RESEARCH BULLETIN 1056 DECEMBER, 1985

UNIVERSITY OF MISSOURI-COLUMBIA
COLLEGE OF AGRICULTURE
AGRICULTURAL EXPERIMENT STATION

ROGER MITCHELL, DIRECTOR

Characteristics of Summer Habitats of Selected Nongame Birds in Missouri

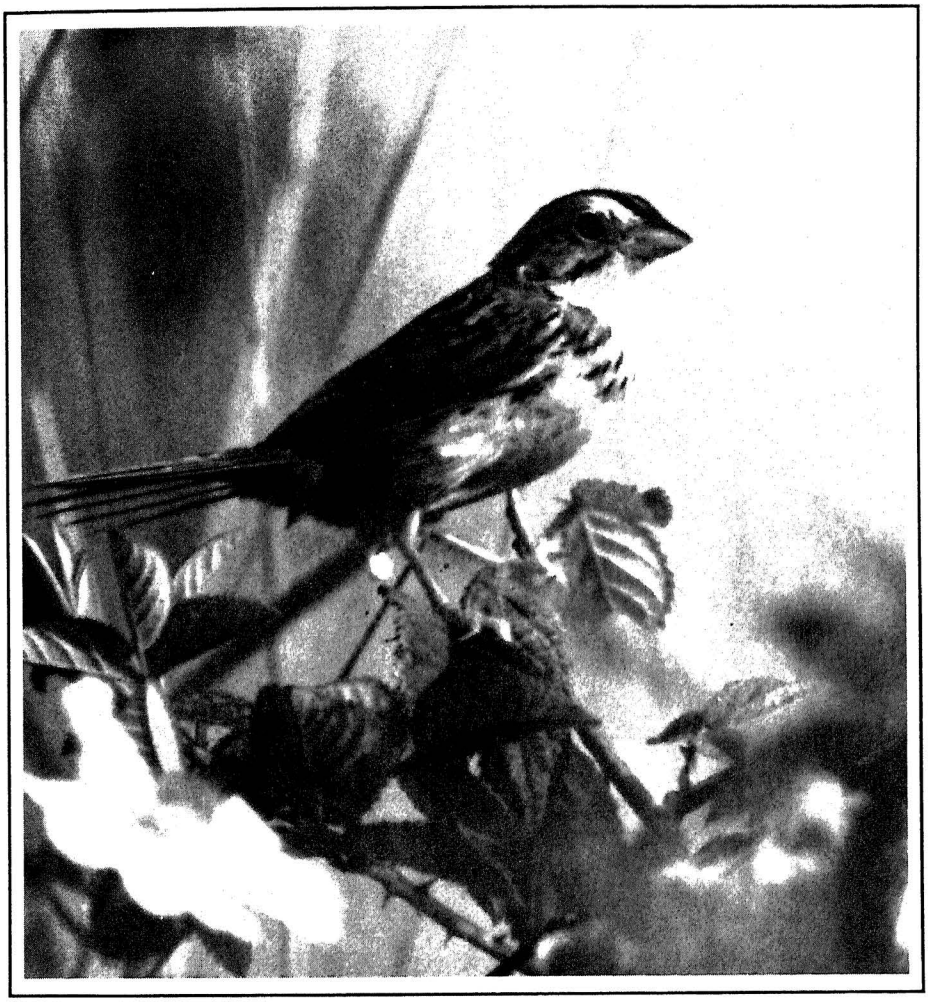
Richard B. Kahl
Thomas S. Baskett
Jonathan A. Ellis
James N. Burroughs

COLUMBIA, MISSOURI

Richard B. Kahl, Missouri Department of Conservation and School of Forestry, Fisheries and Wildlife; Thomas S. Baskett, U.S. Fish and Wildlife Service, Missouri Cooperative Fish and Wildlife Research Unit; Jonathan A. Ellis, School of Forestry, Fisheries and Wildlife, University of Missouri-Columbia; and James N. Burroughs, School of Forestry, Fisheries and Wildlife, University of Missouri-Columbia.

Characteristics of Summer Habitats of Selected Nongame Birds in Missouri

Richard B. Kahl, Thomas S. Baskett,
Jonathan A. Ellis and James N. Burroughs



Jim Rathert photo

Henslow's Sparrow

MISSOURI AGRICULTURAL EXPERIMENT STATION

TABLE OF CONTENTS

Page

INTRODUCTION ..... *v*

STUDY AREAS 1

Central Missouri Upland Hardwoods 1
Southeastern Missouri Upland Hardwoods 1
Central Missouri Bottomland Hardwoods 2
Southeastern Missouri Bottomland Hardwoods 2
Central Missouri Old Fields 2
Central Missouri Grasslands 3
Southwestern Missouri Grasslands 3

METHODS 3

Locating Singing Males 3
Habitat Sampling 3
Analysis of Data 5
Bird Species Associations 5
Habitat Characteristics and Bird Species 5

RESULTS 6

Bird Species Associations 6
Bird Species Accounts 7
Grassland-Managed 7
Eastern Meadowlark 7
Dickcissel 9
Grasshopper Sparrow 11
Henslow's Sparrow 14
Grassland-Unmanaged 16
Eastern Kingbird 16
Common Yellowthroat 18
Lark Sparrow 20
Field Sparrow 21
Overgrown Grassland - Old Field 23
Willow Flycatcher 23
Bell's Vireo 26
Prairie Warbler 28
Yellow-Breasted Chat 30
Orchard Oriole 32
American Goldfinch 34

TABLE OF CONTENTS (CON'T.)

Forest Interior - Forest With Some Large Trees 36
Pileated Woodpecker 36
Red-bellied Woodpecker 39
Great Crested Flycatcher 41
Acadian Flycatcher 43
Eastern Wood Pewee 46
Tufted Titmouse 48
White-breasted Nuthatch 50
Yellow-throated Vireo 52
Red-eyed Vireo 53
Warbling Vireo 56
Prothonotary Warbler 58
Cerulean Warbler 60
Yellow-throated Warbler 62
Summer Tanager 63
Forest Interior - Pole or Sawtimber, Sparse Understory 66
Carolina Chickadee 66
Wood Thrush 68
Northern Parula 71
Northern Oriole 73
Rose-breasted Grosbeak 75
Forest Interior - Pole or Sawtimber, Dense Understory 77
Red-headed Woodpecker 77
Hairy Woodpecker 79
Downy Woodpecker 82
Black-and-White Warbler 85
Worm-Eating Warbler 87
Ovenbird 90
Kentucky Warbler 93
Scarlet Tanager 95
Forest Interior - Open Tree Reproduction 98
Black-capped Chickadee 98
White-Eyed Vireo 100
Louisiana Waterthrush 103
Forest Edge 105
Brown Thrasher 105
Blue-winged Warbler 107
Indigo Bunting 108
Rufous-sided Towhee 111
Disturbed Land 113
Horned Lark 113

TABLE OF CONTENTS (CON'T.)

DISCUSSION 116

Alternative Analyses Explored 116
Suitability Index Curves 116
Coefficients of Variation 116
Discriminant Function Analysis 116
Means and Standard Deviations 117
Frequency Distribution Analysis 117
Limitations of Data and Analyses 117
Habitat Modeling 119

SUMMARY 123

LITERATURE CITED 125

APPENDICES 135-151

I Common and Scientific Names of Plants Mentioned in Text 135
II Common and Scientific Names of Bird Species Mentioned in Text 137
III Supplementary Accounts for 11 Species of Birds 141

FIGURES 153-155

1 Locations of Study Areas in Missouri 153
2 Frequency Distribution for the Northern Oriole 154
3 Phenogram of Habitat Similarities 155

INTRODUCTION

In the United States, concern for wildlife resources has gradually resulted in legislation that requires consideration of environmental quality in resource development planning. Relevant federal laws have recently been summarized by the U.S. Fish and Wildlife Service (1980a). Non-monetary assessment of a prospective project's impact on wildlife is an important element in the planning process. Procedures for non-monetary assessment for nationwide use were based upon a process initially developed by Daniel and Lamaire (1974). Since then, numerous methods have been developed and refined (Whitaker et al. 1976, Flood et al. 1977, Baskett et al. 1980, U.S. Fish and Wildlife Service 1980b, and several others summarized by Erickson et al. 1980).

Through these procedures, biologists assess impacts on fish and wildlife by evaluating habitat quality for several species or groups of species with different life requirements. This evaluation is made by on-site assessment of vegetative or physiographic characteristics considered important to a wildlife species or group of species. These characteristics are determined from literature and personal expertise. Future habitat conditions with and without a development project are then estimated and compared to existing habitat conditions.

Game species with well documented life histories have typically been used as subjects of habitat evaluation. However, many game species are "generalists" with respect to habitat requirements, and evaluations are sometimes difficult and imprecise. In contrast, many species of nongame birds have very specific habitat requirements. Recent trends in use of public lands demand consideration of nongame species.

According to Hilden (1965), visual cues, presumably related to vegetation structures are important in bird habitat selection and release a settling reaction. This implies that measurable habitat variables exist and can be identified for certain bird species. Although published data on specific requirements are limited, numerous studies have already demonstrated a relationship (though not necessarily a dependency) between vegetative structural components and bird species occurrence and diversity (MacArthur and MacArthur 1961, Karr 1968, James and Shugart 1970, James 1971, Anderson and Shugart 1974, Whitmore 1975, K. E. Evans 1978, Anderson 1979, and others).

The present study, conducted during late spring and early summer of 1977 and 1978, was initiated to determine habitat components of nongame birds breeding in central and southern Missouri. Specifically, our objective was to identify measurable components that consistently describe habitat associated with certain species, thus providing quantitative bases for habitat evaluation and habitat modeling.

This study was funded principally through Research Agreements USDI-14-16-0008-2014 and USDI-FWS-14-15-0009-1556-1 between the U.S. Fish and Wildlife Service and the University of Missouri-Columbia. The Missouri Department of Conservation assigned R. B. Kahl as a research coordinator. This publication is a contribution from the Department of Conservation and from the

Missouri Cooperative Wildlife Research Unit: U.S. Fish and Wildlife Service; Missouri Department of Conservation; Wildlife Management Institute; and School of Forestry, Fisheries and Wildlife, University of Missouri, cooperating. Work was supported in part by Missouri Agricultural Experiment Station Projects 182 and 184. For guidance, advice or editorial assistance, we acknowledge M. J. Armbruster, S. S. Clark, D. K. Fleming, and T. S. Taylor, University of Missouri-Columbia; R. L. Clawson, Missouri Department of Conservation; K. E. Evans, U.S. Forest Service; and F. B. Samson, U.S. Fish and Wildlife Service. W. R. Eddleman provided an initial summary of the data useful for the analysis presented here. L. C. Byrne, D. A. Freiling, W. W. Dierker, W. R. Eddleman, G. W. Evans, M. V. Goodwin, P. N. Gray, L. A. Piest, G. M. Sheets, D. J. Tincher, and L. D. Vangilder, University of Missouri-Columbia, provided field assistance. Marianne E. Kurth, University of Missouri Agricultural Editor's Office, edited this publication.

Characteristics of Summer Habitats of Selected Nongame Birds in Missouri

Richard B. Kahl, Thomas S. Baskett,
Jonathan A. Ellis and James N. Burroughs

STUDY AREAS

Habitat of breeding birds was determined on 53 study areas in plant communities of central, southwestern, and southeastern Missouri (Fig. 1). In the listings below, N = number of sites studies in each plant community.

Central Missouri Upland Hardwoods (N = 14)

These forest sites, ranging from 4.1 to 8.1 ha, in Boone and Callaway counties (Fig. 1), were located primarily in hilly terrain and each was traversed by at least one intermittent stream. The dominant overstory species was white oak, although other oaks (red, black, and chinquapin) and hickories were common. (Scientific names of plants are listed in Appendix I.) Mean canopy height ranged from 14.6 to 20.5 m and canopy closure ranged from 63 to 85%. (Means and standard deviations of habitat characteristics for individual study areas were derived from the combined observations of all species on a study area and are listed by habitat type and locale in Kahl et al. 1981.).

Subcanopy closure was quite variable within and among study areas (means, 49-72%). Prevalent subcanopy-understory species included sugar maple, oaks, hickories, hop hornbeam, slippery elm, flowering dogwood, eastern redbud, and shadbush. Ground vegetation was also variable; mean coverage ranged from 51 to 89% and mean height ranged from 0.16 to 0.45 m. Beggar ticks, fragrant sumac, coral berry, goldenrods, Virginia creeper, tick trefoils, bedstraws, and pale touch-me-not were prevalent ground species.

Two study areas differed slightly from the others, as they were located in a broad, flat stream valley. Sugar maple was the dominant overstory species, although oaks and hickories were common. Near the stream, large sycamores were predominant. Subcanopy-understory species included Ohio buckeye, sugar maple, black maple, pawpaw, hop hornbeam and Kentucky coffee tree. Ground vegetation species included poison ivy, Virginia creeper, pale touch-me-not, wood nettle, wild ginger, golden seal, and black cohosh.

Southeastern Missouri Upland Hardwoods (N = 5)

These upland hardwood sites, ranging from 6.3 to 8.0 ha, were adjacent to extensive bottomland hardwoods and swamplands on Mingo National Wildlife Refuge and Duck Creek Wildlife Area in Stoddard, Wayne, and Bollinger counties. Common overstory species were red oak, white oak, and black hickory. Canopy was

high (means, 17.9-28.4 m) and relatively closed (means, 87-90%). Mean subcanopy closure ranged from 52 to 72%. Prevalent subcanopy-understory species included flowering dogwood, sugar maple, white oak, white ash, black hickory, and slippery elm. Ground vegetation was sparse (mean coverages, 17-39%; mean heights, 0.04-0.11 m) and included fragrant sumac, Virginia creeper, muhly grasses, and ferns.

Central Missouri Bottomland Hardwoods (N = 5)

The Missouri River floodplain was the site for these study areas, ranging from 1.8 to 5.0 ha, in Boone and Howard counties. Terrain was generally level, although occasionally interrupted by shallow gullies. Four of the study areas were narrow, forested strips along the river. Predominant overstory species included cottonwood, sycamore, black willow, and silver maple. Canopy was high (means, 18.3-26.4 m), although relatively open (mean closure, 61-80%). Mean subcanopy closure ranged from 57 to 63% and subcanopy-understory species consisted primarily of red mulberry and box elder. Ground vegetation was relatively sparse (mean coverages, 43-70%; mean heights, 0.13-0.46 m). Prevalent ground species included poison ivy, pale touch-me-not, wood nettle, and Virginia creeper.

