AVIAN COMMUNITIES: APPROACHES TO DESCRIBING THEIR HABITAT ASSOCIATIONS

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Abstract.--Four approaches are presented which enable wildlife managers to consider many avian species simultaneously in management objectives. The northeastern Minnesota avifauna is used to test each approach. Three approaches included the classification of avian species into structural successional stages, life forms, or their sociological associations. The fourth approach, habitat niche, depicts species response to quantitative habitat variables. The background, methods, data analysis, interpretation, and advantages/disadvantages of each approach are discussed.

INTRODUCTION

Wildlife managers are faced with the difficult task of predicting the impacts of habitat alterations on wildlife species. Historically, their predictions have been based on empirical data or broadly defined "animal communities." During the last ten to fifteen years, however, the ease of assimilating and integrating large quantities of data by computer has broadened the range of techniques available for modeling natural systems. Our objective is to define and describe four management approaches that are currently available to managers for modeling bird populations. We will briefly discuss the background, methods, data analysis, interpretation, and major advantages and disadvantages of each approach. Hopefully, these discussions will provide recommendations for guiding the future direction of non-game bird management.

The four approaches considered in the following pages are:

Successional Stages - a simplistic approach that identifies the bird species associated with forest types along successional gradients.

Life Form Associations - a multi-level approach that identifies assemblages of species with similar reproductive and feeding strategies.

Species Associations - a multivariate approach that identifies species with similar distributions across a range of defined communities.

Habitat Niche Analysis - a multivariate approach that assumes species occupy a mathematically definable habit hyperspace.

Each approach was utilized in an attempt to model songbird populations from northeastern Minnesota. The successional stage and life form models were examined with data from published reports, our own unpublished data, and empirical data. The species association model was modified from the work of Pfannmuller (1979), while the habitat niche model was modified from the work of Niemi (1977).

Natural Setting

The glacially-influenced landforms of northeastern Minnesota (Wright and Watts 1969; Olcott and Siegal 1978) support a rich mosaic of upland and lowland forests (Ohmann and Ream 1971; Grigal and Ohmann 1975; Dean 1971). Throughout the region glacially deposited features such as end moraines, drumlin fields and glacial lake beds dominate the terrain. This topographical diversity is reflected by similar diversity among vegetation cover types. Located in an ecotone between the northern boreal forests and the eastern deciduous forests of North America, the transitional plant communities of northeastern Minnesota have been described by several plant ecologists since Cooper's (1913) original work on Isle Royale.

The original vegetation of northeastern Minnesota consisted of a complex mosaic of red pine (*Pinus resinosa*), jack pine (*Pinus banksiana*), and white pine (*Pinus strobus*) forests,

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black spruce (Picea mariana) and tamarack (Larix laricina) bogs, and forests of pioneer hardwoods. The latter consisted primarily of quaking aspen (Populus tremuloides) and paper birch (Betula papyrifera) and, in the more mature stands, balsam fir (Abies balsamea). Maintained primarily by lightning-induced fires and insect epidemics, these early communities were dominated by disturbance-adapted species (Heinselman 1973; Ahlgren 1975; Grigal and Ohmann 1975). Because disturbance was a frequent natural occurrence prior to man's intervention, a true 'stable climax' may rarely have developed (Heinselman 1973).

Today, logging activities generally replace natural disturbance as the method of stand renewal. Although the glacially-scoured and fire-controlled terrain of northeastern Minnesota was originally quite heterogeneous, man's activities have added to the disturbed and patchy nature of the forest.

The vegetational diversity that is characteristic of this region is an important influence upon the size and diversity of avian populations. The limited number of density estimates that have been reported for breeding populations in the area (Green et al. 1978) are considerably higher than values reported from similar cover types in Canada (Erskine 1977). Minnesota estimates range from approximately 500 pairs/km^2 in recent clearcuts and stunted conifer bogs to 1000-1500 pairs/km^2 in wetland shrub stands. Even the highest breeding densities reported in Canada rarely exceeded 500-600 pairs/km^2. Several factors may be responsible for this discrepancy. First, the method for determining the number of territorial males per plot was more conservative in the studies by Erskine (1977). Second, many study plots in Minnesota were small; ranging from 2 to 5 ha in size, while study plots in Canada were a minimum of 16 ha in size. The influence of plot size upon population estimates has been noted by Oelke (1966). The difference in plot size, however, reflects an important difference between the forests of Canada and Minnesota. Large, continuous stands of homogeneous cover types, common in Canada, are rare in the disturbed forests of northeastern Minnesota.

Minnesota's northeastern forests are also characterized by a rich diversity of breeding species. Unlike the rest of the state where members of the blackbird family (Icteridae) dominate the avifauna, wood warblers (Parulidae) contribute the largest percentage of both individuals and species to the summer avifauna of northeastern Minnesota (Fig. 1). Other important passerine families include the sparrows, grosbeaks and finches (Fringillidae) with approximately 15 breeding species, the tyrant flycatchers (Tyrannidae) with approximately 8 breeding species, and the thrushes (Turdidae) with approximately 5 breeding species (Green and Janssen 1975). Several species found in our northeastern forests are typically classified as boreal species and are quite rare in the continental United States. These include the black-backed three-toed woodpecker, spruce grouse, goshawk and boreal owl (Green and Janssen 1975). The habitat requirements of these species may deserve the special attention of wildlife managers in areas with a boreal element.

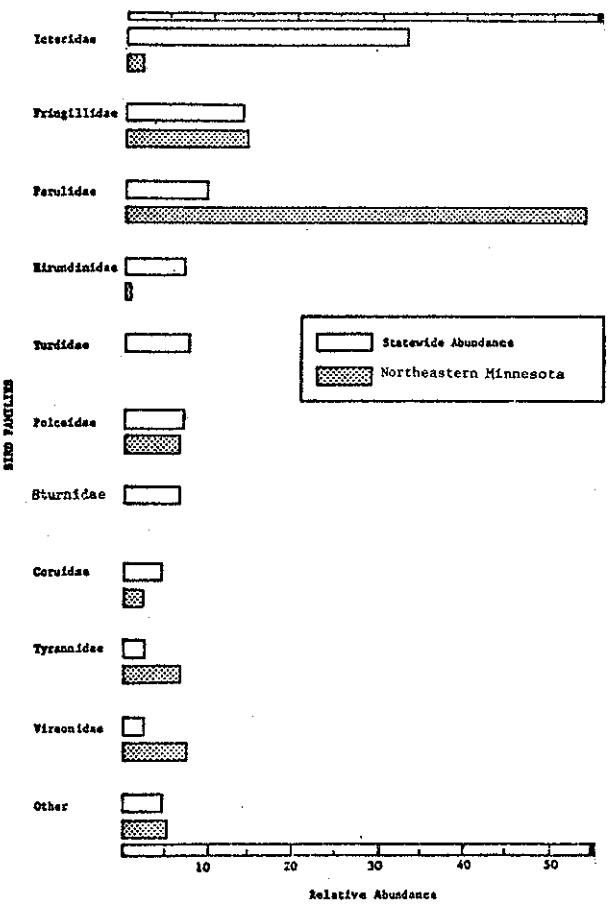


Figure 1.--The relative abundance of major passerine bird families in the State of Minnesota compared with northeastern Minnesota.

Data for this paper were drawn largely from two major studies conducted in northeastern Minnesota. One was conducted in an area of extensive taconite development located east of the mining towns of Hoyt Lakes and Babbitt, Minne-

sota (Pfannmuller 1979). The second study was conducted in an area within and surrounding the 1971 Little Sioux burn, located approximately 20 miles northwest of Ely, Minnesota and near the Island Lake Reservoir, approximately 20 miles north of Duluth, Minnesota (Niemi 1977). Other studies from which data were drawn include Todd and Doran (1976), Green et al. (1978), Bergstedt and Neimi (1974), and Green (1971a).

Bird Species and Data Base

Because more than 250 species of birds are known to occur in northeastern Minnesota, we felt it was practical to limit the number of species considered in this paper. We defined our data base by including only terrestrial species that are summer residents. Terrestrial species were arbitrarily defined as species found in communities ranging from the cattail-sedge marshes (where standing vegetation is present all year) to the drier upland forests. Thus, we excluded species found in the emergent aquatic marshes (where vegetation is present throughout much of the year) and open water areas. Species were further excluded if they could be classified into one of the following four categories:

1. Man-adapted species found commonly near settlements, towns, and cities;
2. Species with specific habitat or niche requirements;
3. Species in which we lack sufficient data; and/or
4. Species in northeastern Minnesota that are on the limit of their breeding range.

The species data base and the classification criteria are shown in table 1.

The concept of excluding species may seem contradictory to multiple species management. However, limiting the number of species in management models is appropriate if the limitations are based on sound rationale. For example, should species found in association with man's settlements be managed in forest ecosystems? Many of these species are much more abundant today than they were in pre-settlement times (Graber and Graber 1963). Species with specific habitat requirements may require special management strategies, especially if those requirements are limited in their availability. Species for which we are lacking data are particularly important. These species should be given research priority in order to determine their habitat requirements and to determine if their population levels are stable or declining. Finally, managing species on the limits of their range may not benefit the species and their inclusion could negatively influence species indigenous to an area.

