crested flycatcher, eastern phoebe, acadian flycatcher, eastern wood pewee, and the American redstart. Because most of these species are canopy or sub-canopy salliers their decrease in logged plots is easily understood.

From this admittedly limited (and highly variable) data set we suggest that extensive habitat disturbance may have its most pronounced effects on the rare species of the community. Their consistent rareness even in their preferred habitat is indicative of an extreme specialization to some aspect of their environment. Current evidence from

temperate bird species indicates that their assessment of acceptable habitat is most frequently expressed as selection for specific structural features of the vegetation. If rare species normally have more stringent requirements in terms of habitat structure, then their sensitivity to habitat disturbance is easily understood. From a management perspective, identifying the specific requirements of these birds is of immediate importance and will require essentially an autecological approach. Until the requirments of these sensitive species are known, we suggest that the populations of the rare species characteristic of undisturbed forests be maintained at high levels by preserving extensive tracts of undisturbed forests. Currently, this appears as the sole means of assuring their persistence.

LITERATURE CITED

Anderson, S. H., and H. H. Shugart.
1974. Habitat selection of breeding birds in an east Tennessee deciduous forest. Ecology 55: 828-837.

Baker, D. F.
1958. Young deciduous forest. Aud. Field Notes 12: 446.

Braun, E. L.
1950. Deciduous forests of eastern North America. The Blankiston Co., Philadelphia, Pennsylvania. 596 p.

Brooks Bird Club.
1953. Young deciduous forest. Aud. Field Notes 7: 338-339.

Chandler, E. R.
1958. Cut-over mature hardwoods. Aud. Field Notes 12: 458-459.

Cody, M. L.
1968. On the methods of resource division in grassland bird communities. Am. Nat. 102: 107-147.

Cohen, J. E.
1966. A model of simple competition. Harvard University Press, Cambridge, Massachusetts.

Cohen, J. E.
1968. Alternative derivations of a species-abundance relation. Am. Nat. 102: 165-172.

Conner, R. N., R. G. Hooper, H. S. Crawford and H. S. Mosby.
1975. Woodpecker nesting habitat in cut and uncut woodlands in Virginia. J. Wildl. Manage. 29: 144-150.

DeGarmo, W. R.
1948. Breeding bird population studies, Pochahantas and Randolph Counties, West Virginia. Aud. Field Notes 2: 219-222.

DeGarmo, W. R.
1953. Mature deciduous forest (northern hardwoods). Aud. Field Notes 7: 339.

Eddy, G.
1973. Young northern hardwood forest. Am. Birds 27: 963.

Haapanen, A.
1965. Bird fauna of the Finnish forests in relation to forest succession. I. Ann. Zool. Fenn. 2: 153-196.

Hagar, D. C.
1960. The interrelation of logging, birds, and timber regeneration in the Douglas-fir region of northwestern California. Ecology 41: 116-125.

Harrison, H. C.
1964. Cut-over mature hardwoods 18: 548.

Hensley, M. M., and J. B. Cope.
1951. Further data on removal and repopulation of the breeding birds in a spruce-fir forest community. Auk 68: 483-493.

Hutton, E. E.
1968. Young northern hardwood forest. Aud. Field Notes 22: 661.

James, F. C.
1971. Ordinations of habitat relationships among breeding birds. Wilson Bull. 83: 215-236.

Kilgore, B. M.
1971. Response of breeding bird populations to habitat changes in a Giant Sequoia forest. Am. Midl. Nat. 85: 135-152.

King, C. E.
1964. Relative abundance of species and MacArthur's model. Ecology 45: 716-727.

Laitsh, N.
1968. Cut-over mature hardwoods. Aud. Field Notes 22: 660.

Likens, G. E., F. H. Bormann, R. S. Pierce and W. A. Reiners.
1978. Recovery of a deforested ecosystem. Science 199: 492-496.

Longust-Higgins, M. S.
1971. On the Shannon-Weaver index of diversity, in relation to the distribution of species in bird censuses. Theor. Pop. Biol. 2: 271-289.

MacArthur, R. H.
1957. On the relative abundance of bird species. Proc. Natl. Acad. Sci. 45: 293-295.

MacArthur, R. H.
1960. On the relative abundance of species. Am. Nat. 94: 25-36.

MacArthur, R. H., and J. W. MacArthur.
1961. On bird species diversity. Ecology 42: 594-598.

MacArthur, R. H., H. Recher, and M. Cody.
1966. On the relation between habitat selection and species diversity. Am. Nat. 100: 319-322.

May, R. M.
1975. Patterns of species abundance and diversity. In M. L. Cody and J. M. Diamond (eds.), Ecology and evolution of communities. Belknap, Cambridge, Massachusetts. 543 p.

Nichols, G. E.
1935. The hemlock-white pine-northern hardwood region of eastern North America. Ecology 16: 403-422.

Noon, B. R.
1977. The ecology of an avian ground-foraging guild in eastern Montans forests. Ph.D. thesis, State University of New York at Albany.

Noon, B. R., and K. P. Able.
1978. A comparison of avian community structure in the northern and southern Appalachian Mountains. U.S. Department of Agriculture, Forest Service, General Technical Report SE-14.

Noon, B. R.
1979. The distribution of an avian guild along a temperate elevational gradient; the importance and expression of competition. MS in review.

Pitelka, F. A.
1941. Distribution of breeding birds in relation to major biotic communities. Am. Midl. Nat. 25: 113-137.

Preston, F. W.
1948. The commonness and rarity of species. Ecology 29: 254-283.

Ricklefs, R. E.
1973. Ecology. Chiron press, Newton, Massachusetts. 861 p.

Shugart, H. H., and B. C. Patten.
1972. Niche quantification and the concept of niche pattern. In B.C. Patten (ed.) Systems analysis and simulation in ecology, Vol. II. Academic Press, New York. 607 p.

Smith, W. H.
1973. Cut-over mature hardwoods. Am. Birds 27: 960-961.

Stewart, R. E., and J. W. Aldrich.
1951. Removal and repopulation of breeding birds in a spruce-fir forest community. Auk 68: 471-482.

Webb, W. L., D. F. Behrend, and B. Saisorn.
1977. Effect of logging on songbird populations in a northern hardwood forest. Wildl. Mongr. 55: 6-36.

Whitmore, R. C.
1977. Habitat partitioning in a community of passerine birds. Wilson Bull.: 253-265.

Whittaker, R. H.
1972. Evolution and the measurement of species diversity. Taxon 21: 213-251.

Wiens, J. A.
1969. An approach to the study of ecological relationships among grassland birds. Ornithological Monogr. 8. American Ornithologist's Union.