Southeastern Missouri Bottomland Hardwoods (N = 7)

These forest sites, ranging from 6.0 to 7.2 ha, were located in extensive, mature bottomland hardwoods on Mingo National Wildlife Refuge and Duck Creek Wildlife Area in Stoddard, Wayne, and Bollinger counties. Terrain was level and often interspersed with small, shallow pools. Predominant overstory species included several oaks (pin, overcup, willow, Shumard, bur), red maple, and sweet gum. Canopy was high (means, 17.3-26.8 m) and relatively closed (means, 79-90%). Subcanopy closure was variable (means, 43-84%). Prevalent subcanopy-understory species included red maple, sweet gum, slippery elm, various oaks and possum haw. Ground vegetation was also quite variable, but generally sparse (mean coverages, 17-52%; and mean heights, 0.05-0.17 m). Common ground species included pale touch-me-not, trumpet creeper, sedges, lizard's tail, red maple seedlings, and false pimpernel.

Central Missouri Old Fields (N = 8)

Old fields, located in Boone and Callaway counties, were small, ranging from 1.7 to 6.2 ha, and irregularly shaped. They included early successional stages (mean canopy height, 6.9 m; mean canopy closure, 14%; and mean density of woody stems ≥2.5 cm diameter at breast height]dbh[, 210/ha). However, they also included late successional stages (almost continuous forest edge with a mean canopy height of 9.5 m, mean canopy closure of 42% and mean density of 1106 woody stems ≥2.5 cm dbh/ha). Small ponds were present on three study areas. Common woody species included persimmon, red cedar, slippery elm, honey locust, plums, smooth sumac, and multiflora rose. Ground vegetation was dense (mean coverages, 91-100%), but height varied considerably (means, 0.36-0.72 m). Coral berry,

goldenrods, brome grasses, timothy, multiflora rose, poison ivy, and fescues were common ground species.

Central Missouri Grasslands (N = 7)

Grassland study sites, ranging from 2.6 to 5.5 ha, in Boone and Callaway counties included ungrazed and recently grazed tracts, and ranged from almost pure fescue stands to 50% grasses-50% forbs and woody species. Small farm ponds were present on five study areas. Woody vegetation was always <2.5 cm dbh and consisted of coral berry, roses, plums, and slippery elm. Ground vegetation was dense on all areas (mean coverages, 97-100%), but height was variable (means, 0.22-0.87 m) due to grazing. Prevalent ground species included fescues, bluestems, orchard grass, goldenrods, and daisy fleabane. Litter was usually abundant (mean coverages, 71-100%) but shallow (mean depths, 1-5 cm).

Southwestern Missouri Grasslands (N = 7)

These grassland sites in St. Clair County, ranging from 8.2 to 12.8 ha, were virgin prairie. They had diverse vegetative structure and composition. Management techniques included annual and biennial burning or haying, grazing, and restoration by removal of most larger trees followed by fire; some were unmanaged in recent years. Density of woody vegetation was quite variable (means, 0-403 stems ≥2.5 cm dbh/ha and 69-9224 stems <2.5 cm dbh/ha). Canopies were low (mean heights, 1.0-6.2 m). Common woody species included rough-leaved dogwood, swamp dogwood, black cherry, persimmon, elms, multiflora rose, dwarf sumac, and smooth sumac. Ground vegetation was dense on all areas (mean coverages, 95-100%), but height was variable (means, 0.23-0.48 m). Prevalent ground species included prairie dropseed, bluestems, fescues, slender mountain mint, ashy sunflower, and blackberries. Litter was quite variable (mean coverages, 26-99%; and mean depths, 0.3-6.0 cm) as a result of the different management practices.

METHODS

Locating Singing Males

Habitat of singing males was determined on the 53 study areas after song perches were located. Twelve of the 53 areas were studied in both years. Singing males were located weekly by the mapping method (Robbins 1970) from 21 May to 30 June 1977 and 10 May to 15 July 1978. On each study area, from one to five transects, 80 m apart, were traversed, the number depending upon study area size and shape. All singing males within 40 m of transect lines were noted and song perches were marked.

Habitat Sampling

Sample plots were centered around song perches (James and Shugart 1970, James 1978). The boundary of a 0.04 ha circular plot was delineated by marking

four points on the perimeter with an 11.5 m rope extended from the song perch. The following habitat variables were measured:

1. Woody stems >1 m tall (subdivided according to stem size and live or dead stems)
2. Ground vegetative cover (%)
3. Ground vegetative height (m)
4. Subcanopy closure (%)
5. Canopy closure (%)
6. Canopy height (m)
7. Litter cover (%) - only in grassland-old field in 1978
8. Litter depth (cm) - only in grassland-old field in 1978
9. Slope (degree) and aspect
10. Distance to water (m) - 1978 only
11. Perch species
12. Perch tree height
13. Singing height

Percent ground cover, ground cover height, litter cover, litter depth, canopy closure, and subcanopy closure were estimated at 20 points along each of two perpendicular transects through the plot center. Percent ground cover and height were estimated by positioning a meter stick perpendicular to the ground. Ground vegetation was recorded as touching (hit) or not touching (miss) the stick. For hits, ground vegetation was measured at the highest point of contact, and recorded as zero for misses. The number of hits was divided by 20 to yield proportion coverage. The recorded ground vegetation height represented average height at maximum density of the vegetation, not maximum height. Litter cover and depth were estimated in the same manner as ground vegetation. Canopy and subcanopy closure were estimated at each of the 20 points by sighting through an ocular tube held vertical at arm's length (Winkworth and Goodall 1962). When vegetation was intersected by crosspieces over the end of the tube, a hit was recorded. Percent closure was calculated in the same manner as ground coverage.

All woody stems >1 m tall were counted and classified in the following size categories: <2.5 cm dbh, 2.5-9.9 cm dbh, 10.0-29.9 cm dbh, and ≥30 cm dbh. Stems ≥2.5 cm dbh were further classified as live or dead. Densities of stems were then converted to stems/ha.

Because of different field procedures, there was a consistent difference between 1977 and 1978 values of densities of woody stems >1 m tall and <2.5 cm dbh on the five central Missouri upland hardwood areas that were studied both years (see Kahl et al. 1981 for details). Thus, for each area studied both years, 1978 observations were corrected by the following formula:

$$\text{Corrected stem density for 1978} = \frac{\overline{X}_{\text{1977 ``i''th study area}}}{\overline{X}_{\text{1978 ``i''th study area}}} \times \text{each 1978 ``i''th study area observation.}$$

For the nine central Missouri upland hardwood areas studied only in 1978, the 1977 and 1978 means of combined observations on the five areas studied both years were used in the correction formula.

Analysis of Data

Bird Species Associations—A cluster analysis based on a similarity index matrix (Barr et al. 1976) was used to distinguish groups or clusters of bird species with similar habitat requirements. Species with nine or more observations were included in the analysis. Cluster analysis usually employs mean values of the attribute data (habitat variables) to compare different samples (bird species). In this study, median values were used instead, as they minimized problems associated with non-normal distributions and outlying points we encountered in attribute data.

Habitat Characteristics and Bird Species—To illustrate terms used and the method of analysis, data for the northern oriole are shown in Fig. 2. (Scientific names of birds are listed in Appendix II.) Habitat variables important to each species with nine or more observations were selected by comparing "individual species" to "all species" frequency distributions for each habitat variable (Fig. 2A). These frequency distributions were produced by arbitrarily subdividing the range of each variable into intervals and expressing the number of observations in each interval as a percent of the total. Two all species distributions for each variable were generated, one incorporating observations of all species in forest habitat; the second, observations of all species in grassland-old field habitat.

Individual species distributions were based on all observations of the species, regardless of habitat type, and therefore delineate all habitat used by a species. However, each species was classified as a forest or a grassland-old field species depending upon where most observations were made. Individual species distributions were then compared only to the appropriate all species distribution. Points of departure between individual species and all species distributions were considered important to the species and were outlined and displayed graphically (examples in Fig. 2B and 2C) in a habitat account for each species. (For complete series of graphs see Kahl et al. 1981.) Differences between individual and all species distributions were analyzed statistically by chi-square goodness of fit (Barr et al. 1976) for each variable at each interval. Expected values were calculated from the following formula:

$$Fi = \frac{Ai}{At} \times It$$

where,

Fi = the expected value for any given interval on the abscissa,
Ai = the number of all species observations in that interval,
At = the total number of all species observations for all intervals, and
It = the total number of individual species observations for all intervals.

Variables considered unimportant to a species were eliminated from further analysis.

Bird species accounts (see "Results") present information about important habitat variables for each species. These variables were subjectively divided into the following two groups:

Primary—Variables with the most marked differences, usually statistically significant, between the all and individual species distributions (Fig. 2B);

Secondary—Variables with lesser differences between the all and individual species distributions (Fig. 2C).

The distributions of each primary and secondary variable were subdivided into the following categories (Fig. 2B and 2C):

Optimum range—Interval with a greater percentage of observations than any other interval in the individual species distribution; or if two or more such intervals exist, the optimum range includes these intervals and all points between;

Main range—Includes the optimum range and successive adjacent intervals to the point that the individual species distribution decreases sharply or falls consistently below the all species distribution; the main range includes most observations of a species (usually >67%), although the exact percentage depends upon the frequency distribution;

Avoided range—Successive intervals with few or no observations for a species or with significantly fewer observations than the all species distribution.

RESULTS

Bird Species Associations

Through cluster analysis, a phenogram was produced, showing percent similarity of habitat (K) vs. bird species (Fig. 3). A vertical line drawn through the phenogram at a given K value (K') separates the species into clusters or groups. A cluster consists of a species represented by an intersected horizontal line and all species above that line until another horizontal line is intersected. Based on the variables measured in this study, members of a cluster in Fig. 3 exhibit the K' level of habitat similarity.

At the 75% habitat similarity level, species are separated into five clusters. Principal habitats represented by species, and subdivisions of these principal habitats are listed below.

I Grassland - prairie, pasture, or early seral old field with few woody stems more than 1 m tall:

(A) Managed grassland without woody vegetation more than 1 m tall;

(B) Unmanaged grassland or old field with a few small shrubs and trees.

II Overgrown grassland or old field with numerous small shrubs and trees.

III Forest interior:

(A) Forest with some large trees and intermediate values for most other habitat variables;
(B) Older pole or sawtimber on level terrain with a high canopy, sparse ground layer, and fairly sparse shrub layer;
(C) Upland pole or sawtimber commonly on sloping terrain, with relatively dense shrub and ground layers;
(D) Sparse tree reproduction with dense ground layer.

IV Forest edge.

V Disturbed land with much bare ground and little woody vegetation.

The phenogram (Fig. 3) provides a basis for determining species that will be affected by certain land management procedures and for selecting species representative of a group for habitat evaluation.

Bird Species Accounts

Species accounts for 49 of the 60 species in Fig. 3 are arranged by the nine habitat clusters identified. Within each cluster, species are arranged in taxonomic order.

Supplementary accounts for the 11 additional bird species appear in Appendix III. These briefer accounts are presented separately because of sampling peculiarities (prairie-chicken, red-winged blackbird, blue grosbeak) or because the birds are "generalists", adapting to such a broad spectrum of habitats that our quantitative findings may be misleading (blue jay, house wren, cardinal, etc.).

Grassland - Managed

Eastern Meadowlark

Eastern meadowlarks were observed primarily in grasslands, but some were found in old fields. Habitat at singing locations usually had few woody stems <2.5 cm dbh (<350/ha) and lacked woody stems ≥2.5 cm dbh (0/ha). Other important features included dense ground vegetation (>90%) and intermediate to dense litter coverage (>65%) (Table 1).

On central Missouri grassland study areas, many males sang from metal or wooden stakes 1-1.5 m tall. They did so on study areas with very low densities of small trees and shrubs and with few tall, herbaceous prairie plants, particularly tall composites, to serve as song perches. Most males (90% of observations) sang from woody vegetation or stakes. They avoided areas with dense woody invasion, and

were observed in only two old fields. Density of woody stems <2.5 cm dbh never exceeded 175/ha, and woody stems ≥2.5 cm dbh never exceeded 100/ha on the song perch plots in old fields. Meadowlarks were not observed on the grassland study area having the greatest amount of woody vegetation.

The above characteristics describe grasslands or early seral old fields with sparse, low woody vegetation and dense ground vegetation.

Table 1. Important characteristics of eastern meadowlark habitat in Missouri (N = 62).

Variable	*Optimum* *Range*	*%*[a]	*Main* *Range*	*%*	*Avoided* *Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	24-350*	50	<350*	90	>350	10
All woody stems ≥2.5 cm dbh/ha	0*	79	0*	79	>100	6
SECONDARY						
Ground vegetative cover (%)	>95*	85	>90	97	<70	0
Litter cover (%)	>95	25	>65	75	<40	11

[a]*Percent of observations.*

**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*

Summary of Other Studies

Woody Vegetation

Arkansas—Meadowlarks were found primarily in mowed hayfields with no woody vegetation, rarely in grassland with abundant small woody stems <7.5 cm dbh and canopy closure of 17% (Shugart and James 1973).

Georgia—Shrub cover was ≤10% (Johnston and Odum 1956).

Illinois—No woody vegetation occurred in immediate vicinity of nest (Roseberry and Klimstra 1970).

Michigan—Stakes 2.0 m tall were selected over shorter stakes as song perches when placed in alfalfa 0.5 m tall (Harrison 1977).

Ground Vegetative Height

Central and Western U.S.—Direct relationship existed between eastern meadowlark populations and grass height (Wiens 1977).

Illinois—Most nests were located in areas with ground cover 0.25-0.50 m tall (Roseberry and Klimstra 1970).

Kansas—Territories had grass cover with a mean height of 0.29 m (Cody 1968).

Dead Vegetation

Illinois—Presence of dead grass stems at ground level was a primary requirement (Roseberry and Klimstra 1970).