One of the primary reasons for defining a species base was to focus attention on species that were particularly dependent on vegetational communities in northeastern Minnesota. Since the data base was established after both the habitat niche and species association analyses were completed, some species that were excluded from the data base, may be included in subsequent tables and figures.

SUCCESSIONAL STAGE APPROACH

Background

The general concept that birds select habitats based on the vegetation structure or habitat physiognomy has been expressed by several researchers (e.g., Lack 1933; Odum 1950; Svardson 1949; Hinden 1965; James 1971). Since succession has been described as an orderly process involving changes in the "structure" of habitats (Odum 1959), it seems natural to classify bird species into communities that are based on the structural categories found along successional gradients. In light of the relationship between bird species and successional stages, it is surprising to note that there are few systematic inventories of the birds inhabiting various stages. Erskine (1977), after discussing the birds of various forest types, comments as follows, "the need for systematic data on birds of successional and edge habitats could hardly be made more obvious." Nevertheless, some pertinent data are available in Kendeigh (1945), Johnston and Odum (1956), Martin (1960), Haapanen (1965), Shugart and James (1973), Holt (1974), and Erskine (1977).

Method

We defined a series of 11 forest types which are the predominant cover types found in northeastern Minnesota. They are described as follows:

Grassland-forbaceous - An open upland area that lacks trees and shrubs. The flora is composed of grasses (Gramineae spp.) and a wide assortment of "weeds" standing up to 1 m high. The cover type is limited and occurs only in early clearcuts, intensely burned areas, or settlements.

Table 1 .--Bird species data base for northeastern Minnesota. Species list includes those considered to be summer residents excluding waterbirds such as loons, grebes, ducks, coot, gulls, and terns as adapted from the annotated list in Green et al. (1978).

SPECIES	CLASSIFICATION CRITERIA 1/ INCLUDED IN ANALYSIS	URBAN ADAPTED	SPECIAL NEEDS	LACK OF DATA	RANGE LIMIT
Double-crested Cormorant			X		
Great Blue Heron			X		
American Bittern	X				
Turkey Vulture				X	
Goshawk				X	
Cooper's Hawk				X	X
Sharp-shinned Hawk				X	
Red-tailed Hawk	X				
Broad-winged Hawk	X				
Bald Eagle			X		
Marsh Hawk	X				
Osprey			X		
Merlin				X	
American Kestrel	X				
Spruce Grouse	X				
Ruffed Grouse	X				
Sandhill Crane				X	
Virginia Rail					X
Sora	X				
Killdeer		X			
American Woodcock	X				
Common Snipe	X				
Upland Plover					X
Spotted Sandpiper			X		
Mourning Dove		X			X
Black-billed Cuckoo					X
Great Horned Owl				X	
Barred Owl				X	
Long-eared Owl				X	
Short-eared Owl				X	
Common Nighthawk		X			
Chimney Swift		X			
Ruby-throated Hummingbird			X		
Belted Kingfisher			X		
Common Flicker	X				
Pileated Woodpecker	X				
Red-headed Woodpecker					X
Yellow-bellied Sapsucker	X				
Hairy Woodpecker	X				
Saw-whet Owl				X	
Whip-poor-will					X
Downy Woodpecker	X				
Black-backed 3-toed Wood				X	
Eastern Kingbird	X				
Great-crested Flycatcher					X
Eastern Phoebe			X		
Yellow-bellied Flycatcher	X				
Alder Flycatcher	X				
Least Flycatcher	X				
Eastern Wood Pewee	X				
Olive-sided Flycatcher	X				
Tree Swallow	X				
Bank Swallow			X		
Rough-winged Swallow			X		

Table 1.--Continued

SPECIES	INCLUDED	URBAN ADAPTED	SPECIAL NEEDS	LACK OF DATA	RANGE LIMIT
Barn Swallow		X	X		
Cliff Swallow		X	X		
Purple Martin		X			
Gray Jay	X				
Blue Jay		X			
Common Raven			X	X	
Common Crow		X			
Black-capped Chickadee	X				
Boreal Chickadee	X				
White-breasted Nuthatch					X
Red-breasted Nuthatch	X				
Brown Creeper			X	X	
House Wren		X			
Winter Wren				X	
Short-billed Marsh Wren	X				
Catbird	X				
Brown Thrasher	X				
Robin		X			
Wood Thrush					X
Hermit Thrush	X				
Swainson's Thrush	X				
Veery	X				
Eastern Bluebird			X		
Golden-crowned Kinglet	X				
Ruby-crowned Kinglet	X				
Cedar Waxwing		X			
Starling		X			
Solitary Vireo	X				
Red-eyed Vireo	X				
Philadelphia Vireo				X	
Warbling Vireo		X			
Black & White Warbler	X				
Golden-winged Warbler					X
Tennessee Warbler				X	
Nashville Warbler	X				
Parula Warbler	X				
Yellow Warbler		X			
Magnolia Warbler	X				
Cape May Warbler	X				
Yellow-rumped Warbler	X				
Blk-throated Green Warbler	X				
Blackburnian Warbler	X				
Chestnut-sided Warbler	X				
Bay-breasted Warbler	X				
Pine Warbler				X	
Palm Warbler				X	
Ovenbird	X				
Northern Waterthrush			X		
Connecticut Warbler	X				
Mourning Warbler	X				
Yellowthroat	X				
Wilson's Warbler				X	
Canada Warbler	X				
American Redstart	X				
House Sparrow		X			
Bobolink		X			
Eastern Meadowlark		X			

Table 1.--Continued

SPECIES	INCLUDED	URBAN ADAPTED	SPECIAL NEEDS	LACK OF DATA	RANGE LIMIT
Western Meadowlark		X			
Yellow-headed Blackbird					X
Redwinged Blackbird		X			
Baltimore Oriole		X			X
Rusty Blackbird				X	X
Brewers Blackbird		X			
Common Grackle		X			
Brown-headed Cowbird		X			
Scarlet Tanager	X				
Rose-breasted Grosbeak	X				
Evening Grosbeak	X				
Purple Finch	X				
Pine Siskin				X	
American Goldfinch	X				
Red Crossbill				X	
White-winged Crossbill				X	
Savannah Sparrow		X			
Vesper Sparrow		X			
Dark-eyed Junco	X				
Chipping Sparrow	X				
Clay-colored Sparrow					X
White-throated Sparrow	X				
Lincoln's Sparrow	X				
Swamp Sparrow	X				
Song Sparrow		X			
TOTAL SPECIES					

1/ See text for explanation.

Cattail-sedge marsh - An open, wet area that lacks trees and shrubs. The flora is composed primarily of cattails (Typhaceae) and sedges (Cyperaceae) standing up to 2 m high. The cover type has a limited distribution in northeastern Minnesota.

Heath muskeg bog - An open lowland area that lacks trees; shrubs are rarely present. The flora is composed primarily of heath species (Ericaceae) standing up to 1 m high. The cover type is common in northeastern Minnesota.

Young open shrub - An upland shrub with scattered dead and/or live trees. Structurally, the habitat consists of a dense shrub layer, up to 3 m high, and a well-developed herbaceous layer. The flora may be composed of deciduous saplings such as quaking aspen, paper birch, or shrub species such as hazel (Corylus cornuta) or juneberry (Amelanchier spp.). The cover type is very common and is present within 3 to 12 years following logging or forest fire.

Wetland shrub - A lowland shrub area with scattered live and/or dead trees. Structurally the habitat consists of a dense shrub layer, approximately 3 m high and a variable herbaceous layer. The dominant floral species are alder (Alnus rugosa) and willow (Salix spp.). The cover type is quite common.

Young deciduous - An upland, medium-aged, tree stand with variable shrub and herbaceous layers. Structurally, the vegetation consists of a dense, deciduous tree layer, ranging from 3 to 9 m high. The typical tree species are quaking aspen and paper birch. The cover type is common 12 to 30 years following forest fire or logging.

Young coniferous - An upland, medium-aged, tree stand with sparse shrub and herbaceous layers. Structurally the vegetation consists of a dense coniferous tree layer, ranging from 3 to 9 m high. The typical tree species may be jack pine, red pine, white pine, white spruce (Picea glauca) or balsam fir. The cover type is common 12 to 30 years following forest fire or logging.

Semi-open conifer lowland - A stand whose structure is intermediate between that of the heath muskeg bog and the mature lowland conifer bog. Structurally the vegetation consists of a dense, low-lying heath layer, up to 1 m high, and a low to moderately dense tree layer up to 6 m high. The tree species are usually black spruce or tamarack. The cover type is fairly common.

Mature deciduous upland - A closed-canopy, deciduous upland stand with a moderate to dense tree layer, ranging from 9 to 20 m high, and a variable shrub and herbaceous layer. The tree species are usually quaking aspen or paper birch, although northern hardwoods (e.g., maple and basswood) may predominate near Lake Superior. The cover type is very common.