Conclusions

The results in our study generally agree with qualitative descriptions of meadowlark habitat in other published accounts. Throughout their range, eastern meadowlarks inhabit a wide variety of open land areas, but apparently prefer grasslands and meadows with sparse or no woody vegetation (Bent 1958, Mengel 1965, DeGraaf et al. 1980). Male eastern meadowlarks require some erect structures (woody vegetation, tall forb, stake, fence post, telephone wire, etc.) for singing, and females require dense ground vegetation for nesting and some litter accumulation for nest construction (Bent 1958, Harrison 1975, DeGraaf et al. 1980). The characteristics selected as important in our study delineate habitat that would provide these requirements.

Dickcissel

Dickcissels were observed primarily on grassland study areas, although several were also noted on old field study areas. Habitat around song perches was consistently characterized by few or no woody stems <2.5 cm dbh (<350/ha), no woody stems ≥2.5 cm dbh (0/ha) and by dense ground vegetation (>95%, never <85) (Table 2).

These characteristics describe most managed grasslands or early seral old fields.

Summary of Other Studies

Woody Vegetation

Arkansas—Dickcissels were found primarily in recently disturbed grasslands with a few woody stems 1.2-1.5 m tall, occasionally in mowed hayfields lacking woody vegetation or in grassland with many small woody stems (Shugart and James 1973).

Kentucky—The species occurred in grassy areas, sometimes with dense clumps of shrubs and small trees (Mengel 1965).

Ground Vegetative Cover

Kansas—Volume of ground vegetation in territories determined the numbers of mates per male (Zimmerman 1971).

Ground Vegetative Height

Kansas—Ground vegetation, particularly the forb component, was much taller in territories of monogamous and polygynous males (average 1.2 m for forbs) than in territories of unmated males (average about 0.8 m for forbs). Nests typically were in vegetation >0.60 m tall (Zimmerman 1966).

Grass-Forb Composition

Central U.S.—Females preferred areas with more forb than grass cover; therefore, grass-forb composition of territory possibly affected males' success in attracting mates (Verner 1975).

Colorado—Forb cover and height were not different in occupied *vs.* unoccupied areas, but twice as many individual forb plants were in occupied as in unoccupied habitat (Wiens 1973a).

Table 2. Important characteristics of dickcissel habitat in Missouri (N = 84).

	Optimum		*Main*		*Avoided*	
Variable	*Range*	*%*[a]	*Range*	*%*	*Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	0*	49	<350	86	>350	14
All woody stems ≥2.5 cm dbh/ha	0*	89	0*	89	>0	11
Ground vegetative cover (%)	>95*	86	>95*	86	<85	1
SECONDARY						
(none)						

[a]*Percent of observations.*

**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*

Conclusions

In general, characteristics of dickcissel habitat determined in our study agreed with qualitative descriptions in several other published accounts (Fitch 1958, Bent 1968, DeGraaf et al. 1980). However, there were some discrepancies.

First, throughout the breeding range, male dickcissels sing from fence posts (Fitch 1958), tall weed stalks (Bent 1968), and forbs or woody vegetation about 1.5-4 m tall (Zimmerman 1966). Our own observations showed that males always sang from low (often <1 m) woody vegetation. These woody stems were not recorded in our study because tallies of woody stems included only those >1 m tall; thus our tallies were somewhat misleading in this connection.

Second, ground vegetation height averaged >0.20 m on most song perch plots but was typically <0.60 m in our study. This measurement represents the average height at maximum density of the vegetation, not maximum height. In Kansas, ground vegetation averaged 0.50-1.20 m within territories of successful males (Zimmerman 1966). The discrepancy possibly reflects different methodologies.

Third, tall forb cover or low woody vegetation also provides nesting cover. In diverse locations, most nests were located at heights of 0.08-4.25 m in tall forbs or low woody vegetation (Overmire 1962, Meanley 1963, Von Steen 1965, Harmeson 1974). Again, our procedure failed to adequately reflect the presence of the low-growing woody vegetation.

Characteristics selected as important to dickcissels in our study only partially describe preferred habitat as reported in the literature. Some measure of grass-forb composition, maximum height of ground vegetation, and abundance of low woody vegetation (<1 m tall) must be included before dickcissel habitat can be adequately assessed in most parts of the breeding range.

Grasshopper Sparrow

Grasshopper sparrows were observed primarily in grasslands, although several were also noted in an old field. Habitat around song perches consistently lacked woody stems ≥2.5 cm dbh (0/ha, never >50) and woody stems <2.5 cm dbh (0/ha), and had short to intermediate ground vegetation (0.10-0.40 m). Other important features included dense ground vegetation (>85%) and shallow to intermediate litter accumulation (0.1-2 cm) (Table 3).

These characteristics describe a managed grassland (introduced or native grasses) with no woody invasion >1 m tall. Grasshopper sparrows utilized all southwestern Missouri grasslands studied except the two with the greatest woody invasion and tallest herbaceous vegetation. In central Missouri, grasshopper sparrows utilized the two grassland study areas with the shortest herbaceous and least woody vegetation. These overgrazed grasslands accounted for 34% of all observations.

Table 3. Important characteristics of grasshopper sparrow habitat in Missouri (N = 111).

Variable	*Optimum* *Range*	*%*[a]	*Main* *Range*	*%*	*Avoided* *Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	0*	88	0*	88	>0*	12
All woody stems ≥2.5 cm dbh/ha	0*	99	0*	99	>0*	1
Ground vegetative height (m)	.20-.30*	42	.10-.40	87	<.10 or >.40*	13
SECONDARY						
Ground vegetative cover (%)	>95	74	>85	98	<85	2
Litter depth (cm)	.1-1.0*	46	.1-2.0	73	<.1 or >2.0	27

[a]*Percent of observations.*
**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*

Summary of Other Studies

Woody Vegetation

Arkansas—Grasshopper sparrows were found in recently disturbed grassland with little or no woody vegetation (Shugart and James 1973).

Colorado—No difference was detected between occupied and unoccupied grasslands with respect to coverage by woody vegetation (Wiens 1973a).

Georgia—Grasshopper sparrows were found in early successional study plots with ≤10% coverage by shrubs; not in old fields with shrub coverage ≥35% (Johnston and Odum 1956).

Ground Vegetative Cover

Northeastern U.S.—Grasshopper sparrows used uplands with ground vegetation of various densities, but with continuous, tall herbaceous cover (DeGraaf et al. 1980).

Vermont and Pennsylvania—Preferred habitat had dense vegetation below 0.60 m (MacArthur et al. 1962).

Ground Vegetative Height

Arkansas—Grasshopper sparrows preferred short vegetation in a mowed hayfield (Shugart and James 1973).

Central and Western U.S.—Moderately grazed grassland with relatively short vegetation supported the greatest numbers of grasshopper sparrows (Wiens 1977).

Colorado—Forb height was shorter (15.2 cm) on occupied than unoccupied habitat (Wiens 1973a).

Missouri—Most sightings were in prairie plots with short grass having maximum density at 1 cm and appreciably lower density at 25 cm (Skinner et al. 1984).

North America—Vegetation was 0.31-0.36 m tall on several grasslands inhabited by this species (Cody 1968).

Vermont and Pennsylvania—Vegetation <0.60 m tall was preferred (MacArthur et al. 1962).

Wisconsin—Effective vegetation height (vegetation covering 90% of a vertical board) was 0.08 m for this sparrow (Wiens 1973b).

Litter Cover

Colorado—Average coverage was 57% in occupied areas, more in unoccupied areas (Wiens 1973a).

West Virginia—Litter coverage averaged 73%; this characteristic was selected as one of several important variables by Whitmore (1979).

Litter Depth

Colorado—Litter was 1.2 cm deep on occupied areas, more on unoccupied areas (Wiens 1973a).

Wisconsin—Litter was 1.9 cm deep on grasslands used by this sparrow (Wiens 1973b).

Bare Ground, Grass, and Forb Cover

Colorado—Occupied and unoccupied plots did not differ in proportion of ground that was bare, or covered by grasses or forbs (Wiens 1973a).

West Virginia—Percentage of bare ground (24%) and coverage by grasses (28%) appeared important in habitat selection by grasshopper sparrows (Whitmore 1979).

Conclusions

Habitat selection by grasshopper sparrows in Missouri generally was consistent with selection in other areas of the U.S. Grasshopper sparrows inhabit a wide variety of open land situations lacking dense or tall woody vegetation, including prairies, hay fields, and old fields (Smith 1963, Mengel 1965, Bent 1968, DeGraaf et al. 1980). A few woody stems apparently are tolerated and habitat with scattered tall forbs or low woody stems is preferred. In our study, grasshopper sparrows avoided areas with encroaching woody vegetation, but they apparently required a few low woody stems (<1 m tall) or tall forbs for song perches. Males usually sang from low woody vegetation (72% of observations). In Pennsylvania, males sang from the tallest perches within the territory, but used low perches if restricted to low vegetation (Smith 1963).

Ground vegetation height and coverage also appeared important to grasshopper sparrows in several other studies. Short, relatively dense vegetation was preferred in most parts of the breeding range. Although differences in height measurements are apparent among studies, these discrepancies probably reflect dissimilar methods of defining and measuring height. Clumped vegetation is preferred, including such plant species as orchard grass, alfalfa, red clover, or lespedezas (Smith 1963, Bent 1968, DeGraaf et al. 1980).

Depth of litter was consistent among studies, but the apparent importance and degree of litter coverage varied considerably. No preference was apparent in our study as coverage ranged from 0-100%.

The prominent features of grassland sparrow habitat in our study provide a general outline for assessing habitat throughout the breeding range. But several other characteristics should be considered in any evaluation of grasshopper sparrow habitat. These include the amount of woody vegetation <1 m tall or tall forbs, degree of clumping of vegetation (heterogeneity), and a standard measure of vegetation height.

Henslow's Sparrow

Male Henslow's sparrows were observed singing only on grassland study areas and were very selective of song perch habitat on these areas. The characteristics most consistently describing habitat around song perches were no woody stems ≥2.5 cm dbh (always 0/ha), few or no woody stems <2.5 cm dbh (0/ha, never >100), and dense ground vegetation (>95%, never <90) of intermediate height (0.20-0.40 m, never <0.10 or >0.50). Another important feature was dense litter coverage (>95%, never <25) (Table 4).

Henslow's sparrows did not use the two grassland study areas with the greatest woody invasion. Although males avoided areas with woody vegetation >1 m tall, most (61%) sang from dead woody vegetation <1 m tall. These conditions are characteristic of grasslands that have not been overgrazed or recently mowed or burned. However, unmanaged grasslands with woody vegetation >1 m and ground vegetation >0.5 m tall were avoided.

Table 4. Important characteristics of Henslow's sparrow habitat in Missouri (N = 59).

Variable	*Optimum* *Range*	*%*[a]	*Main* *Range*	*%*	*Avoided* *Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	0*	92	0*	92	>0	8
All woody stems ≥2.5 cm dbh/ha	0*	100	0*	100	>0*	0
Ground vegetative cover (%)	>95*	98	>95*	98	<95	2
Ground vegetative height (m)	.30-.40*	54	.20-.40*	81	<.20 or >.50	5
SECONDARY						
Litter cover (%)	>95*	59	>95*	59	<60	14

[a]*Percent of observations.*
**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*

Summary of Other Studies

Woody Vegetation

U.S.—Henslow's sparrows selected grassy fields, sometimes with widely scattered, low woody vegetation (Bent 1968, DeGraaf et al. 1980).

Ground Vegetative Cover

Michigan—Habitat had dense, low-growing vegetation, or at least frequent dense patches (Robins 1971).

Ground Vegetative Height

Missouri—Most sightings of Henslow's sparrows were in prairie plots with maximum grass density at a height of 25 cm (Skinner et al. 1984).

Litter Cover

Michigan—Some litter was required (Robins 1971).

Conclusions

Few published quantitative data on habitat requirements of Henslow's sparrows are available. Habitat used by this sparrow in our Missouri study was similar to habitat qualitatively described in other studies. Henslow's sparrows occupy neglected grassy fields, pasturelands, and wet meadows with dense herbaceous vegetation, and sometimes inhabit areas with widely scattered, low woody vegetation (Bent 1968, DeGraaf et al. 1980).

The only discrepancy between our findings and other published results was for ground vegetative height which was typically 0.20-0.40 m tall and never >0.50 m in this investigation. Bent (1968) reported ground vegetation of at least 0.30-0.60 m tall. This possibly represents maximum height, not height at maximum density as measured in our study.

Presence of song perches probably also affects habitat suitability. In Michigan, males sang just below the top of the general vegetation cover, occasionally using woody plants (Robins 1971). In our study, males usually sang from low woody vegetation (80% of observations) at heights <1 m above ground.

With the exception of some measure of song perch availability, the characteristics in our study appear to describe Henslow's sparrow habitat for most of the breeding range.

Grassland - Unmanaged

Eastern Kingbird

Eastern kingbirds were observed primarily on grassland study areas, although several were also noted on old field study areas. Because this species is a generalist, no variables could be classified as primary. Habitat features of secondary importance included few or no live stems 2.5-9.9 cm dbh (<50/ha, never >500), few or no live stems 10.0-29.9 cm dbh (<50/ha, never >100), and dense litter coverage (>85%) (Table 5).

Summary of Other Studies

Woody Vegetation

Arkansas—Eastern kingbirds were located in a range of habitats from grassland with a few small trees and woody stems to old field with intermediate densities of woody stems <7.5 cm dbh (805/ha) and stems ≥ 7.5 cm dbh (305/ha). Canopy closure was about 17%. Kingbirds were absent or scarce in areas without woody vegetation or areas with densities of trees ≥315/ha and canopy closures ≥25% (Shugart and James 1973).

Kansas—Eastern kingbirds occurred in open areas with high perches (Fitch 1958).

Ontario—Eastern kingbirds inhabited wet and dry bogs with brush vegetation, but not young black spruce forests with clumps of trees 7.5 cm dbh and 6 m tall (Martin 1960).

Ground Vegetative Cover and Height

Kansas—Eastern kingbird habitat had short to intermediate ground vegetation of low to intermediate density (Fitch 1958).

Table 5. Important characteristics of eastern kingbird habitat in Missouri (N = 23).

Variable	*Optimum* *Range*	*%*[a]	*Main* *Range*	*%*	*Avoided* *Range*	*%*
PRIMARY						
(none)						
SECONDARY						
Live stems 2.5-9.9 cm dbh/ha	0	61	<50	78	>500	0
Live stems 10.0-29.9 cm dbh/ha	0	78	<50	96	>100	0
Litter cover (%)	85-90*	24	>85	57	<85	43

[a]*Percent of observations.*

**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*

Conclusions

Eastern kingbirds occur in a wide range of situations ranging from open woodlands to grasslands (Bent 1942, Mengel 1965, Graber et al. 1974, Harrison 1975).

Possibly, eastern kingbirds can adjust to most open areas within their geographic range having several perches for courtship displays and foraging. The need for perches was evident in other studies but not clearly so in ours. Most eastern kingbirds in our study sang from woody vegetation 1-8 m tall (92% of observations).

Results of our study cannot be adequately assessed against other studies. No characteristics were selected as of primary importance in our study, and the results do not clearly delimit eastern kingbird habitat.

Common Yellowthroat

Common yellowthroats were observed primarily in old fields and grasslands, although several were also noted in central Missouri bottomland hardwoods. Habitat around song perches was characterized only by lack of canopy closure (0%) and intermediate to tall ground vegetation (0.30-0.80 m, never <0.20). Other important features included dense ground vegetation (always >85%), a low canopy when one was present (<6 m, never >16), and a small number of woody stems ≥2.5 cm dbh (<100/ha, never >900) (Table 6).

Song perches were located in old fields and grasslands with dense, often brushy, vegetation, but few larger trees.

Table 6. Important characteristics of common yellowthroat habitat in Missouri (N = 43).

	Optimum		*Main*		*Avoided*	
Variable	*Range*	*%*[a]	*Range*	*%*	*Range*	*%*
PRIMARY						
Ground vegetative height (m)	.50-.70*	37	.30-.80	86	<.30*	9
Canopy closure (%)	0*	84	0*	84	>0	16
SECONDARY						
All woody stems ≥2.5 cm dbh/ha	0	44	<100	81	>250	5
Ground vegetative cover (%)	>95	79	>85	100	<85	0
Canopy height (m)	2-4*	35	<6	88	>6	12

[a]*Percent of observations.*

**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*

Summary of Other Studies

Ground Vegetative Cover and Height

Illinois—On habitat supporting low numbers of common yellowthroats,

ground vegetation <0.6 m tall had average coverages of 78-83% (Karr 1968).

Utah (isolated valley in UT, AZ, NV)—Moderate ground vegetation coverage was selected by multivariate analysis (MVA) as an important habitat variable for yellowthroats (Whitmore 1977).

Vermont and Pennsylvania—Dense vegetation <0.6 m tall and moderately dense vegetation >0.6 m tall provided suitable habitat (MacArthur et al. 1962).

Canopy Closure

California—Habitat was suitable for common yellowthroats in grass-forb, shrub-sapling, and pole and older forests with various degrees of canopy closure in the Sierra Nevadas (Verner 1980).

Georgia—Yellowthroats were found in locations with 10% shrub cover but not in areas with ≥35% shrub cover or in areas without woody vegetation (Johnston and Odum 1956).

Utah—Little canopy closure was an important component of habitat (Whitmore 1977).

Canopy Height

Georgia—Yellowthroat habitat had woody vegetation ≤1.8 m tall but did not include areas with most woody vegetation 3.0-6.0 m tall (Johnston and Odum 1956).

Michigan—Habitat included areas with scattered shrubs and trees 0.9-4.5 m tall and dense woody thickets <0.9 m tall (Stewart 1953).

Vermont and Pennsylvania—Yellowthroat habitat was brushy fields with moderately dense vegetation of heights 0.6-4.5 m and sparse or no vegetation >4.5 m tall (MacArthur et al. 1962).

Wyoming—Yellowthroats were found where canopy heights were 0.6-1.2 m, with a few stems 3.0-3.6 m tall, but not in otherwise suitable habitat with canopy heights 12-21 m (Salt 1957).

Conclusions

Principal habitat of common yellowthroats is usually described as damp sites with dense herbaceous vegetation and low, woody stems. Yellowthroats will also nest in uplands with dense, tall herbaceous vegetation (Bent 1953, Stewart 1953, Mengel 1965, DeGraaf et al. 1980). Use of moist sites may simply reflect the species' need for the dense vegetation found in low, damp sites (Stewart 1953).

Habitat characteristics selected in our study compare favorably with those described in other studies except that ground vegetative cover was 78-83% in Illinois habitats (Karr 1968). In our study, on the other hand, ground coverage was never <85% but included all vegetation <1 m tall.

In our study, preferred canopy height was 2-4 m, and males usually sang at heights 1-4 m above ground (90% of observations) in woody vegetation 1-8 m tall

(93%). However, this woody vegetation was so sparse that canopy closure was tallied as 0%. Male common yellowthroats typically sing from perches near the ground, especially low bushes, but will also sing at heights of 12 m (Kendeigh 1945).

Except for the sparseness of low woody vegetation coverage we observed, the characteristics selected in our study appear to delineate common yellowthroat habitat in most parts of the breeding range.

Lark Sparrow

Lark sparrows were found only on one southwestern Missouri grassland study area. The characteristics most consistently describing habitat around song perches were shallow litter (always 0.1-1.0 cm), a low to intermediate canopy (4-12 m, never <2 or >14), and sparse litter coverage (15-50%, never >50). Other important features included a small number of woody stems ≥2.5 cm dbh (24-450/ha, never >450) and intermediate to tall ground vegetation (always 0.20-0.80 m) (Table 7).

The only grassland study area utilized by lark sparrows had been recently cleared of most trees and burned; litter was sparse.

Table 7. Important characteristics of lark sparrow habitat in Missouri (N = 12).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Canopy height (m)	4-12	83	4-12	83	<2 or >14	0
Litter cover (%)	40-45*	25	15-50*	95	>50*	0
Litter depth (cm)	.1-1.0*	100	.1-1.0*	100	>1.0*	0
SECONDARY						
All woody stems ≥2.5 cm dbh/ha	24-50*	50	24-450	92	0*	8
Ground vegetative height (m)	.20-.30	42	.20-.80	100	<.20	0

[a]*Percent of observations.*

**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*

Summary of Other Studies

No other quantitative data were found.

Conclusions

Lark sparrows inhabit a variety of openlands from open woodland and park-like areas to brushy pastures and completely treeless meadows and pastures. Preferred habitat appears to be open areas with a few small trees and shrubs and some bare ground (Mengel 1965, Bent 1968). Lark sparrows often nest in bare or eroded places (Harrison 1975). Larger shrubs and small trees provide song perches. In our study, most males (83% of observations) sang from tops of woody vegetation 4-12 m tall. Habitat characteristics selected in our study adequately describe this preferred habitat. However, because of the lack of published quantitative data for comparison, these results should be considered cautiously for other areas.

Field Sparrow

Field sparrows were observed on all old field and two grassland study areas. Habitat around song perches was characterized by a low to intermediate canopy (2-8 m, never >8) and a small number of woody stems <2.5 cm dbh (25-1050/ha, never 0). Other important features included an intermediate number of woody stems ≥2.5 cm dbh (25-250/ha) and dense ground vegetation (always >85%) (Table 8).

These characteristics describe brushy old fields and grasslands containing a few larger trees. Considering all grassland study areas, canopy height and density of stems <2.5 cm dbh were greatest on the two used by field sparrows.

Table 8. Important characteristics of field sparrow habitat in Missouri (N = 51).

	Optimum		*Main*		*Avoided*	
Variable	*Range*	*%*[a]	*Range*	*%*	*Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	350-700*	33	25-1050	73	0*	0
Canopy height (m)	2-4*	35	2-8*	92	<2* or >8	8
SECONDARY						
All woody stems ≥2.5 cm dbh/ha	25-50*	41	25-250	70	0*	10
Ground vegetative cover (%)	>95	67	>85	100	<85	0

[a]*Percent of observations.*

**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*

Summary of Other Studies

Woody Vegetation

Arkansas—Preferred habitat included several mid-successional areas, ranging from grassy plots with many small woody stems to a woody field plot with a well-developed understory. The latter plot had 520 small trees/ha ≥7.5 cm dbh and about 11,000 woody stems/ha <7.5 cm dbh (Shugart and James 1973).

Michigan—More breeding pairs of field sparrows inhabited fields as woody invasion progressed, especially red cedar. The trees were used for nesting cover (E.W. Evans 1978).

Pennsylvania—Preferred habitat was old fields invaded by blackberries, dogwoods, and birches, and also several forest types with various stem densities. Open grasslands with few woody stems were avoided (Davis and Savidge 1971).

Ground Vegetative Cover

Vermont and Pennsylvania—Dense vegetation <0.6 m tall was preferred (MacArthur et al. 1962).

Canopy Closure

Arkansas—Field sparrows were abundant in woody old fields with as much as 25% canopy closure, but were less abundant where closure was 47% and lacking where canopy was 74% closed (Shugart and James 1973).

Georgia—Sparrows were found in grassy-shrubby areas with 10-35% shrub cover, and in young pine forest with 33% coverage by pines and 23% by thickets. The species was absent from areas lacking woody vegetation (Johnston and Odum 1956).

Indiana—Of several brushy plots, the least preferred by field sparrows had the greatest amount of woody invasion with 50% canopy closure (Nolan 1963).

Canopy Height

Georgia—Preferred habitat of field sparrows had woody stems 1.8-7.5 m tall (Johnston and Odum 1956).

Illinois—Field sparrows inhabited shrub-grasslands with trees <8 m tall, but not grassland lacking trees (Best 1977).

Indiana—Grassy and brushy old fields, some with numerous small trees <7 m tall, supported higher populations than brushy fields with half the ground shaded by saplings ≥7 m tall (Nolan 1963).

Vermont and Pennsylvania—Field sparrows inhabited areas with few woody stems >4.5 tall, and with sparse to moderate vegetation at heights of 0.6-4.5 m (MacArthur et al. 1962).

Conclusions

As the name implies, field sparrows are found in old field or brushy grassland-pasture habitat (Fitch 1958, Mengel 1965, Bent 1968, DeGraaf et al. 1980). The main requirement appears to be presence of low to intermediate densities of small trees and shrubs. Canopy height and woody stem densities found on field sparrow song perch plots in our study reflect this requirement.

Male field sparrows apparently prefer small trees or shrubs for song perches (Bent 1968, Gates and Gysel 1978). In our study, most males sang from woody vegetation 1-8 m tall (98% of observations). Additionally, most nests, except early ones, are placed in low, woody vegetation (Crooks and Hendrickson 1953, Bent 1968, Best 1978, E. W. Evans 1978).

Habitat characteristics selected as important in our study describe most mid-successional stages between grassland or recently disturbed land and forest. These characteristics appear to delineate field sparrow habitat in most parts of the breeding range.

Overgrown Grassland - Old Field

Willow Flycatcher

Willow flycatchers were found only on one grassland study area; it was unmanaged and had a small stream flowing through it. The characteristics most consistently describing habitat around song perches were intermediate to tall ground vegetation (0.40-0.70 m, never <0.35), and a low (always 4-10 m), open canopy (always 5-30%). Other important features included dense ground vegetation (always >90%), at least a few woody stems ≥2.5 cm dbh (always 24-300/ha), an intermediate to high number of woody stems <2.5 cm dbh (always >350/ha), and a litter layer of intermediate depth (l-4 cm) and intermediate to dense coverage (>60%) (Table 9). Proximity of water was an important feature of song perch habitat; distance to water averaged 11.1 m.

Willow flycatchers used a specific portion of the available habitat, consisting of unmanaged grasslands with abundant woody vegetation and nearby water. Most males sang from dense thickets near a stream. Therefore, clumping of low, woody vegetation probably is a habitat prerequisite.

Summary of Other Studies

Woody Vegetation

Utah (isolated valley in UT, AZ, NV)—High shrub density was selected by MVA as an important habitat factor (Whitmore 1977).

Various Localities—Presence of numerous small tree and shrub thickets seemed to be a requirement for willow flycatcher habitat (Bent 1942, Berger and Parmelee 1952, Meanley 1952, King 1955, Stein 1958, Graber et al. 1974).

Ground Vegetative Cover

Utah—Moderate ground vegetative cover was a prominent feature of willow flycatcher habitat (Whitmore 1977).

Wyoming—Ground cover was abundant in aspen grove habitat (Salt 1957).

Canopy Closure

Utah—Little canopy closure was an important factor (Whitmore 1977).

Table 9. Important characteristics of willow flycatcher habitat in Missouri (N = 12).

Variable	*Optimum Range*	*%*[a]	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Ground vegetative height (m)	.50-.60*	42	.40-.70*	92	<.40† or >.70	8
Canopy closure (%)	5-10*	33	5-30	100	<5* or >30	0
Canopy height (m)	4-6*	50	4-10*	100	<4* or >10	0
SECONDARY						
All woody stems <2.5 cm dbh/ha	6300-6650*	25	>350	100	<350*	0
All woody stems ≥2.5 cm dbh/ha	24-50	33	24-300	100	0* or >300	0
Ground vegetative cover (%)	>90	100	>90	100	<90	0
Litter cover (%)	>95	33	>60	92	<60	8
Litter depth (cm)	1.0-4.0	75	1.0-4.0	75	<1.0†	8

[a]*Percent of observations.*

**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, $P<0.05$).*

†$P<0.10$.

Wyoming—Aspen groves frequented by this flycatcher had open canopies (Salt 1957).

Canopy Height

Utah—Presence of a few large trees was an important habitat factor for willow flycatchers as determined by MVA (Whitmore 1977).

Wyoming—Habitat included shrublands with irregular cover of willows 0.6-1.2 m tall and a few clumps 3.0-3.6 m tall, and aspen groves with trees 12-21 m tall (Salt 1957).

Proximity of Water

Various Localities—Habitat selection was partly dependent on proximity of water in some areas (Bent 1942, Walkinshaw 1966), but no preference for mesic sites was shown in many other localities (Bent 1942, Meanley 1952, King 1955, Stein 1958, Graber et al. 1974, DeGraaf et al. 1980).