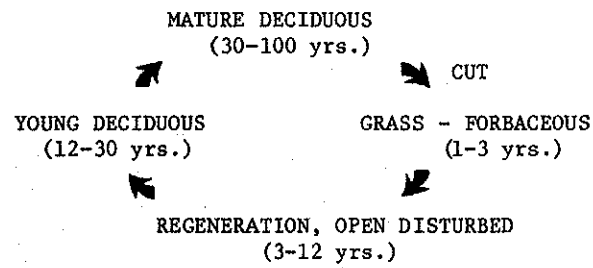
Mature coniferous upland - A closed-canopy, coniferous upland stand with a moderate to dense tree layer, ranging from 9 to 20 m high, and a sparse shrub and herbaceous layer. The tree species may include red pine, jack pine, white pine, white spruce, or balsam fir. The cover type is common and is often an actively-managed community.

Mature conifer lowland - A closed-canopy, coniferous lowland stand with a moderate to dense tree layer, up to 20 m high, a sparse shrub layer, and a dense herbaceous layer (comprised of moss and heath species). The tree species are usually black spruce or tamarack or occasionally white cedar (Thula occidentalis). The cover type is very common.

Bird species were then classified into one or more of these 11 cover types, depending on their use of each habitat for either reproduction and/or feeding. Data were extracted from a variety of sources including Pfannmuller (1979), Green and Niemi (1977), Todd and Doran (1976), Bergstedt and Niemi (1974), Green (1971a), field experience, or consultation with local experts.

Data Analysis and Interpretation

The results of the classification are shown in Table 2. The table provides a framework for modeling the habitat distributions of bird species in northeastern Minnesota. Using these data, the manager can predict some of the impacts of habitat alteration. For example, the following successional sequence would result if a mature deciduous forest were cut:



The rotation of species through this deciduous sere could be approximated from the information in Table 2.

As shown in Table 2, there is a general pattern of increasing number of species from the grass-forb type to the mature deciduous upland. Since the grass-forb and cattail-sedge types are the least complex (essentially one-layered) and the mature deciduous upland is the most complex (multi-layered), this increase generally reflects the complexity of the vegetation. The young open shrub and wetland shrub types are intermediate in structural complexity and the number of species generally associated with these types are also intermediate. However, if the number of dead or live trees is substantial in these types, then the numbers of bird species and individuals can also be quite high.

Advantages

1. The approach provides a baseline to build more sophisticated and realistic models for predicting the impacts of forest management.

2. The successional types are easily interpreted by most users.

3. The model permits the manager to make broad generalizations regarding the impact of forest management on non-game birds.

Table 2.--Life form association, successional stages used for reproduction (X), feeding (O), and adaptability index for the bird species data base defined in Table 1.

SPECIES	Life form 1/	Grass-Forb	Cattail-Sedge	Muskeg Bog	Young Open Shrub 2/	Young Deciduous	Young Coniferous	Mature (upland) Deciduous	Mature Coniferous Upland	Semi-Open Conifer Lowland	Mature Conifer Lowland	Wetland Shrub	ADAPTABILITY 3/ Total X	Total O	Index
American Bittern	3		X O	X O									2	2	3
Red-tailed Hawk	9	O			X O			X					2	2	3
Broad-winged Hawk	11	O			O			X O					1	3	2.5
Marsh Hawk	5	O	X O	X O	O								2	4	4
American Kestrel	14	O			X O								1	2	2
Spruce Grouse	10			X					X O	X	X O		4	2	5
Ruffed Grouse	5				X O	X O		X O					3	3	4.5
Sora	3		X O									X O	2	2	3
American Woodcock	3,5	X	O		X	X	X					X O	5	2	6
Common Snipe	3	X	X O	X O								X O	4	3	5.5
Common Flicker	13	O			X O			X					2	2	3
Pileated Woodpecker	13							X O					1	1	1.5
Yellow-bellied Sapsucker	13							X O	X O				2	2	3
Hairy Woodpecker					X O			X O					2	2	3
Downy Woodpecker	13				X O	X O		X O				O	3	3	4.5
Eastern Kingbird	8,11	X O			X O							X O	3	3	4.5
Yellow-bellied Flycatcher	6								X O	X O	X O		3	3	4.5
Alder Flycatcher	8				X O							X O	2	2	3
Least Flycatcher	8,11					X O		X O	X O				3	3	4.5
Eastern Wood Pewee	8,11							X O	X O				2	3	3
Olive-sided Flycatcher	8,11				X O					X O		X O	3	3	4.5
Tree Swallow	14	X O		X O	X O					X O			4	4	6
Gray Jay	10								X O	X O	X O		3	3	4.5
Black-capped Chickadee	14					X O	X O	X O					3	3	4.5
Boreal Chickadee	14								X O	X O	X O		3	3	4.5
Red-breasted Nuthatch	14							X O	X O		X O		3	3	4.5
Short-billed Marsh Wren	3,6,8	X O	X O	X O									3	3	4.5
Catbird	5,6,7,8				X O							X O	2	2	3
Brown Thrasher	5,6,7,8				X O							X O	2	2	3
Hermit Thrush	5					X O	X O	X O	X O	X O	X O		6	6	9
Swainson's Thrush	7,8								X O	X O	X O		3	3	4.5
Veery	5,6				X O	X O		X O					3	3	4.5
Ruby-crowned Kinglet	10							X O		X O			2	2	3
Golden-crowned Kinglet	10							X O		X O			2	2	3
Solitary Vireo	8,11						X O	X O		X O			3	3	4.5
Red-eyed Vireo					X O	X O		X O					3	3	4.5
Black and White Warbler	6				X O	X O		X O	X O	X O		X O	6	6	9

Table 2.--continued

SPECIES	Life Form	Grass-Forb	Cattail-Sedge		Muskeg Bog		Young Open Shrub		Young Deciduous		Young Coniferous		Mature Deciduous Upland		Mature Coniferous Upland		Semi-open Coniferous Lowland		Mature Conifer Lowland		Wetland Shrub		ADAPTABILITY Total X	Total O	Index
Nashville Warbler	6										X	O	X	O 4/	X	O	X	O	X	O			5	5	7.5
Parula Warbler	11												X	O 4/	X	O			X	O			3	3	4.5
Magnolia Warbler	8,10,11										X	O	X	O 4/					X	O			3	3	4.5
Cape May Warbler	10																X	O	X	O			2	2	3
Yellow-rumped Warbler	10										X	O	X	O 4/	X	O	X	O	X	O			5	5	7.5
Black-throated Green Warbler	8,10,11												X	O 4/									1	1	1.5
Blackburnian Warbler	10														X	O			X	O			1	1	1.5
Chestnut-sided Warbler	8						X	O	X	O	X	O	X	O							X	O	5	5	7.5
Bay-breasted Warbler	10,11																X	O	X	O			2	2	3
Ovenbird	5								X	O	X	O	X	O	X	O							4	4	6
Connecticut Warbler	6														X	O	X	O	X	O			3	3	4.5
Mourning Warbler	6,8						X	O	X	O	X	O											3	3	4.5
Yellowthroat	3,6,8		X	O	X	O											X	O			X	O	4	4	6
Canada Warbler	6,8								X	O			X	O	X	O							3	3	4.5
American Redstart	8,9,11								X	O			X	O							X	O	3	3	4.5
American Goldfinch	5,6,7,8	X	O				X	O													X	O	3	3	4.5
Purple Finch	10,11														X	O							1	1	1.5
Scarlet Tanager	9,11												X	O									1	1	1.5
Evening Grosbeak	10,11						X	O			X	O			X	O			X	O			4	4	6
Rose-breasted Grosbeak	8,9,11								X	O			X	O									2	2	3
Dark-eyed Junco	5										X	O			X	O	X	O	X	O			4	4	6
Chipping Sparrow	7,8,10,11										X	O			X	O	X	O	X	O			4	4	6
White-throated Sparrow	5,6								X	O	X	O	X	O	X	O	X	O	X	O	X	O	8	8	12
Lincoln's Sparrow	5,6						X	O									X	O	X	O			3	3	4.5
Swamp Sparrow	3,6,8		X	O	X	O											X	O			X	O	4	4	6
Total species feeding		9		8		8		23		16		12		27		25		17		21		18			
Total species reproducing		6		7		9		22		17		13		29		25		18		21		17			

1/ Life form categories as defined in table 3.
2/ Snags or live trees are necessary for some species classified in this type.
3/ Index calculated by [2 (Reproduction stages) + Feeding stages] / 2.
4/ Species generally requires some coniferous component in this habitat type.

Disadvantages

1. Since systematic data is often lacking to quantify the species population levels within each successional range and to pinpoint the range of habitats occupied by each species, we were forced to make subjective judgements regarding a species classification. Such judgements are always prone to individual bias.

2. The approach also forces a subjective judgement of habitat classification when habitats themselves are difficult to classify. Obviously one may define more than 11 forest types in northeastern Minnesota. Many habitats, for example, are mixed associations resulting from such events as forest fire, logging, insect infestation, or natural disasters. Few forest stands are homogeneous cover types.

3. Realistically, we believe the successional approach is too simplistic and does not account for many factors that are important to the distribution of individual species.

LIFE FORM APPROACH

Background

The life form approach to wildlife management was recently introduced by wildlife biologists and foresters working in the Blue Mountains of northeastern Oregon and Washington (Thomas et al. 1975, Thomas et al. 1976). The approach was an attempt to develop a management model broad enough to be applicable to all vertebrate species and yet detailed enough to consider species-specific management issues. An additional criterion focused on the ability of the model to relate directly to present silvicultural practices. Because demands for timber production currently guide nearly all facets of forest management, it was important for wildlife managers to incorporate forestry concepts in their management models. Together these considerations led to the development of the life form approach to species management.