Wyoming—Willow flycatcher habitat consisted of mesic sites (Salt 1957).

Plant Species

U.S.—Close association with willow thickets was noted in some localities (Bent 1942, Graber et al. 1974).

Utah—Crowding out of stream-side willows by the introduced shrub tamarix, perhaps unsuitable for willow flycatcher nesting, may have accounted for a drastic decrease in flycatcher population in an isolated valley (Whitmore 1977).

Conclusions

Throughout their range, willow flycatchers use a wide variety of open, brushy habitats under both mesic and xeric conditions. Some discrepancies appear in the published literature on habitat preferences in different geographical locations. Identification and classification problems of the alder-willow flycatcher complex (Graber et al. 1974) probably account for much of the confusion about habitat preferences.

Proximity of water, especially in western areas, is probably related to the selection of low, relatively dense, woody vegetation which commonly grows near water or on moist sites. An apparent preference for willow thickets may simply reflect the fact that willows in low, moist sites frequently provided the acceptable vegetative structure pattern for willow flycatchers.

All published accounts agree on the requirement of numerous small trees and shrubs, but the upper and lower size limits (canopy height) are questionable. In our study, willow flycatchers were not found in areas with a canopy >10 m high. In contrast, a few larger trees were an important component of habitat in the Virgin River Valley of Utah, Arizona, and Nevada (Whitmore 1977). Groves of larger trees

(12-21 m tall) also were used in Wyoming (Salt 1957). Small woody stems provide nest sites and song perches. Most nests are located 1.2-2.1 m above ground in small trees or shrubs (Graber et al. 1974, DeGraaf et al.
1980). In our study, all song perches were located in woody vegetation 1-10 m tall.

The most consistent features of habitat in the published studies were numerous small trees and shrubs, a few larger trees, and a moderate to well developed ground layer. With the exception of canopy height and litter layer characteristics, the results of our study appear to describe willow flycatcher habitat adequately in most locations.

Bell's Vireo

Bell's vireos were observed in old field, grassland, and bottomland forest-edge habitats. Habitat around song perches most consistently had intermediate to tall ground vegetation (>0.40 m), an intermediate to large number of woody stems <2.5 cm dbh (>700/ha, never <145), and a low to intermediate canopy (2-8 m). Another important feature was few to intermediate numbers of woody stems ≥2.5 cm dbh (24-1100/ha) (Table 10).

These characteristics describe brushy grassland-old field or forest edge habitat with tall ground vegetation. Of all grassland study areas, woody invasion was greatest on the two utilized by Bell's vireos.

Table 10. Important characteristics of Bell's vireo habitat in Missouri (N = 54).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	1700-2100*	11	>700	94	<700*	6
Ground vegetative height (m)	.40-.70*	56	>.40	83	<.40*	17
Canopy height (m)	2-4*	28	2-14	87	<2*	6
SECONDARY						
All woody stems ≥2.5 cm dbh/ha	24-100	28	24-1100	91	0*	6

[a]*Percent of observations.*

**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*

Summary of Other Studies

Woody Vegetation

Arkansas—Presence of a few large trees was selected as an important habitat factor by MVA (James 1971). Habitat included grasslands with few to numerous small woody stems, but not mowed fields with no woody stems. Old fields with >800 woody stems <7.5 cm dbh/ha and with >300 woody stems ≥7.5 cm dbh/ha were also excluded (Shugart and James 1973).

Indiana—Habitat consisted of areas with abundant low shrubs, thickets, or brier tangles (Mumford 1952). Habitat included areas with high densities of small woody stems and trees, but not old fields with sparse woody cover (Nolan 1963).

Kansas—Thickets or old fields were favored Bell's vireo habitat (Barlow 1962).

Ground Vegetative Cover

Arkansas—Dense ground cover was selected as an important factor for Bell's vireos (James 1971).

Indiana—Acceptable habitat had dense ground cover (Mumford 1952, Nolan 1963).

Canopy Height

Indiana—Areas with numerous small trees 0.3-0.5 m tall provided habitat, but not areas with numerous larger trees 1.0-7.0 m tall (Nolan 1963).

Plant Species

Indiana—Small trees of several species including plum provided suitable habitat (Mumford 1952).

U.S.—A preference for wild plum thickets was shown by Bell's vireos in some localities (Bent 1950, Fitch 1958).

Conclusions

Throughout their range, Bell's vireos inhabitat brushy thickets in a variety of open situations ranging from forest openings and orchards to grassland-old field areas (Bent 1950). These vireos possibly respond to any brushy area in whatever open habitat and of whatever species available. Dense, brushy cover provided nest sites in Indiana (Mumford 1952). Bell's vireos in Illinois were observed below 1.8-2.1 m in shrubby vegetation (Pitelka and Koestner 1942). In our study, most Bell's vireos were observed singing at heights of 1-8 m (94%) in woody vegetation 1-8 m tall (80%).

Density of small woody stems is the only habitat characteristic selected in our study that probably would describe habitat in most parts of the breeding range.

Some measure of openness of vegetation (canopy closure or density of larger woody stems) might also be useful in quantifying habitat characteristics of Bell's vireos.

Prairie Warbler

Prairie warblers were found primarily in old fields, although two were also observed in grasslands. The most consistent characteristics of habitat around song perches were ground vegetation of intermediate height (0.30-0.50 m, never <0.30 or >0.65) and a low canopy (2-10 m, never <2 or > 14). Other important features included an intermediate number of woody stems <2.5 cm dbh (24-2100/ha, never <24), few woody stems ≥2.5 cm dbh (24-800/ha) and dense ground vegetation (always >80%) (Table 11).

These characteristics describe brushy grassland-old field or forest edge habitat. Of all grassland study areas, the two utilized by prairie warblers had the greatest densities of small trees and shrubs.

Table 11. Important characteristics of prairie warbler habitat in Missouri (N = 21).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Ground vegetative height (m)	.40-.50*	43	.30-.50*	81	<.30* or >.65	0
Canopy height (m)	6-8*	52	2-10	95	<2* or >14	0
SECONDARY						
All woody stems <2.5 cm dbh/ha	24-350	24	24-2100	77	0*	0
All woody stems ≥2.5 cm dbh/ha	24-100	29	24-800	86	0*	5
Ground vegetative cover (%)	>95	71	>80	100	<80	0

[a]*Percent of observations.*

**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*

Summary of Other Studies

Woody Vegetation

Arkansas—Habitat of prairie warblers included burned grasslands with a few dead woody stems, grasslands with numerous shrub and small tree stems, and old fields with about 1100 woody stems <7.5 cm dbh/ha, and 525 stems ≥7.5 cm dbh/ha. Also included were red cedar glades with few woody stems <7.5 cm dbh (675/ha) and about 315 stems ≥7.5 dbh/ha. Mowed hayfields lacking woody vegetation, forest edge, and oak forest were not used (Shugart and James 1973).

Massachusetts—Burned-over pine barrens with about 13,000 live trees/ha and an oak shrub layer of 9400 clumps/ha were preferred to an area with about 800 dead trees/ha (Moore 1980).

Ground Vegetative Cover

Indiana—Habitat for prairie warblers consisted of old fields with sparse ground cover, fields with dense cover of low woody vegetation and herbs, and brushy fields with 50% canopy coverage by saplings ≥ 7 m tall (Nolan 1963).

U.S.—Preferred habitat in various localities had ≥90% ground coverage, but sometimes 80% (Nolan 1978).

Vermont and Pennsylvania—Suitable habitat had moderate to dense vegetation at 0-0.6 m and at 0.6-4.5 m (MacArthur et al. 1962).

Canopy Closure

Arkansas—Burned grasslands with a few dead small trees, old fields with 25% canopy closure, and cedar glades with 47% closure were used by prairie warblers. Mowed hayfields lacking woody vegetation, forest edge, and oak forest with ≥ 64% closure did not provide suitable habitat (Shugart and James 1973).

Georgia—Grass shrubland with 35% shrub cover and 25 year-old pine forest with 33% coverage by pines and 23% by thickets were used. Grassland with ≤10% coverage, and older pine forest were not used (Johnston and Odum 1956).

Indiana—All types of deciduous shrub habitat ranging from old fields with little tree or brush coverage to fields with 50% canopy closure provided by saplings were used (Nolan 1963).

Massachusetts—A pine barren burned 13 years earlier, having live trees covering 26% and a shrub layer covering 53% of the area constituted prairie warbler habitat (Moore 1980).

U.S.—Habitat of prairie warblers in various parts of the U.S. had 6-25% canopy closure, sometimes as high as 50% (Nolan 1978).

Canopy Height

Georgia—Habitat included grassy-shrubby areas with woody vegetation 2-8 m tall, but not areas with woody vegetation <2 m tall (Johnston and Odum 1956).

U.S.—Preferred habitat in various localities had canopy heights 6-13 m, sometimes >13 m (Nolan 1978).

Virginia—Prairie warblers preferred 12-year-old clearcut areas with woody vegetation 3-5 m tall to areas clearcut 3-7 years previously, with vegetation 1.5-3.5 m tall. The birds seldom used or avoided 1-year-old clearcuts with canopy heights of 0.3-1.0 m, and pole or older forest stands with canopy heights >8 m (Conner and Adkisson 1975).

Plant Species

Northeastern U.S.—A preference for coniferous cover was recorded (DeGraaf et al. 1980).

Conclusions

Prairie warblers inhabit a wide variety of shrubby habitat including open southern pine forest with a well developed shrub layer, sand dunes with a sparse, open belt of shrubby plants, mangroves of varied density, jack pine plains with sparse ground cover, abandoned fields with woody vegetation of varying amounts, grassland-forest edge, forest disturbed by lumbering or fire, and the Great Dismal Swamp of the southeastern U.S., with a closed canopy (Nolan 1978).

Ground vegetation height and coverage appear to vary with specific habitat types. Amount of woody vegetation at heights >0.6 m is probably more important. Prairie warblers nest in small trees or shrubs and males sing from this relatively low, woody vegetation. Nests are typically 1-10 m above ground (Harrison 1975). Males in our study always sang at heights >1 m, in shrubs or trees 2-14 m tall.

Preferred habitat in various localities consisted of trees 6-13 m tall, sometimes >13 m tall; 6-25% canopy closure, sometimes as high as 50%; coverage by shrubs and trees <2 m tall usually <50%; and ground cover of ≥90%, but often as low as 80% (Nolan 1978).

Prairie warbler habitat selection appears to depend on the amount of woody vegetation available. Prairie warblers occur in many different habitat types with various densities of shrubs and small trees. Habitat with no woody vegetation or with numerous large trees apparently does not usually support prairie warbler populations.

Yellow-breasted Chat

Yellow-breasted chats were observed primarily in old fields, although several were also noted in grassland and all forest habitat types. Habitat around song perches consistently had a low to intermediate canopy (4-10 m) and a low to intermediate number of woody stems <2.5 cm dbh (350-6300/ha, never <120). Other important features included at least a few woody stems ≥2.5 cm dbh (100-2000/ha) and intermediate to tall ground vegetation (>0.30 m) (Table 12).

These characteristics describe late seral old field or forest edge habitat with tall

ground vegetation. Woody invasion was prominent on the only two grassland study areas used by chats.

Table 12. Important characteristics of yellow-breasted chat habitat in Missouri (N = 39).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	700-1050*	21	350-6300	80	<350*	8
Canopy height (m)	6-8*	51	4-10	77	<4* or >16	5
SECONDARY						
All woody stems ≥2.5 cm dbh/ha	400-500*	18	100-2000	85	0*	3
Ground vegetative height (m)	.50-.60†	23	>.30	82	<.30	18

[a]*Percent of observations.*
**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*
†P<0.10.

Summary of Other Studies

Woody Vegetation

Arkansas—Old fields with 675-1138 woody stems <7.5 cm dbh/ha and 305-525 stems ≥7.5 cm dbh/ha provided primary habitat, but not mowed hayfields lacking woody vegetation or oak forest (Shugart and James 1973).

Canopy Closure

Arkansas—Preferred habitat included old fields with 17-47% canopy closure, but not mowed hayfields with no canopy or oak forest with ≥64% canopy closure (Shugart and James 1973).

Georgia—Suitable chat habitat was provided by shrub-grasslands with 10-35% shrub cover, but not areas lacking woody vegetation or young pine forest with 33% canopy coverage by pines and 23% coverage by shrubs (Johnston and Odum 1956).

Indiana—Several old field types provided adequate habitat, but not brushy fields with saplings shading 50% of the ground, or nearly continuous stands of

large, dense hawthorn (Nolan 1963).

Tennessee—Important features of habitat selected by MVA included dense overstory and open subcanopy in a forested area (Anderson and Shugart 1974).

Vermont and Pennsylvania—Habitat had moderate to dense vegetation at 0.6-4.5 m (small tree and shrub layer) and sparse vegetation above 4.5 m (MacArthur et al. 1962).

Canopy Height

Georgia—Shrub grasslands with woody vegetation <7.5 m tall provided suitable habitat, but not young pine forest (Johnston and Odum 1956).

Indiana—Fields with blackberry thickets and stands of small trees 1-7 m tall were preferred chat habitat, as were old fields with numerous small trees 0.3-5.0 m tall. Brushy fields with saplings ≥7 m tall were not preferred (Nolan 1963).

Virginia—Chat habitat included bottomland forest with trees 9-12 m tall (Dennis 1958). Woody vegetation 1-5 m tall in areas clearcut 3-12 years previously was used by chats (Conner and Adkisson 1975).

Conclusions

Yellow-breasted chats usually occur in dense thickets in most wooded habitats from overgrown old fields to forests (Bent 1953, Griscom and Sprunt 1957, Fitch 1958, Mengel 1965, DeGraaf et al. 1980). Although density of brushy vegetation was variable on an Indiana study area inhabited by chats, males concentrated their activities in areas with the densest vegetation (Thompson and Nolan 1973). The amount of low woody vegetation apparently was the most important determinant of habitat suitability for chats. Habitat descriptions in other studies were based primarily on woody vegetation. Low woody stems provided nesting and feeding substrates (Whitmore 1977, DeGraaf et al. 1980), and song perches (our study, vegetation 1-14 m tall).

As concluded from our study, chats typically are found in habitat with a relatively low canopy (4-12 m), numerous small woody stems, and a few larger trees. However, the exact number of woody stems was quite variable. Spatial heterogeneity of shrubs and small trees (clumping) probably is more important than the number of stems per area. Ground vegetation development possibly is not important, but is indicative of preferred brushy habitat in various geographic locations.

Coverage by shrubs and small trees (1-10 m) and possibly heterogeneity should be considered when assessing yellow-breasted chat habitat.

Orchard Oriole

Orchard orioles were observed in grassland, old field, and bottomland hardwood habitats. Habitat around song perches usually had a low to intermediate canopy (4-20 m) and few woody stems ≥2.5 cm dbh (24-400/ha, never 0). Another

important feature was a low to intermediate number of woody stems <2.5 cm dbh (24-3150/ha) (Table 13).

These characteristics loosely describe overgrown grassland-old field, forest edge, or open forest habitat. Grassland study plots used by orchard orioles in our investigation were those having the greatest amount of woody invasion.

Table 13. Important characteristics of orchard oriole habitat in Missouri (N = 25).

Variable	*Optimum* *Range*	*%*[a]	*Main* *Range*	*%*	*Avoided* *Range*	*%*
PRIMARY						
Ground vegetative height (m)	24-100	24	24-400	64	0*	0
Canopy height (m)	6-8†	36	4-20	92	<4 or >20	8
SECONDARY						
All woody stems ≥2.5 cm dbh/ha	24-350	16	24-3150	72	0*	4

[a]*Percent of observations.*
**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*
†P<0.10.

Summary of Other Studies

No published quantitative data were found suitable for comparison with our data on habitat surrounding song perches.

Conclusions

Orchard orioles are found in a variety of sparsely wooded habitats including orchards, woodland edge, open woodland and shade trees near human habitations (Bent 1958, Fitch 1958, Mengel 1965, DeGraaf et al. 1980); but this oriole avoids heavily wooded forests (Harrison 1975). A distinct shrub layer with a few larger trees provides foraging habitat (Evans and Kirkman 1981) and nesting habitat (Harrison 1975). Nests are commonly located 3.0-6.1 m above ground in shrubs or trees.

Published quantitative descriptions of habitat requirements for comparison to the results of our study are lacking. Moreover, broad ranges for the selected habitat characteristics discussed above preclude accurate habitat delineation.

American Goldfinch

American goldfinches were observed on old field and grassland study areas. Habitat around song perches was most consistently characterized by a low to intermediate canopy (3-8 m, never <3 or >12) and intermediate to tall ground vegetation (0.40-0.80 m, never <0.35). Other important features included a low to intermediate number of woody stems ≥2.5 cm dbh (always 50-550/ha), a low to intermediate number of woody stems <2.5 cm dbh (always >400/ha), dense ground vegetation (always >80%), and shallow litter (always <3.0 cm) (Table 14).

The above characteristics describe late successional old fields and grasslands, or forest edge. In our investigation, the two grassland study areas having the greatest woody invasion were utilized by goldfinches.

Table 14. Important characteristics of American goldfinch habitat in Missouri (N = 11).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Ground vegetative height (m)	.40-.80†	82	.40-.80†	82	<.40	9
Canopy height (m)	6-8*	55	3-8	91	<3* or >12	0
SECONDARY						
All woody stems <2.5 cm dbh/ha	400-700†	27	400-5250	91	<400	0
All woody stems ≥2.5 cm dbh/ha	100-550	91	50-550	100	<50 or >550	0
Ground vegetative cover (%)	>95	82	>80	100	<80	0
Litter depth (cm)	1.0-2.0	50	.1-3.0	100	>3.0	0

[a]*Percent of observations.*
**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*
†P<0.10.

Summary of Other Studies

Woody Vegetation

Arkansas—Brushy old fields with 805-1138 woody stems <7.5 cm dbh/ha and 305-525 stems ≥7.5 cm dbh/ha provided suitable habitat, but not mowed hayfields

lacking woody vegetation, red cedar glades, forest edge, or forested areas (Shugart and James 1973).

Indiana—Optimum habitat consisted of old fields with relatively little woody vegetation, but goldfinches were also found in several types of deciduous scrublands with sparse to dense, low woody vegetation (Nolan 1963).

Oregon—Goldfinches inhabited Oregon white oak stands with varying densities of trees (110-378/ha) (Anderson 1970).

Ground Vegetative Cover

Indiana—Of several types of scrublands with low woody vegetation, those with thin ground cover were preferred (Nolan 1963).

Wyoming—Aspen groves with a well-developed ground layer were used by goldfinches, but not scrub meadows with abundant ground cover (Salt 1957).

Canopy Closure

Arkansas—Suitable goldfinch habitat was provided by brushy old fields with canopy closures 17-25%, but not forested areas with >45% canopy closure, cedar glades, nor areas lacking woody vegetation (Shugart and James 1973).

Oregon—Stands of Oregon white oak with canopy closure 44-82% provided goldfinch habitat, but areas with 44-61% closure were preferred (Anderson 1970).

Canopy Height

Indiana—Habitat consisted of several types of deciduous scrublands with canopies 0.3-7.0+ m high (Nolan 1963).

Oregon—Several types of Oregon white oak stands with trees 9-18+ m tall provided goldfinch habitat (Anderson 1970).

Virginia—Goldfinches used 1-year-old clearcuts with woody vegetation 0.3-1.0 m tall, and to a lesser extent, 3- to 12-year old clearcuts with woody vegetation 1-5 m tall (Conner and Adkisson 1975).

Wyoming—Groves of aspen trees 12-21 m tall provided American goldfinch habitat, but not scrub-meadow and willow-sedge swamp with trees 0.6-3.6 m tall (Salt 1957).

Conclusions

Throughout their breeding range, American goldfinches are associated with a variety of habitats including open weedy fields, pastures with scattered trees, forest edge, orchards, groves, farms and villages (Harrison 1975, DeGraaf et al. 1980). Some of the highest population densities occurred in open swamp habitat (Nickell 1951). This generalist nature is reflected in the seeming inconsistencies in habitat descriptions of the above studies.

Habitat characteristics included canopy heights of 1-21 m, ground vegetative heights of 0.4-0.8 m (our study only), a few to many small woody stems and

0-500+ larger trees per ha, sparse to dense ground vegetative cover, shallow litter layer (our study only), and canopy closures of 0-82%. The primary criterion appears to be presence of a few to many small woody stems. Shrubs and small trees provide nest sites (Stokes 1950, Nickell 1951, Berger 1968) and song perches (this study). Males always sang from woody vegetation 1-12 m tall in our study. In a Louisiana bottomland forest, most goldfinches restricted their activity (singing males excluded) to heights of 0.6-7.6 m above ground (Dickson and Noble 1978).

Another essential component of habitat possibly is proximity of thistles or other composites. All nests located in a Michigan study were within 180-270 m of thistle patches (Nickell 1951). Goldfinches forage on thistle seeds and incorporate thistle down into nests. (Harrison 1975). In the northeastern U.S., feeding areas can be >1.6 km from nest sites (DeGraaf et al. 1980).

Although goldfinches appeared to require a specific habitat type in our study, they typically occurred in a wide variety of habitats from grassland-old fields with sparse woody vegetation to bottomland forest with relatively dense canopy closure and tall trees in other studies. Thus, results of our study may not apply in many other locations.

Forest Interior - Forest With Some Large Trees

Pileated Woodpecker

Pileated woodpeckers were found primarily in central Missouri upland hardwoods, but were also noted in all other forest types. The most consistent characteristic of habitat around song perches was an intermediate canopy height (15-20 m, never <15). Other important features included short ground vegetation (0.02-0.30 m), a nearly closed to closed canopy (>80%), intermediate ground vegetation coverage (50-70%), a relatively low number of woody stems ≥2.5 cm dbh (800-1200/ha, but never <800), and an intermediate number of dead stems 2.5-9.9 cm dbh (50-100/ha) (Table 15).

Summary of Other Studies

Density of Trees

Oregon—Nesting habitat of pileated woodpeckers had a mean number of 440 stems >10 cm dbh/ha; the range was 230-973 stems/ha (Bull and Meslow 1977).

Dead Stems

Oregon—Density of snags >10 cm dbh ranged from 10-130/ha, and averaged 47/ha at nest sites (Bull and Meslow 1977).

Various Localities—Large dead stems (>45 cm dbh) numbering 13-24/40 ha

were required to maintain good populations of pileated woodpeckers (Bull and Meslow 1977, Evans and Conner 1979, Bull et al. 1980). The presence of larger snags (>33 cm dbh) is critical for nesting and roosting cavities (Conner et al. 1975, Hardin and Evans 1977, Evans and Conner 1979, Thomas et al. 1979, Bull et al. 1980).

Canopy Closure

California—Closure was >39% in optimum habitat in the Sierra Nevadas (Verner 1980).

Eastern U.S.—Canopy closure was positively correlated with pileated woodpecker abundance (Robbins 1978).

Canopy Height

California—Mature forests with trees >15 m tall constituted optimum pileated woodpecker habitat in the Sierra Nevadas (Verner 1980).

Table 15. Important characteristics of pileated woodpecker habitat in Missouri (N = 18).

	Optimum		*Main*		*Avoided*	
Variable	*Range*	*%*[a]	*Range*	*%*	*Range*	*%*
PRIMARY						
Canopy height (m)	16-20	56	15-20	78	<15	0
SECONDARY						
All woody stems ≥2.5 cm dbh/ha	900-1000*	33	800-1200	61	<800 or >1200	39
Dead stems 2.5-9.9 cm dbh/ha	50-100†	39	50-100†	39	<50	17
Ground vegetative cover (%)	55-60*	22	50-70	56	>70	11
Ground vegetative height (m)	.02-.20	67	.02-.30	89	<.02 or >.30	11
Canopy closure (%)	>95	22	>80	67	<55	6

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

†P<0.10.

Virginia—Tall canopy was selected as an important habitat feature by MVA (Conner and Adkisson 1977).

Size of Contiguous Habitat

Various Localities—Extensive forest tracts are required by pileated woodpeckers (Bent 1939, DeGraaf et al. 1980). These woodpeckers are seen in forested tracts of 40 ha (C.S. Robbins, personal communication) but territory size in Virginia was 70 ha (Evans and Conner 1979). Several small woodlots may suffice in Missouri (J.E. Rathert, personal communication).

Tree Species Composition

Eastern U.S.—A positive correlation existed between oak composition and pileated woodpecker abundance (Robbins 1978).

Illinois—In apparent contrast, a negative correlation existed between the percentage of oak and hickory trees and pileated woodpecker abundance. Forests with a more even balance of tree species were preferred. But there was a positive correlation between the number of hackberry trees >22 cm dbh and abundance of this species in bottomlands (Graber et al. 1977).

Proximity of Water

Virginia—All of 18 nests were within 150 m of water, and usually <50 m (Conner et al. 1975).

Conclusions

The results of our study appear inconsistent in some respects with those of several other studies. Dissimilar methods of data collection and analysis at least partly explain these inconsistencies.

Habitat with tall ground vegetation was preferred by pileated woodpeckers in Oregon (Bull and Meslow 1977) but this layer primarily consisted of shrubs. Shrubs >1 m tall were not included in the ground layer in our study. Selection for short ground vegetation of intermediate coverage probably reflects other, more important attributes of pileated woodpecker habitat. For instance, ground layer development is affected by the extent of canopy closure which was relatively complete. However, pileated woodpeckers sometimes forage on or near the ground (Bent 1939, Dickson and Noble 1978, Brawn 1979), and a short ground layer would allow easier foraging.

Statements about importance of stand density and large-tree density varied considerably among publications. Densely stocked stands were preferred in many localities (Conner et al. 1975, Conner and Adkisson 1977, Hardin and Evans 1977, Scott et al. 1977). Although pileated woodpecker song perch plots typically had 800-1200 stems ≥2.5 cm dbh/ha in our study, these plots had relatively low densities

of trees when compared to forest habitat used by other species. Mean density of stems ≥10 cm dbh in our study compared favorably with mean density in Oregon nesting habitat (Bull and Meslow 1977). Apparent lack of selection in our study for densely stocked stands possibly indicates that all our forest study areas were sufficiently dense to support pileated woodpeckers.

A preference for forest areas with large trees was not evident from the tree size categories (≥30 cm dbh) used for data analysis in our study. Habitat around song perches always had relatively high densities of trees >23 cm dbh (>70/ha). Pileated woodpeckers prefer forest areas with most trees >22 cm dbh and several trees 38-54 cm dbh (Conner et al. 1975, Hardin and Evans 1977).

Information on requirements for various sized snags was also inconsistent. In our study, the importance of snags 2.5-9.9 cm dbh possibly was related to foraging behavior, as pileated woodpeckers in the same general location often foraged on smaller trees (Brawn 1979). Additionally, the presence of numerous large snags did not appear critical in our study. Large snags were sparsely distributed in most forest habitat, as 78% of all forest song perch plots (all bird species) had no snags ≥30 cm dbh. A large number of our relatively small sample plots (0.04 ha) would be needed to sample large snags adequately over extensive areas. A minimum of 3-4 snags is required within the 70-240 ha territory of a pileated woodpecker pair (Bull and Meslow 1977, Evans and Conner 1979, Bull et al. 1980).

We did not investigate several characteristics of habitat that appeared important in other studies. These included size of contiguous habitat, proximity of water to the nest, and tree species preferences.

The selected habitat characteristics in our study probably would not readily assess suitable habitat in most other locations. Pileated woodpeckers appear to respond most to older forest stands (canopy height >15 m and numerous trees >38 cm dbh), the presence of a few large snags >33 cm dbh per territory, relatively high tree densities (although not in our study), and large forest area.

Red-bellied Woodpecker

Red-bellied woodpeckers were observed in all forest habitats. Several were also found on isolated large trees in old fields. These woodpeckers are generalists, and no primary variables were identified. Secondary habitat characteristics included intermediate ground vegetation height (0.10-0.50 m), an intermediate to high canopy (16-24 m), and a large number of dead stems 2.5-9.9 cm dbh (50-200/ha) (Table 16).