Similar to the guild concept used by avian ecologists (Salt 1957; Cody 1974), the life form is defined as an assemblage of species with similar reproductive and feeding strategies. For example, all birds that nest in shrubs and feed on the ground would be considered as belonging to one life form. The utility of the approach is based on the premise that species with similar habitat requirements will generally respond in a similar manner to habitat alterations. If shrubs were removed from a forest stand one would no longer expect to find shrub nesting species.

Alterations to the habitat are interpreted as changes that will either advance or retard a plant community's rate of succession. Logging, for example, will revert an upland stand back to a young herb-dominated community. A life form's response to such alterations represents the average response of all species within the particular life form category. A species response, in turn, is determined by examining its utilization of the major habitat types and successional stages in the region of interest. By summarizing the response of different species, the life form approach permits the wildlife manager and forester to manage for many species simultaneously, rather than the cumbersome task of initially having to consider each species separately. If needed, the data are also available for predicting the response of individual species.

Thomas and his co-workers considered several other factors in their life form model, such as a species use of special and/or unique habitats. A vulnerability index was also calculated to determine a species (or life form's) degree of adaptability or vulnerability to habitat manipulation.

Methods

We used the sixteen life form categories that Thomas et al. (1976) defined for their work in the Blue Mountains (table 3). The category or categories to which each bird species was assigned is shown in Table 2.

Each species utilization of plant communities in northeastern Minnesota was also determined (Table 2). Unlike the model of Thomas et al. (1975) which dealt separately with a species use of timber types and with its use of successional stages, we attempted to combine these responses by considering the eleven structural communities we previously defined. One reason we eliminated this separation was due to the small age spread for upland habitats in northeastern Minnesota and the corresponding lack of bird data across such fine categories.

Table 3. Life Form Definitions.[1/]

Life Form 1:	Reproduces in the water and feeds in the water.
Life Form 2:	Reproduces in the water and feeds on the ground, in bushes or in trees.
Life Form 3:	Reproduces on the ground around water, feeds on the ground, in bushes or in water.
Life Form 4:	Reproduces on or in cliffs, caves, rim and talus slopes, feeds on the ground or in the air.
Life Form 5:	Reproduces on the ground, without specific water, cliff, rim or talus association, and feeds on the ground.
Life Form 6:	Reproduces on the ground, feeds in bushes and trees or in the air.
Life Form 7:	Nests in bushes, feeds on the ground, in water and in the air.
Life Form 8:	Nests in bushes, feeds in trees and bushes or in the air.
Life Form 9:	Nests primarily in deciduous trees, feeds in trees and bushes.
Life Form 10:	Nests primarily in conifers, feeds in trees and bushes, or in the air.
Life Form 11:	Nests in conifers or deciduous trees and feeds in trees or bushes, on the ground or in the air.
Life Form 12:	Nests on very thick branches, feeds on the ground or in water.
Life Form 13:	Excavates own hole, feeds in trees, brush or air.
Life Form 14:	Nests in a hole made by another species or in a naturally occurring hole-feeds on the ground, in water or in the air.

1/ From Thomas et al. (1976)

Table 3. (cont.)

Life Form 15:	Reproduces in a burrow (underground) and feeds on or under the ground.
Life Form 16:	Reproduces in a burrow (underground) and feeds in the air or in the water.

Stands older than 60-70 years are scarce. In addition, because both upland and lowland habitats were considered in our model, we did not feel that the age boundaries nor the response of bird species for successional stages in uplands were necessarily applicable to the successional stages in lowlands.

With the bird data for each of the eleven habitats, we calculated a vulnerability index for each species (Table 2). As specified by Thomas et al. (1975), the index value was calculated by doubling the number of reproductive habitats the species uses, adding it to the number of feeding habitats used and dividing the sum by two. Although a species orientation to unique and or special habitats (e.g., snags, cliffs, etc.) may be included in the model, we did not incorporate such an analysis in this investigation.

Data Analysis and Interpretation

A major objective of the life form approach is to predict the response of vertebrates with similar habitat requirements to various habitat alterations. To illustrate, we examined life form 13 (species that excavate their own nesting cavities in a tree and feed either on the ground, in bushes, in trees or in the air). In northeastern Minnesota we identified eight species in life form 13 (Table 2). In addition to the woodpecker species, we have also included the boreal and black-capped chickadees. Although these chickadees may utilize either nesting cavities constructed by other species or natural cavities, they may also excavate their own (Harrison 1975). Based on the information in Table 2, the distribution of life form 13 in our eleven structural communities is shown in Figure 2. The figure provides the wildlife manager and forester with two types of information: 1) presence/absence information regarding the distribution of the life form within the communities; and 2) a means for predicting the impact of various habitat alterations. For example, the mature deciduous community satisfies the habitat requirements for a larger proportion of species in life form 13 than any other community. If a 50-year-old aspen stand were clearcut, one

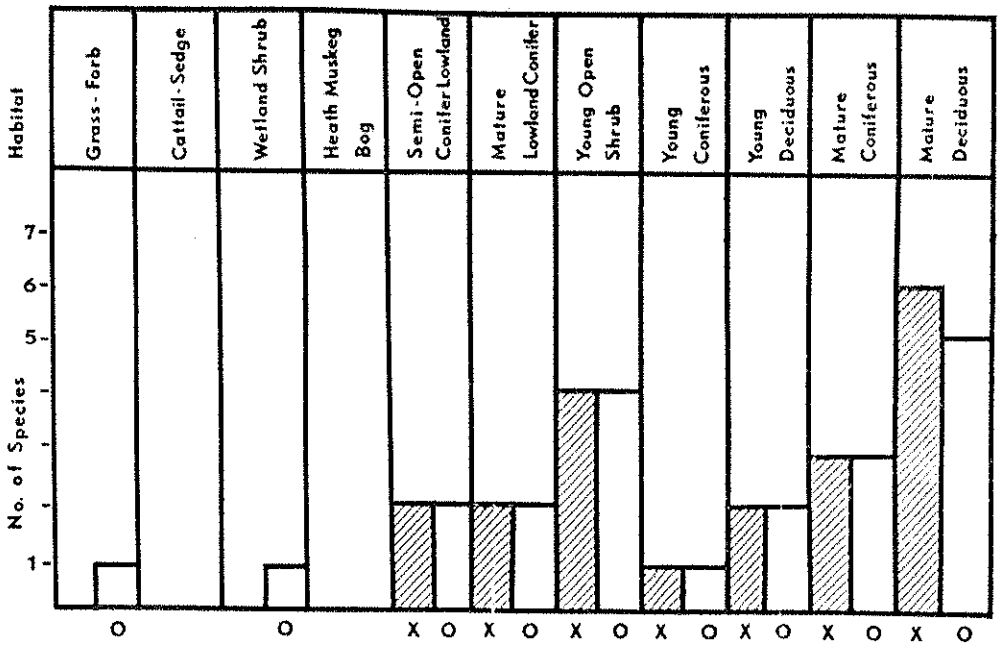


Figure 2.-- Distribution of Life Form 13 among the major habitats in northeastern Minnesota.
x= nesting 0=feeding

would predict a small decrease in the number of self-excavating cavity nesters, as long as some snags were left standing. If snags were removed, then the impact to cavity nesting species would be much greater.

Consideration of life forms provides helpful generalizations, but it is still important to consider the response of individual species. Information regarding species in life form 13 has been summarized in Table 4. An important question to consider when contemplating management alternatives is, 'Are some species within the life form more vulnerable to habitat alterations than other species?' Using the previous example, are there species within life form 13 that are so narrowly confined to the mature deciduous habitat that its loss would be detrimental to the species population in northeastern Minnesota? Our table indicates that the loss of the aspen stand might be more detrimental to the pileated woodpecker than to other species within the life form. Another important consideration is the availability of the particular habitat with regards to both time and space. Loss of a rare habitat is obviously more likely to be detrimental to a vulnerable species than the loss of an abundant habitat.

Advantages

1. The life form approach integrates the information available for each species into the framework of a single model. It's value in establishing a data base for all vertebrate species should not be overlooked.

2. Condensing species information into a "workable" number of life form categories permits the manager to consider many taxa simultaneously.

3. The life form approach is flexible enough to allow for the incorporation of new data.

4. The approach generates a "rough" index of a species (and life forms) vulnerability to habitat manipulation. Although the index is a valuable indicator for predicting species composition changes on a broad scale, neither the index, nor the entire management approach, were intended as more than initial steps when dealing with specific management problems.

Species / Habitat	Grass-Forb	Cattail-Sedge	Wetland Shrub	Heath Muskeg	Semi-open Conifer	Mature Lowland Conifer	Young open Shrub	Young Coniferous	Young Deciduous	Mature Coniferous Upland	Mature Deciduous Upland	Adaptability-Vulnerability
Common Flicker	o				x o						o	3
Pileated Woodpecker											x o	1.5
Yellow-bellied Sapsucker										x o	x o	3
Hairy Woodpecker							x o				x o	3
Downy Woodpecker							x o		x o		x o	4.5
Black-backed 3-toed Woodpecker					x o	x o	x o			x o		6.0
Black-capped Chickadee								x o	x o		x o	4.5
Boreal Chickadee					x o	x o					x o	4.5

Table 4. The distribution of species in Life Form 13 among the major habitats in northeastern Minnesota.

Disadvantages

1. The original classification of structural communities is subjective rather than objective. In addition, the biologist's decision concerning species utilization of a structural community for feeding or reproduction is also subjective. The manager must make a judgement which is subject to bias and which is based generally on a limited amount of available information.

2. When a species ecology is inadequately known, its' adaptability/vulnerability may be inaccurately judged - another reason why the model is intended only as an initial approach to impact analysis. For example, in our earlier illustration, the model predicts that the black-backed three-toed woodpecker is more adaptable to habitat alterations than other species in life form 13 - a prediction many ornithologists might dispute.

3. Many species may be classified in more than one life form category. In many cases, this probably reflects the insufficient data that is available to the ecologist, particularly with respect to feeding habits. On the other hand, the adaptability of some species is reflected by classifying them in more than one category.

MULTIVARIATE APPROACHES

One of the principal criticisms of the two approaches we presented above is their reliance on subjective judgements. Although these judgements were based on field experience and familiarity with the literature, a need clearly exists for more objective approaches to modeling natural systems. Such concern has prompted avian ecologists (e.g., James 1971; Whitmore 1977; Smith 1977) to investigate various multivariate approaches to avian community analysis. Multivariate techniques were implemented in the species association approach described below in order to analyze the relationships among species and in the habitat - niche analysis to analyze the relationships between species and their environment.

SPECIES ASSOCIATIONS AND AVIAN COMMUNITIES

Background

The following approach to community analysis implements multivariate techniques to classify avian communities and to delineate species associations within those communities. As we stated earlier, the classification of avian communities has, historically, been rather subjective (e.g., Kendeigh 1945; Martin 1960). Most avian ecologists have assumed that the "boundaries" of avian communities directly reflect the "boundaries" of plant communities. Though the plant community framework is satisfactory for a preliminary assessment, the wildlife manager should not assume that the same boundaries always apply to avian communities. Our intent was to derive a classification scheme for bird communities with the use of parameters that quantified the bird species composition rather than the plant species composition. Compared with the numerous studies using rigorous mathematical approaches to plant community classification (e.g., Grigal and Ohmann 1975; Nobles et al. 1977), few studies have dealt with such an approach to avian community classification.

The second objective of the association approach was to delineate species associations; a species association being a group of species that are distributed in a similar manner among avian communities. Few species, either plant or animal, are restricted in their occurrence to one community. Several species may often occur together in different communities because they require a similar environmental feature. Our objective was to characterize the bird species associations in northeastern Minnesota and to illustrate their occurrence and abundance within the different avian communities.

We chose cluster analysis (Boesch 1977; Pielou 1977) as the mathematical technique for defining avian communities and associations. The technique operates by combining sets of data, or entities, on the basis of their overall similarity. In this example the 'sets of data' corresponded to the set of avian population censuses for all study plots, while the 'entities' corresponded to each of the individual bird species. The degree of similarity among plot censuses, or among the distribution of individual species, was mathematically interpreted as the distance between sample points. The clustering process may be graphically represented by a dendogram which illustrates the hierarchial arrangement of the data sets or entities (e.g., see Cody 1974).

Cluster analysis operates under the assumption that the sample units naturally fall into discrete and recognizable communities. The validity of this assumption however, has been challenged by ecologists who allege that discrete discontinuities between communities are not realistic (e.g., Gleason 1926; Curtis 1959). Those ecologists who maintain that species are geographically distributed independently of one another favor the use of ordination techniques that graphically portray the relationships among sample stands. Ordination arranges the stands within a uni-dimensional coordinate frame so that the relative continuity or discontinuity in their distribution is illustrated. The ordination technique commonly used for this purpose is discriminant analysis. Discriminant analysis operates by defining linear combinations of the components of each stand (e.g., species) so that, within a coordinate frame, the distances between communities are maximized. In avian ecology, discriminant analysis has recently been used by several authors to graphically illustrate the distribution of individual species (James 1971; Whitmore 1977; Smith 1977; Thomas et al. 1977). We have implemented discriminant analysis to portray the degree of similarity/dissimilarity among the species composition of the different study plots.

Methods

The procedures for implementing cluster analysis were applied to avian census data collected in 43 forest stands. The sample stands were selected to represent the portions of all major cover types in northeastern Minnesota. Territory mapping (Williams 1936) was selected for collecting census data from each plot during the 1977 summer season. Although we will briefly review our analysis procedures in the following paragraphs, Pfannmuller (1979) should be consulted for further details.

In order to define both the avian communities and species associations that characterize northeastern Minnesota, we needed to implement the technique of cluster analysis in two different ways. The first, referred to as normal analysis, (Boesch 1977) was used to classify communities. Normal analysis grouped together the 43 sample stands on the basis of their overall similarity in bird species composition. For example, we would predict that the bird censuses from two mature jack pine stands would be recognized as representing one avian community. Discriminant analysis was also

applied to graphically portray the 'distance' or similarity in the avian composition of the sample stands. The second type of cluster analysis, referred to as inverse analysis (Boesch 1977), was used to define species associations. Inverse analysis grouped together bird species that showed similar distribution among the 43 sample stands. For example, we might predict that the red-eyed vireo and ovenbird, species that are both commonly observed in mature upland forest stands, would be members of one species association.

Computer programs designed to conduct cluster analysis were written by E.J. Cushing of the University of Minnesota and by G. Burnett, of the State of Minnesota (State Planning, Regional Copper-Nickel Study). The input variables for the program, and the distance equations for computing similarity, were systematically altered by the authors. Further details can be found in Pfannmuller (1979).

Data Analysis and Interpretation

By varying both the nature of the input variables and the distance equations, several dendrograms were generated with normal cluster analysis; one such example is shown in Figure 3. The figure clearly suggests an appropriate scheme for classification. For example, the bird species composition in eight of the eleven deciduous upland plots was recognized as similar and they were distinct from the species composition on the remaining thirty-five sample plots. It is appropriate at this point to advance a warning - the ecologist should not interpret the classification suggested by any one dendrogram as definitive. Rather, all dendrograms generated from normal analysis should be analyzed before proposing a reasonable classification (which may not directly reflect any one particular dendrogram). Based on the 1977 breeding bird data, nine avian communities were delineated for northeastern Minnesota (see Fig. 5). A graphical illustration of the similarity of their species composition is shown in Figure 4. Several dendrograms were also generated from inverse cluster analysis. Although we have not included any of the dendrograms here, the final classification of species associations is detailed in Table 5. In addition, the relative abundance of the species associations in each avian community is illustrated in Figure 5.

The delineation of avian communities with the use of dendrograms suggests structural features of the vegetation that are

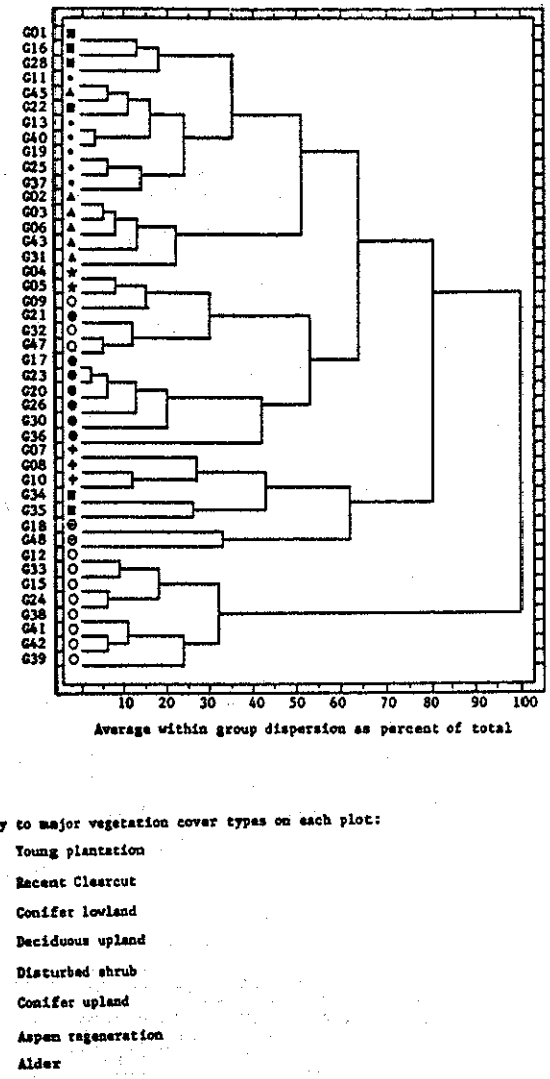


Figure 3.--Dendrogram showing the hierarchial relationships among bird communities of 43 stands based on the density of 56 breeding bird species.