These characteristics loosely describe a pole to mature forest with numerous small snags.

Summary of Other Studies

Density of Trees

Arkansas—Habitat included forested areas with 558-1825 woody stems <7.5 cm dbh/ha and 315-918 stems ≥7.5 cm dbh/ha (Shugart and James 1973).

Dead Stems

U.S.—Approximately 220-270 large snags (optimum size, 36-53 cm dbh) were required per 40 ha of habitat (Evans and Conner 1979).

Canopy Closure

Arkansas—Forested areas with canopy closure 47-74% provided habitat for red-bellied woodpeckers, but not wooded areas with ≤25% closure or forest edge (Shugart and James 1973).

Size of Contiguous Habitat

Eastern U.S.—Forest areas of at least 3.0-7.5 ha were required for red-bellied woodpecker habitat (Galli et al. 1976, Robbins 1979).

Tree Species Composition

Illinois—Maple-ash associations were important forest habitat (Williams 1975, Graber et al. 1977).

Kansas—Oak-hickory woodlands were preferred habitat for red-bellied woodpeckers (Fitch 1958).

Table 16. Important characteristics of red-bellied woodpecker habitat in Missouri (N = 43).

Variable	*Optimum* *Range*	*%*[a]	*Main* *Range*	*%*	*Avoided* *Range*	*%*
PRIMARY						
(none)						
SECONDARY						
Dead stems 2.5-9.9 cm dbh/ha	50-100	26	50-200	58	<50†	12
Ground vegetative height (m)	.10-.20	30	.10-.50	85	<.10†	9
Canopy height (m)	16-20	51	16-24	72	<12	2

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

Conclusions

Red-bellied woodpeckers are forest generalists; therefore, no habitat characteristics consistently delineated habitat in the above studies. In a Tennessee study, no habitat characteristic of 28 tested was strongly correlated with red-bellied woodpecker abundance (Anderson and Shugart 1974).

Large, dead trees are not necessarily required for nesting since red-bellied woodpeckers often excavate cavities in dead limbs of live trees (Bent 1939, Reller 1972, Graber et al. 1977, Scott et al. 1977); but in some areas most nests are in snags (Jackson 1976). Red-bellied woodpeckers require a minimum of four cavities for roosting and nesting within the territory, and territories are approximately 6 ha in size. To maintain good population levels under these conditions, 220-270 large snags are required for 40 ha of habitat (Evans and Conner 1979), or trees with large dead limbs.

Snags of various sizes also provide feeding, perching and drumming sites. Possibly such uses of small snags explain the seeming importance of dead stems 2.5-9.9 cm dbh observed in our study. However, our results do not agree well with those of another central Missouri study (Brawn 1979) in which snags considerably larger than 10 cm dbh were frequented by red-bellied woodpeckers for nesting and other uses. In our study, 41% of red-bellied woodpeckers located were on dead trees.

Habitat other than forest is sometimes used for foraging and includes shrubland or pasture (Graber et al. 1977) and cornfields (DeGraaf et al. 1980). Winter habitat can also differ from breeding habitat. Red-bellied woodpeckers in Illinois ofter wintered in more open habitats than they used during the breeding season (Graber et al. 1977).

Throughout the range, red-bellied woodpeckers occur in most forest types, but appear to prefer larger expanses of mature forest (Scott et al. 1977), especially bottomland forest (Bent 1939, Bond 1957, Graber et al. 1977, DeGraaf et al. 1980). The main range of canopy height (16-24 m) in our study reflects this preference for older forest areas. The primary requirements appear to be forest with a minimum canopy height of approximately 12-16 m (presence of larger trees for nesting and roosting) and minimum area size of 3.0-7.5 ha.

Great Crested Flycatcher

Great crested flycatchers were found in all forest habitat types except upland hardwoods in southeastern Missouri. The only characteristic consistently describing habitat around song perches was an intermediate to high canopy (16-28 m, never <12) (Table 17). Canopy height averaged <15 m on the only central Missouri upland hardwood study area in which these flycatchers were not observed. Discriminant function analysis selected canopy height as the most important variable differentiating this study area from all other central Missouri upland study areas.

Table 17. Important characteristics of great crested flycatcher habitat in Missouri (N = 79).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Canopy height (m)	16-20*	49	16-28	84	<12	0
SECONDARY						
(None)						

[a]*Percent of observations.*
**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

Summary of Other Studies

Dead Stems

U.S.—Large snags (optimum 30 cm dbh) were required for nesting and perching (Evans and Conner 1979).

Understory Development

Georgia—Older forest habitat with well-developed understory was preferred over younger forest with a distinct but spotty understory (Johnston and Odum 1956).

Ohio—Grazed woodlots supported lower populations of great crested flycatchers than ungrazed woodlots (Good and Dambach 1943).

Canopy Closure

Arkansas—Crested flycatcher habitat consisted of oak forests with 64-74% closure, but not red cedar glades with 47% canopy closure, or forest edge (Shugart and James 1973).

Georgia—Several older forest types provided flycatcher habitat, but not young pine with 33% canopy closure (Johnston and Odum 1956).

Ontario—A positive relationship existed between great crested flycatcher abundance and canopy closure along road census routes (Weber and Theberge 1977).

Canopy Height

Georgia—Primary habitat was 100-year-old pine forests, followed by 150-year-old climax oak-hickory forest with canopies 25.5-30.0+ m high. Pine forest 60

years old with canopy 18 m high was less frequently used (Johnston and Odum 1956).

Virginia—Highest populations of great crested flycatchers were in a pole stand with canopy heights 8-11 m; less favored was a mature stand with canopy 23-25 m high; a 12-year-old clearcut with a 3-5 m canopy was seldom used (Conner and Adkisson 1975).

Size of Contiguous Habitat

Eastern U.S.—The minimum woodlot or forest tract size was 0.8 ha (Galli et al. 1976) and 10.0 ha (Robbins 1979).

Tree Species Composition

Illinois—Oak forest habitat was preferred (Graber et al. 1974).

Conclusions

Great crested flycatchers are common in most deciduous or mixed forests, but prefer mature or nearly mature forests, especially open forest areas or edge (Bent 1942, Fitch 1958, Graber et al. 1974). Of 16 oak forests with widely different structures, all provided suitable habitat (Probst 1979).

Great crested flycatchers were probably a forest interior species but have been adapting to more open situations as forestry operations have removed most snags in forest interiors (Bent 1942, Scott et al. 1977). Only 16% of all perches were snags in our study.

Habitat in the above studies had canopy heights of 8-30+ m, canopy closure >60% (often oak trees), a minimum size of 0.8 ha, and well-developed understories. The most consistent requirements of great crested flycatchers appear to be presence or proximity of pole to mature forest and cavities available in live or dead trees.

Acadian Flycatcher

Acadian flycatchers were observed primarily on central Missouri upland hardwood and southeastern Missouri bottomland hardwood study areas. The characteristic most consistently describing habitat around song perches was an intermediate number of live stems ≥30 cm dbh (25-125/ha). Other important features included an intermediate to high canopy (16-24 m, never <10) and intermediate to closed canopy (>60%, never <50) (Table 18).

Summary of Other Studies

Density of Large Trees

Arkansas—Of several successional types, only climax forest with larger (≥7.5

cm dbh) trees averaging 483/ha provided Acadian flycatcher habitat (Shugart and James 1973).

Eastern U.S.—Presence of numerous large trees was selected as an important variable by multiple regression analysis (Robbins 1978).

Georgia—Acadian flycatcher habitat consisted of climax oak-hickory forest with mature trees averaging 45 cm dbh (Johnston and Odum 1956).

Michigan—Areas with trees >56 cm dbh were inhabited by these flycatchers (Walkinshaw 1966).

Wisconsin—Density of trees >10 cm dbh ranged from 373-380/ha (Bond 1957).

Understory-Subcanopy Development

Various Localities—Distinct or dense understories were a feature of preferred habitat (Hespenheide 1971, Graber et al. 1974, DeGraaf et al. 1980); populations were lower in grazed than ungrazed woodlots (Good and Dambach 1943).

Vermont and Pennsylvania—Sparse or moderate vegetation <4.5 m tall and dense vegetation >4.5 m were present in suitable Acadian flycatcher habitat (MacArthur et al. 1962).

Canopy Closure

Arkansas—Climax forest with 74% closure, but not subclimax forest with 64% closure, provided Acadian flycatcher habitat (Shugart and James 1973).

Various Localities—Dense canopy was an important component of Acadian flycatcher habitat (Walkinshaw 1966, Hespenheide 1971, Robbins 1978, DeGraaf et al. 1980).

Wisconsin—These flycatchers inhabited areas with 80-95% canopy closure (Bond 1957).

Canopy Height

Georgia—Mature trees in flycatcher habitat were taller than 30 m (Johnston and Odum 1956).

Michigan—Acadian flycatcher territories always contained tall trees (Walkinshaw 1966).

Virginia—Suitable habitat consisted of mature oak stands with canopy heights 23-25 m, but not pole stands 8-11 m tall (Conner and Adkisson 1975).

Size of Contiguous Habitat

Eastern U.S.—Population densities of this species were considerably lower in forest tracts <30 ha than in forests >30 ha (Robbins 1979).

Conclusions

Acadian flycatchers are usually associated with mature, dense, mesic forest,

Table 18. Important characteristics of Acadian flycatcher habitat in Missouri (N = 63).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Live stems ≥30 cm dbh/ha	65-100*	26	25-125	84	<25 or >125	16
SECONDARY						
Canopy closure (%)	85-90	19	>60	95	<60	5
Canopy height (m)	16-20	44	16-24	70	<16	13

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

especially bottomland forest or cool shady ravines in uplands (Bent 1942, Mengel 1965) with well developed subcanopy and understory layers (Graber et al. 1974, DeGraaf et al. 1980). In our study, a key characteristic on uplands appeared to be distance to water. Song perches on upland sites were always within 20 m (X = 6.4 m) of streams; the perches were typically in shaded ravines.

The importance of understory-subcanopy development in this flycatcher's ecology is evident. Acadian flycatchers nest in the lower canopy of understory layers at heights of 2.4-6.1 m (Harrison 1975). They also forage beneath the canopy (Williamson 1971, Graber et al. 1974, DeGraaf et al. 1980). Song perches are located in the understory-subcanopy layers. In our study, males typically sang from woody stems 1-16 m tall at heights of 1-8 m above ground. Subcanopy coverage was variable in areas used by Acadian flycatchers in our study ranging from 15 to 95%, but usually 35-85%.

The selected habitat characteristics in our study adequately delineate general habitat requirements of relatively numerous large trees, a resulting high canopy, and dense canopy closure. Multiple regression analysis for several eastern U.S. locations selected high, dense canopy, numerous large trees, and areas with high precipitation as the most important features of Acadian flycatcher habitat (Robbins 1978). However, other specific requirements exist which include a well developed understory layer, possibly with openings, habitat moistness or proximity to water, and a relatively large forest size (>30 ha).

Eastern Wood Pewee

Eastern wood pewees were found in all forest habitat types, although most were observed on central Missouri upland hardwood study areas. The characteristic most consistently describing habitat around song perches was an intermediate to high canopy (12-24 m, never <12). Other important features included short to intermediate ground vegetation (0.01-0.40 m), an intermediate to high number of woody stems <2.5 cm dbh (corrected values 2100-7700/ha, never <320), an intermediate number of live stems 10.0-29.9 cm dbh (50-300/ha, never <49) and an intermediate number of live stems 2.5-9.9 cm dbh (250-900/ha, never <120) (Table 19).

These characteristics loosely describe pole to mature forest with relatively short ground vegetation, a well-developed shrub-understory layer, and numerous smaller trees. However, value ranges were so large that habitat requirements were not clearly delineated.

Table 19. Important characteristics of eastern wood pewee habitat in Missouri (N = 58).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Canopy height (m)	16-20*	56	12-24	89	<12	0
SECONDARY						
All woody stems <2.5 cm dbh/ha	2100-2800	18	2100-7700	77	<2100	23
Live stems 2.5-9.9 cm dbh/ha	550-600*	16	250-900	85	<250 or >900	15
Live stems 10.0-29.9 cm dbh/ha	150-200†	23	50-300	82	<50 or >350	9
Ground vegetative height (m)	.10-.20*	43	.01-.40	93	<.01 or >.40	7

[a]*Percent of observations.*
**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*
†P<0.10.

Summary of Other Studies

Density of Small Woody Stems

Various Localities—Habitat descriptions range from prominent to open or

spotty shrub or small tree layers (Bent 1942, Johnston and Odum 1956, Martin 1960, Robbins 1978, DeGraaf et al. 1980).

Density of Trees

Eastern U.S.—Important components of habitat included few small trees and many large trees as selected by MVA (Robbins 1978).

Canopy Closure

Arkansas—Red cedar glades with canopy closure of 47% supported more wood pewees than did oak forests with 64-74% canopy closure (Shugart and James 1973).

Ontario—A direct relationship existed between canopy closure and pewee abundance (Weber and Theberge 1977).

Canopy Height

Georgia—Pine forest 60 years old with a canopy 18 m high was preferred over several other coniferous and deciduous forest types with canopy heights 7.5-30+ m (Johnston and Odum 1956).

Ontario—Wood pewee habitat consisted of a mature sugar maple forest with canopy 24-30 m high, but not other forest types with lower canopies (Martin 1960).

Virginia—Mature oak stands with trees 23-25 m tall provided habitat, but not pole stands with trees 8-11 m tall (Conner and Adkisson 1975).

Size of Contiguous Habitat

Eastern U.S.—Minimum size of area was 2-4 ha, and seemed to be a critical habitat feature (Galli et al. 1976, Robbins 1979).

Tree Species Composition

Eastern U.S.—Presence of numerous oaks was a key habitat component for wood pewees (Robbins 1978); pewees were strongly associated with oaks (DeGraaf et al. 1980).

Illinois—Wood pewees were associated with oaks (Graber et al. 1974).