important to birds in northeastern Minnesota. For example, the avian composition of mature deciduous uplands was recognized as distinctly different from the avian composition of mature coniferous uplands. Therefore, a major structural distinction important to many species in their selection of a breeding habitat was the distinction between deciduous and coniferous vegetation. However, the distinctions between different deciduous cover types or different coniferous cover types were apparently not important to birds. The species composition of mature red pine stands, for example, were not recognized as faunistically distinct from the species composition of mature jack pine stands. The community in Figure 4 also

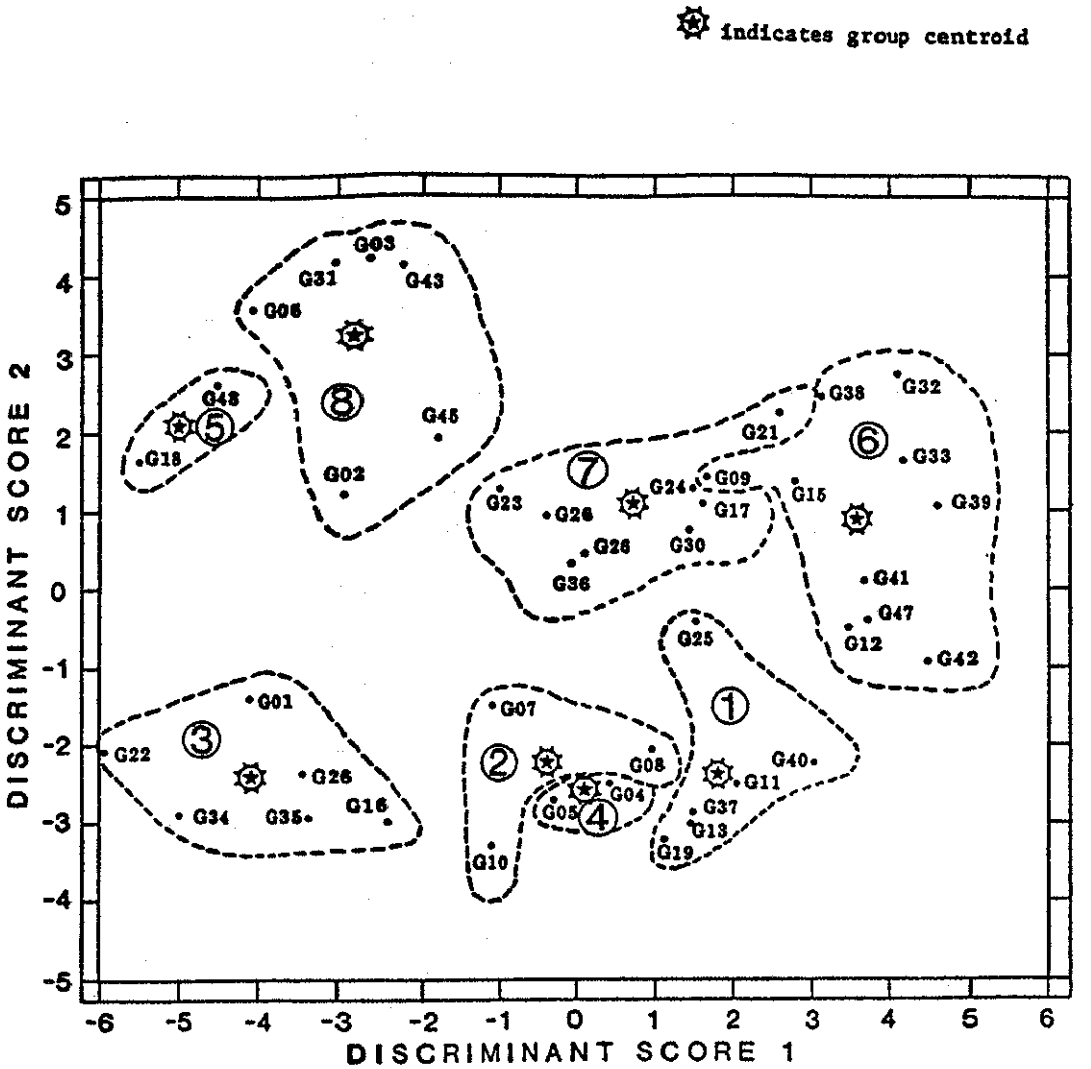


Figure 4.--Spatial relationships of bird communities on 43 of the 1977 sites when plotted using 2 discriminant functions.

provides the wildlife manager with important information. The ordination graphically portrays the degree of community "distinctness." The greater the distance between the centers of each cluster, the larger the difference in species composition.

By examining the relative abundance of the species associations within the bird community we can also generate information regarding the relative "distinctness" of the communities. The alder bird community, for example, is unique in it's abundance of species belonging to the gray catbird/swamp sparrow species association. In addition, we can see that members of this association have a narrower tolerance of different habitats than members of the mourning warbler/chestnut-sided warbler association. As with any model of a natural system, the larger the number of sample stands that are included in the original data base, the stronger are the predictions that the model can make.

Advantages

1. The approach recognizes avian communities on the basis of avian attributes rather than forcing avian community boundaries into the boundaries of vegetation communities. It thereby demonstrates similarities among avian communities that may not be intuitively obvious from a vegetation analysis alone.

Table 5. -- Species composition of the 9 major bird species associations in northeastern Minnesota.[1/]

I. Mourning Warbler/Chestnut-sided Warbler	II. Red-eyed Vireo/ Ovenbird	III. Common Flicker/Brown-headed Cowbird
Blue Jay Robin Cedar Waxwing Black-and-white Warbler Nashville Warbler Magnolia Warbler Chestnut-sided Warbler Mourning Warbler	Yellow-bellied Sap-sucker Least Flycatcher Red-eyed Vireo Ovenbird Canada Warbler Rose-breasted Grosbeak	Common Flicker Great Crested Flycatcher Alder Flycatcher Tree Swallow Golden-winged Warbler Brown-headed Cowbird
IV. Black-capped Chickadee/ Golden-crowned Kinglet	**V. Gray Catbird/Swamp Sparrow**	**VI. Yellow-bellied Flycatcher/ Connecticut Warbler**
Spruce Black-capped Chickadee Brown Creeper Golden-crowned Kinglet	Killdeer Ruby-throated Humming-bird Gray Catbird Red-winged Blackbird Swamp Sparrow	Gray Jay Yellow-bellied Flycatcher Winter Wren Ruby-crowned Kinglet Cape May Warbler Connecticut Warbler
VII. Sparrow Hawk/Brown Thrasher	**VIII. Hermit Thrush/ Blackburian Warbler**	**IX. Eastern Wood Pewee/ Scarlet Tanager**
Sparrow Hawk Brown Trasher Brewer's Blackbird Lincoln's Sparrow	Hermit Thrush Solitary Vireo Yellow-rumped Warbler Blackburnian Warbler Evening Grosbeak Dark-eyed Junco Chipping Sparrow	Eastern Wood Pewee Red-breasted Nuthatch Black-throated Green Warbler Scarlet Tanager American Goldfinch

1/ The strength of the relationships among the species in each association is dependent upon: 1) the amount of information available for each species and 2) the range of habitat tolerance for each species. The weaker associations in the above table include associations IV, VII and IX; all represent species that were relatively uncommon.

2. Because the boundaries of vegetation and avian communities are often similar, one can predict the relative importance of various structural features of the vegetation upon the composition of avian communities.

3. The species composition of bird communities are characterized by the relative importance of different species associations. Each species association is composed of species with similar habitat distributions.

4. Discriminant analysis allows the wildlife manager to graphically perceive the degree of faunal distinctness among the bird communities.

Disadvantages

1. Although broad vegetational requirements of a species are defined, information regarding specific niche dimensions are lacking. Data of this form are necessary prerequisites to species-oriented habitat management.

2. The technique has not been widely applied.

3. Some subjective judgements are still involved in the classification of communities and associations.

4. As was indicated in Table 5, the strength of the classification, for species associations or communities, depends on the amount of data available. For example, the strength of a species association that includes several uncommon or rare species may be less

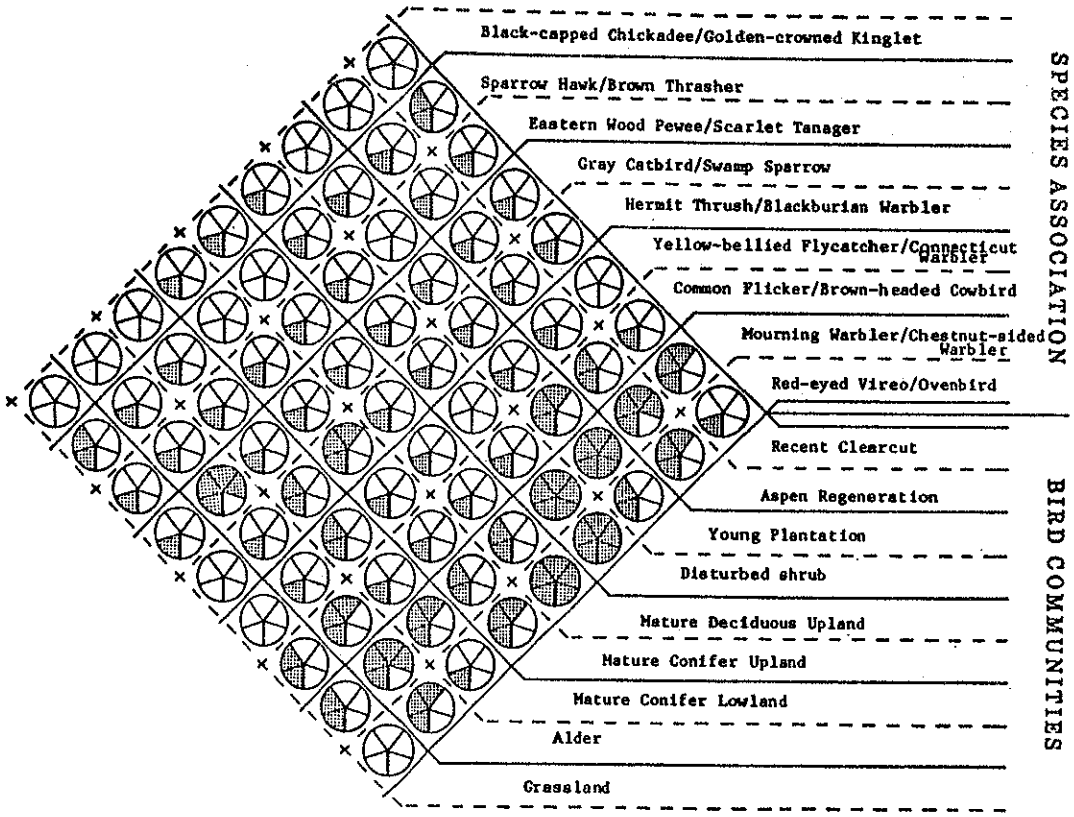


Figure 5.--The relative abundance of major species associations within bird communities of northeastern Minnesota.

(i.e., less stable) than an association that includes several abundant species.

HABITAT NICHE ANALYSIS

Background

Like the previous approach, this technique is a multivariate approach that relates habitat variables to bird distributions. Most naturalist's have recognized for a long time that certain birds occur in particular environments (Adams 1908). Some species may respond to one particular factor while others may respond to a combination of factors, thereby illustrating the need for multivariate techniques. The multivariate approach to habitat selection, and more specifically to the niche concept, was formalized by Hutchinson (1965). Hutchinson viewed the niche as an n-dimensional Euclidean space with each axis of the space corresponding to some relevant variable in the species biology. This approach has been used by Shugart and Patten (1972), Anderson and Shugart (1974), Shugart et al. (1975), Whitmore (1975), and Noon and Able (1978).

The basic premise of the approach assumes that the habitat selected by birds can be measured mathematically (see Green 1971b, 1974). If we assume that it is possible to accurately measure all niche habitat components, then it is possible to mathematically predict the probability that a species will occur in a given habitat. A key to understanding this approach involves viewing the space a species occupies as a hyperellipsoid because the individual components that define the niche are intercorrelated. For example, the density of trees directly effects the density of shrubs and herbs. Such correlations between components of the habitat implies that graphically, their axes are not orthogonal (i.e., they are not independent of one another). Subsequently, to make predictions from field data, a new coordinate system must be defined such that the axes are orthogonal or independent. These new independent axes are simply linear combinations of the original data set.

For this paper we have used principal component analysis (PCA) as modified from the work of Niemi (1977). PCA is a rotation of coordinates into a sampled hyperellipsoid. The principal component coordinates are independent and explain decreasing amounts of

variation in the sample data. In PCA, a series of habitat measurements (vectors) are made within an area occupied by a species. These measurements essentially quantify the amount of a given habitat variable (e.g., tree density) that appears necessary to provide suitable habitat for the species. With an appropriate number of samples, a mean vector position or "centroid" can be calculated for each sample vector. In general, for a given habitat, the closer a habitat vector is to the species centroid position, the more suitable the habitat is for the species. A probability model can be designed to predict the occurrence of a species within a given habitat. These predictions are based on measurements of the same habitat variables used to establish the specific model. Such a model may also allow interpretation of species preference both within and between habitats (Shugart et al. 1975).

Method

We will briefly explain the methodology, but a more detailed description can be found in Niemi (1977). We constructed a model based on a PCA analysis of eight measured habitat variables (Table 6) collected within the territorial boundaries of 21 bird species found in northeastern Minnesota. These bird and habitat data were collected in four different stands during June and July of 1974 and 1975. Three stands were in young altered habitats while the fourth stand was in a mature forest habitat. The three altered stands consisted of: 1) a burned, virgin jack pine stand (BVP) which was never logged but burned in 1971, 2) a burned, cut jack pine stand (BCP) which was logged and then burned in 1971, and 3) an aspen clear-cut (ACC) stand which was logged in 1973. The mature stand was a mixed balsam - birch forest (BBF) with some aspen. These habitats were selected to demonstrate the microhabitat preferences of bird species within early successional stages and to show how a principal component model can be useful to compare changes occurring in bird populations following alteration.

Data Analysis and Interpretation

The principal component model is shown in Figure 6. The figure clearly delineates a group of species to the right, that are typically associated with mature forests, and species to the left, that are typically associated with early successional stages. Table 7 shows the correlation of the original habitat variables with the principal components for proper interpretation of the axes of the model. Those species between the two groups, such as the red-eyed vireo, veery, blue jay, and least flycatcher, are typically associated with a wide variety of habitats ranging from the early successional stages to the mature forest stages. Within the species group associated with the early successional stages, there is a noticeable gradient of species preferences from the common yellowthroat on top to the hermit thrush at the lower left (Figure 6). The yellowthroat prefers the open areas in the early successional stages along with a high density of low shrubs, and a low density of saplings and trees. The hermit thrush, however, prefers areas with high tree and sapling densities. Many species are rather ubiquitous in the early successional

Table 6.--Description of 8 variables used in the principal component analysis shown in Figure 6 including mnemonic code and method.

Variable Mnemonic	Description	Method
GC	Percent ground cover divided by 10	20(+ presence or-absence readings of green vegetation (James and Shugart 1970)
HS	High shrub density	Number of shrub stems >1m. high <2.5cm dbh/10^{-3}ac. (Ohmann 1973)
LS	Low shrub density	Number of shrub stems >.3m high <1m. high/$4^{x}10^{-3}$ac. (Ohmann 1973)
SH	Shrub height	Average of 4 readings in m./10^{-1}ac.
SLOP	Slope	Change in elevation for diameter of 10^{-1}ac. circle
SDIV	Shrub diversity	Shannon and Weaver (1963) diversity index
SAPS	Sapling density	Number of saplings 2.5-7.6cm dbh/ 10^{-1}ac.
T2	Tree density	Number of trees 15.1-22.9cm dbh/ 10^{-1}ac.

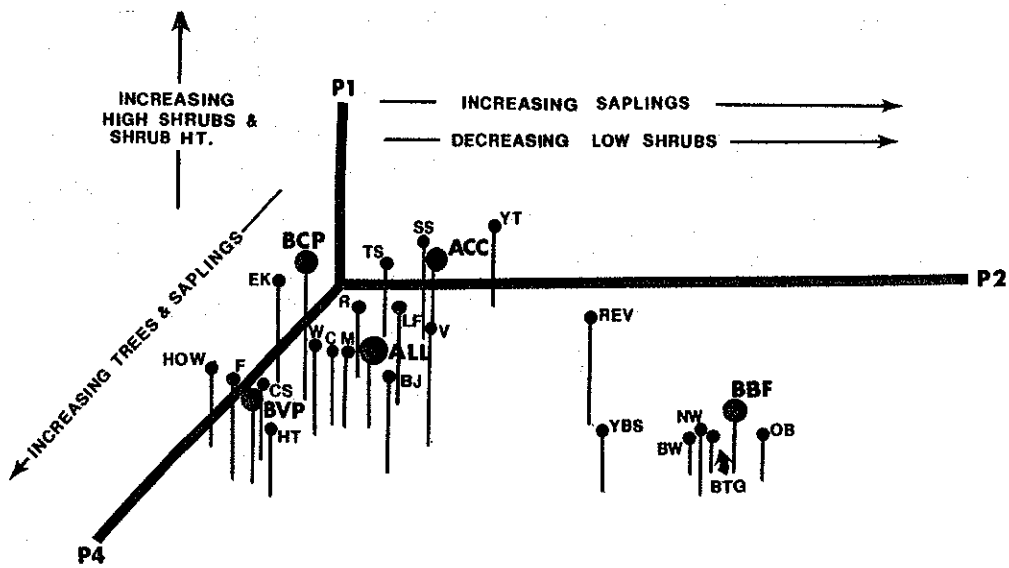


Figure 6.--Mean principal compoent vectors for twenty-one bird species and four sampled stands (described in text) on the best three principal components separating species habitat. Each axis is an orthogonal component composed of linear combinations of the eight habitat components shown in Table 7. Species include common flicker (F), yellow-bellied sapsucker (YBS), eastern kingbird (EK), least flycatcher (LF), tree swallow (TS), blue jay (BJ), house wren (HOW), American robin (R), hermit thrush (HT), veery (V), red-eyed vireo (REV), nashville warbler (NW), black-throated green warbler (BTG), blackburnian warbler (BW), chestnut-sided warbler (C), ovenbird (OB), mourning warbler (M), common yellowthroat (YT), chipping sparrow (CS), white-throated sparrow (W), and song sparrow (SS).

stages, such as the chestnut-sided warbler, mourning warbler, and white-throated sparrow; they tend to cluster around the mean position for all (ALL) the altered habitats.

One of the interesting discoveries of this study regards an index value (Z value, Table 7) that was calculated to test the relative strength of each principal component to separate the habitats selected by species. We found that although each principal component explained a decreasing amount of variation in the habitat data (Table 7), those same components did not necessarily explain decreasing amounts of variation in the bird species selection of habitats. The descriptive model was constructed by using the best three principal components which separated species habitat, not habitats alone. Birds may not differentiate between habitats based simply on those variables with high variations, but rather on variables which provide the best discriminating cues between habitats, variables which provide a specific need, or for other more subtle reasons. Thus, in Figure 6 and Table 7, P2, P4, and P1 were ordered for best separating species habitats while P1, P2, and P4 were ordered in explaining variation in the habitat data.

Figure 6 provided a means to view multiple species habitat selection by multiple measurements of structural habitat components. These measurements could also include additional niche components such as food requirements, or other behavioral traits which more accurately define a species niche hyperspace. We have used principal component analysis, but discriminant function analysis may also be used to maximize the separation between species groups (James 1971; Shugart and Patten 1972; Shugart et al. 1975). Further sophistication of multivariate analysis and a more thorough testing of its field methodology will eventually provide better techniques for use in practical applications.

Advantages

1. A multivariate perspective can potentially allow a large number of species to be considered simultaneously in management objectives.

2. Presuming the assumption for collecting data are appropriate, this approach can ultimately test the strength of species associations (e.g., how closely associated are

species in a defined community) and provide a measure of the niche breadth of specific species.

3. Subjective judgements are substantially minimized relative to the approaches listed above.

Disadvantages

1. Unless an intimate understanding of both multivariate procedures and wildlife species requirements are obtained by users, these techniques may be improperly interpreted and easily abused.

2. By using the multivariate techniques, interpretation of species habitat preferences are more difficult and abstract.

3. Whether niche requirements are measurable is questionable. Presumably, there are many intangible factors which are difficult to quantify but important to the well-being of a species. See final discussion for more details.

DISCUSSION

We briefly examined four broad and diverse techniques that ecologists have implemented in their efforts to describe the relationship between animal species and their environment. We have chosen the four models presented above because they portray, in our estimation, the most realistic approaches currently available for managing many species simultaneously. A brief summary of the philosophy supporting each approach was presented, a short discussion of it's methodology, and an example of it's application. Several brief statements were also made regarding the relative merits and drawbacks of each approach. The discussion of each approach was of necessity rather general.

Giving any of the approaches justice, however, should include a detailed review of the publications cited. Hopefully our summary has provided a general review of each approach and has demonstrated that none of the techniques will provide the wildlife biologist with an all encompassing approach to species management. Since it is almost a classic response that most scientific investigations reveal far more problems than they answer, we feel it is important at this point to outline many of the problems that continually frustrate wildlife biologists who attempt to answer seemingly simple questions regarding wildlife distributions. The items listed below are drawbacks that are generally inherent to all multi-specie approaches to habitat management:

Table 7.--Z values, explained variation, and correlation coefficients of the eight habitat variables associated with the three principal components used in Figure 6. Mnemonic habitat codes are from Table 6.

	Principal Components		
Z value 1/	P2	P4	P1
Exp. Var. 2/	46.	17.	10.
Correlations 3/	21.	14.	26.
GC	.27	-.14	.39
GS	-.45	.27	.84
LS	.67	-.57	.55
SH	-.28	.27	.73
SLOP	-.02	-.20	.09
SDIV	.37	-.09	.43
SAPS	.43	.64	.29
TS	.24	.63	-.01

1/ A measure of relative strength of the principal component to separate species habitat as described in text.

2/ Variation explained by the principal component with respect to the habitat data.

3/ Correlation coefficients of the principal components with the original habitat variables.

1. The delineation of communities, either plant or animal, is questionable. All but one of the models described above incorporated a subjective judgement regarding community boundaries. It is sufficient to note that some form of classification is necessary only from the perspective of human communication, but any static classification seems useless.

4. Habitat selection by birds may be partially controlled by factors beyond those that can be measured within an individual's territory or home range. The size of a habitat (Whitcomb 1977, Diamond 1975) and it's spatial relationship to other habitats (Leopold 1932, Wiens 1975) are factors which

have received little attention from avian ecologists. Such factors, however, may be important components in the habitat selection process. For example, what size should clearcuts be to maintain natural populations and how should they be juxtapositioned with other habitats to benefit wildlife or a particular species?

3. Generalized approaches to wildlife management, such as those presented above, often do not take into account special habitat requirements of some species. Such democratic techniques, which manage for the "majority," may be extremely detrimental to species with specific requirements. Snags, the unmeasured variable described by Balda (1975), is an example of a neglected yet important habitat requirement for many birds. DeGraaf (1978) recently estimated that among the 800 bird species found in the United States approximately 85 are cavity nesters. For many species such as these, the absence of a single feature in the habitat could critically reduce population levels. It is crucial that potential 'limiting factors' be identified.

4. Wiens (1977) has recently summarized a concept called "ecological crunch" whereby species experience population fluctuations in response to changing environmental conditions. During times of resource limitation or stress (e.g., during drought), species may become restricted to their optimum habitats-habitats where their behavioral and morphological adaptations are best suited for securing resources. In response to these limitations, population levels may be greatly reduced. During resource abundance, however, species diffuse into submarginal habitats and, consequently, their population levels increase. This emphasizes the importance of long term studies of species populations - studies which, to date, have been seriously lacking.

5. The factors that limit population levels are poorly understood. Although most bird population studies have been conducted during the breeding season, there is a growing concern that events on the wintering grounds may be the most important factors influencing bird populations (Lack 1971), Fretwell 1973). Once again long term investigations that cover the entire life history of the species, from it's breeding grounds, to migration resting areas, and finally to wintering grounds, have been neglected.

6. A realistic approach to wildlife management must establish a means to limit the species under consideration in order to be workable. Although we have attempted such a procedure here, an important question remains - how can a wildlife manager objectively (not subjectively, as we have) decide which species to include in his management plan? The federal endangered species list, state threatened or endangered species lists, and the American Birds Blue List provide some direction for identifying species of concern. Nevertheless, these lists are also subject to individual bias and are rarely substantiated by systematic field investigations. The entire concept of "uniqueness" has escaped a much needed quantitative definition. Uniqueness criteria are difficult to define and an evaluation does not exist. Should species uniqueness be determined by niche breadth, distribution, public opinion, importance to man, importance to the ecosystem, or some other criterion? Environmental evaluations using birds and habitats, such as that presented by Graber and Graber (1976), have been progressive in this regard and deserve further attention.

7. Many ecological concepts have not been included in the models discussed above. Included among these concepts are predator-prey relationships, competition, and diversity. Until their importance is fully understood, any approach to wildlife management will, of necessity, be "simplistic" in nature.

In listing these drawbacks we do not wish to frighten wildlife biologists who endeavor to implement management approaches such as the ones we have presented here. By their very nature, all models are beset with limitations. Their objectives are to simplify natural systems, to identify the major components of the system, and to determine the species ultimate dependence upon one another, Nevertheless, we are better prepared to employ the practical applications of such models when we understand their inherent limitations.

The four approaches to non-game bird management that we have presented will serve as a framework to be expanded as our data base grows. At present we need to continue

research efforts that are designed to identify species habitat requirements. Nevertheless, we have reached a starting point for wildlife impact analysis. Although we are still far from the point where the impacts of all habitat management problems can be accurately predicted, non-game bird managers can predict gross population changes based on the data we have presented.

All four management models have also been effective methods of data reduction. Beginning with an extensive list of variables that quantify the environment, principal component analysis has, after linearly combining the variables, identified those that are best able to define the response of different species in the community to environmental parameters. Features of the habitat are thereby reduced to a few 'components' that are important in the species distributions. The successional stage, life form, and species association models have, by different techniques, identified various assemblages of species. The assemblages include species which by various methods, are recognized as responding to the environment in a similar manner. As a result, the biologist can deal with groups of species rather than individual species. Work at effective methods of data reduction must continue if non-game biologists are to effectively communicate pertinent information to foresters which will aid them in understanding the implications of various habitat management alternatives.

CONCLUDING REMARKS

There are many approaches to wildlife management. The four we have examined are attempts to construct models that will simultaneously examine many species. Although the successional stage and life form approaches establish an important data base for each species, when the habitat requirements of hundreds of vertebrate species is considered, the problems are nearly incomprehensive. Thus, if managers realistically want to consider all vertebrates in the planning process, the necessity for using some form of multivariate analysis is essential. Such analyses are useless, however, unless they can be comprehended by the ecologist and wildlife manager alike. Bridging the gap between theoretical and applied ecology is not an easy task and may prove to be one of our most challenging tasks. The manager who attempts to put ecologist's models to practical use must be able to perceive how generalizations derived from the model relate to the real system he manages. In time, it would be beneficial for either theoretical ecologists to attempt interpretations of their data for practical use or a concerted effort be made to integrate theoretical findings into practical management approaches.

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