Conclusions

Eastern wood pewees are common in a variety of wooded habitats including interior and edge of deciduous and coniferous forests, farm woodlots, old orchards, roadsides and parks (Mengel 1965, Harrison 1975, DeGraaf et al. 1980). Wood pewees were found in 16 eastern deciduous forests with widely different structures (Probst 1979). In some localities, this pewee prefers forest edge, forest openings, or discontinuous forest habitat (Bent 1942, Fitch 1958, Hespenheide 1971). The wide range of habitats suitable for pewees explains the many inconsistencies and

discrepancies in published habitat descriptions.

Although degree of development of the shrub-small tree layer varied betwen studies, it possibly is important as a foraging zone. Eastern wood pewees foraged in the lower part of or just below the lower tree canopy (Graber et al. 1974), and the mid to lower canopy (DeGraaf et al. 1980), especially near forest openings.

A minimum area size of 2-4 ha appears critical to pewees (Galli et al. 1976, Robbins 1979). However, there may be a low maximum area size as pewee abundance was negatively correlated with forest size in several eastern U.S. locations (Robbins 1978).

The only habitat characteristic selected as important in our study that also appeared consistent with most other studies was a relatively high canopy (>12 m). Other factors affected eastern wood pewee habitat selection, as pewees were not found in all forest areas with tall trees. In our study, 66% of the singing sites of pewees were in oaks, agreeing with several other studies.

Distribution of pewees in a Tennessee deciduous forest was correlated with many variables, but none appeared to exert a dominant force (Anderson and Shugart 1974).

Tufted Titmouse

Tufted titmice were observed on all central Missouri upland hardwood areas. Several were also noted in all other forest habitats, and one song perch was in an old field. As a result, only two secondary variables appeared important and values of these variables describe most pole to mature hardwood forests. Tufted titmice were usually seen in areas with an intermediate to closed canopy (>75%) of intermediate to great height (12-24 m) (Table 20).

Table 20. Important characteristics of tufted titmouse habitat in Missouri (N = 65).

	Optimum		*Main*		*Avoided*	
Variable	*Range*	*%*[a]	*Range*	*%*	*Range*	*%*
PRIMARY						
(None)						
SECONDARY						
Canopy closure (%)	>75	75	>75	75	<55	5
Canopy height (m)	16-20	41	12-24	84	<12	5

[a]*Percent of observations.*

Summary of Other Studies

Density of Pole or Mature Trees

Eastern U.S.—MVA selected density of trees 16-38 cm dbh as a fairly important habitat feature (Anderson 1979).

Ground Vegetative Cover

Eastern U.S.—Percent ground cover was a key component of titmouse habitat (Anderson 1979).

Understory - Subcanopy Development

Eastern U.S.—Open understory and well-developed subcanopy were prominent features of habitat in Tennessee (Anderson and Shugart 1974), and density of shrub stems was an important variable affecting habitat suitability in eastern U.S. (Anderson 1979), as determined by MVA.

Georgia—Mature forest habitat had well-developed understory layers (Johnston and Odum 1956).

Missouri—Titmice were most abundant in mature oak-hickory forests with open understories, but also were common in forest types with dense understory (Evans and Kirkman 1981).

Canopy Closure

Arkansas—Tufted titmice used red cedar glades with 47% canopy closure, and climax oak forest with 74% closure, but not forest edge or several grass-scrub types (Shugart and James 1973).

Canopy Height

Eastern U.S.—Canopy height was selected as an important feature of titmouse habitat (Anderson 1979).

Georgia—Preferred habitat consisted of older pine and oak-hickory forest types with canopy height >25.5 m; forest or grass-scrub type with canopies <18 m were not used (Johnston and Odum 1956).

Virginia—Pole to mature oak stands with canopy heights >8 m provided suitable habitat for titmice, but not recently logged stands with canopies <5 m high (Conner and Adkisson 1975).

Distance to Edge

Eastern U.S.—Distance to edge was a key habitat variable (Anderson 1979).

Kansas—Habitat suitability was affected by distance to edge (Fitch 1958).

Conclusions

The tufted titmouse did not appear to respond consistently to any habitat characteristic described in the above studies. A wide variety of wooded types provide suitable habitat including grass-shrub savannah, forest edge, glades, and pole to mature deciduous and coniferous forests (Evans and Kirkman 1981), as well as river bottom forests, swamps, orchards, and residential shade trees (Bent 1946).

The most consistent requirement apparently was the presence of a few trees >8 m tall. Several large, dead or partially dead trees (optimum size of 30 cm dbh) with secondary cavities are required for nesting and roosting (Evans and Conner 1979). Some degree of shrub-subcanopy development probably is also important, as titmice commonly forage in these layers (Evans and Kirkman 1981). In the northeastern U.S., special habitat requirements include nest cavities and mixed woodland (DeGraaf et al. 1980).

White-breasted Nuthatch

White-breasted nuthatches were observed primarily in central Missouri upland hardwoods, although several were also noted in southeastern Missouri upland and bottomland hardwoods. Habitat around song perches was most consistently characterized by an intermediate to high canopy (12-24 m, never <10) and a slight to moderate slope (1-15°). Other important features included an intermediate number of woody stems <2.5 cm dbh (corrected values 1400-5600/ha), intermediate ground vegetation coverage (30-70%, never <15), and an intermediate to large number of live stems ≥30 cm dbh (24-125/ha) (Table 21). These characteristics pertain to most older pole to mature upland hardwood forests in central Missouri.

Summary of Other Studies

Density of Small Woody Stems

Eastern U.S.—Density of shrub stems was a prominent component of nuthatch habitat selected by MVA (Anderson 1979).

Ontario—Mature hardwood forests with a prominent shrub layer provided nuthatch habitat (Martin 1960).

Oregon—The least preferred of five Oregon white oak stands was heavily grazed and had few shrub stems (318/ha) (Anderson 1970).

Tennessee—In contrast, preference for sparse understory was indicated by MVA (Anderson and Shugart 1974).

Density of Large Trees

Northeastern U.S.—Presence of nuthatches was positively associated with numbers of trees 8-15 cm dbh (Anderson 1979); presence of large trees was a special habitat requirement (DeGraaf et al. 1980).

Table 21. Important characteristics of white-breasted nuthatch habitat in Missouri (N = 45).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Canopy height (m)	16-20*	58	12-24	89	<12 or >24	11
Slope (degrees)	1-5*	38	1-15	87	0	13
SECONDARY						
All woody stems <2.5 cm dbh/ha	2800-3500	18	1400-5600	76	<1400	13
Live stems ≥30 cm dbh/ha	50-125	56	24-125	87	0	2
Ground vegetative cover (%)	50-55	13	30-70	69	<20	2

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

Canopy Closure

Arkansas—Nuthatch habitat included pole to mature oak forests with 64-74% canopy closure (Shugart and James 1973).

California—Forest stands with <70% canopy closure were preferred by white-breasted nuthatches in the Sierra Nevadas (Verner 1980).

Eastern U.S.—One of several prominent habitat variables selected was canopy closure (Anderson 1979).

Ontario—Habitat consisted of mature hardwood forests with a closed canopy (Martin 1960).

Oregon—Oregon white oak stands with 44-82% canopy closure provided suitable habitat (Anderson 1970).

Canopy Height

California—Suitable habitat for white-breasted nuthatches in the Sierra Nevadas was provided by forests with canopy >15 m high (Verner 1980).

Eastern U.S.—Canopy height appeared to be a primary habitat variable (Anderson 1979).

Ontario—Habitat consisted of mature sugar maple forest with canopy height 24-30 m, but not mixed or conifer stands with canopies <21 m high (Martin 1960).

Virginia—A mature oak stand with trees 23-25 m tall provided nuthatch habitat, but not a pole stand with trees 8-11 m (Conner and Adkisson 1975).

Tree Species Composition

U.S.—Deciduous woodlands were preferred (Scott et al. 1977), especially oaks (Bent 1948, Fitch 1958, Mengel 1965).

Conclusions

Most characteristics in the above studies did not consistently describe suitable habitat. White-breasted nuthatches are common in most deciduous and mixed woodlots containing some large trees, orchards, and residential shade trees (Harrison 1975, McEllin 1979, DeGraaf et al. 1980).

In our study, canopy height and slope were primary characteristics. The features selected as important pertain to most older pole or mature upland hardwood forests in central Missouri. Almost all of the upland hardwood study areas were used by nuthatches. Other studies did not mention slope as a conspicuous feature of nuthatch habitat. Possibly slope values only reflect the hilly terrain of our central Missouri plots.

The only critical requirements of white-breasted nuthatches appear to be forested areas with an intermediate to high canopy (>12 m) and at least a few larger trees. Secondary cavities in large trees (optimum 30 cm dbh) provide nest and roost sites (Evans and Conner 1979). In Colorado, nests were located in large live trees with an average dbh of 54 cm (McEllin 1979). Deciduous stands apparently are preferred, especially oaks. In our study, nuthatches were usually located on white oaks (53% of observations) 12-20 m tall. Overall, 67% were observed on several oak species. Oaks were the most common overstory trees. In another study, Probst (1979) found white-breasted nuthatches using most of 16 oak forest types with widely different structures.

Yellow-Throated Vireo

Yellow-throated vireos were observed in all forest habitats except central Missouri bottomland hardwoods. The characteristics most consistently describing habitat around song perches were a high canopy (>16 m, never <15) with intermediate to nearly complete closure (70-90%, never <55). Another important feature was an intermediate to nearly closed subcanopy (50-90%, never <35) (Table 22).

Summary of Other Studies

Size of Contiguous Habitat

Eastern U.S.—Woodlands of 100+ ha were preferred by yellow-throated vireos (Robbins 1979).

Table 22. Important characteristics of yellow-throated vireo habitat in Missouri (N = 32).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Canopy closure (%)	85-90	22	70-90	69	<70	15
Canopy height (m)	16-20	41	>16	91	<15	0
SECONDARY						
Subcanopy closure (%)	50-55*	25	50-90	81	<50	12

[a]*Percent of observations.*
**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

Conclusions

Throughout the range, yellow-throated vireos occur in a variety of wooded habitats with tall deciduous trees, including partially open forest, forest edge, groves, orchards, and roadside trees (Bent 1950, Harrison 1975, DeGraaf et al. 1980). The principal requirements appear to be tall trees and a partially open canopy; high but relatively dense canopy was the primary characteristic of habitat in our study. Another critical feature possibly is size of contiguous forest habitat.

In our study, males usually sang from tops of trees >12 m tall, mostly oaks (75% of observations), which were the most common overstory trees. The upper canopy also provides the main foraging zone for yellow-throated vireos (Hamilton 1962, Williamson 1971, DeGraaf et al. 1980). Subcanopy possibly was important in our study by adding depth to this foraging zone. Yellow-throated vireos also forage in the shrub layer (Evans and Kirkman 1981).

Qualitative and quantitative information on habitat requirements of yellow-throated vireos from published accounts is limited.

Analysis of data obtained in our study did not delineate habitat differing from that found in most mature or nearly mature hardwood forests in Missouri.

Red-eyed Vireo

Red-eyed vireos were studied only on central Missouri upland and southeastern Missouri bottomland hardwood study areas. Habitat around song perches most consistently had an intermediate to high number of live stems ≥30 cm dbh (50-275/ha) and an intermediate to nearly closed canopy (65-90%, never <50). Other

important features included short ground vegetation (0.01-0.30 m, never >0.40), an intermediate to high canopy (always >12 m) and an intermediate subcanopy closure (40-60%) (Table 23). These characteristics apply to most older pole to mature hardwood stands.

Table 23. Important characteristics of red-eyed vireo habitat in Missouri (N-53).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Live stems ≥30 cm dbh/ha	50-75	23	50-275	92	<50*	8
Canopy closure (%)	70-75*	23	65-90	83	<65 or >95	8
SECONDARY						
Ground vegetative height (m)	.10-.20	34	.01-.30	92	>.30	6
Subcanopy closure (%)	50-55*	17	40-60	53	--	-
Canopy height (m)	16-20*	58	12-20	79	<12	0

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

Summary of Other Studies

Ground Vegetative Height

Vermont and Pennsylvania—Red-eyed vireo habitat had sparse vegetation below 0.6 m and moderate to sparse vegetation 0.6-4.5 m tall (MacArthur et al. 1962).

Subcanopy Development

Tennessee—Large subcanopy trees appeared essential as determined by MVA (Anderson and Shugart 1974).

Various Localities—Primary habitat had a well-developed shrub and sapling layer (Bent 1950, Lawrence 1953, Johnston and Odum 1956, Martin 1960, MacArthur et al. 1962, DeGraaf et al. 1980).

Canopy Closure

Arkansas—Primary habitat was climax oak forest with 74% canopy closure; subclimax forest with 64% closure also was used, but not areas with <50% closure (Shugart and James 1973).

Various Localities—MVA of habitat data selected a well-developed canopy as a prominent feature of red-eyed vireo habitat in Arkansas (James 1971), Eastern U.S. (Robbins 1978), and Tennessee (Anderson and Shugart 1974).

Wisconsin—Forests with canopy closures of 57-95% were acceptable, but the stands with greater closure were preferred (Bond 1957).

Canopy Height

Canada—Habitat in northern areas rarely had canopy heights >20 m, but in southern areas canopy height was typically 20-30 m (Barlow and Rice 1977). Presence of tall trees was a key characteristic (Lawrence 1953).

Georgia—Primary red-eyed vireo habitat had canopies ≥30 m, then areas of 18+ m, but not younger forests or shrublands (Johnston and Odum 1956).

Ontario—Several forest types with canopies >9 m high provided habitat (Martin 1960).

Pennsylvania—Preferred habitat was mature forest, but younger forests with canopy heights 5-7 m were also used (Davis and Savidge 1971).

Virginia—Forests with canopies 23-25 m high were preferred, but pole stands 8-11 m tall were also used (Conner and Adkisson 1975).

Tree Stand Age

Various Localities—When compared with stands of various other ages, mature hardwoods supported the greatest numbers of red-eyed vireos (Johnston and Odum 1956, Martin 1960, Davis and Savidge 1971, Shugart and James 1973, Conner and Adkisson 1975).

Size of Contiguous Habitat

Maryland—Frequency of occurrence of red-eyed vireos declined sharply in areas <100 ha (Robbins 1979).

New Jersey—Woodlots <3 ha were not suitable (Galli et al. 1976).

Tree Species Composition

Eastern U.S.—Forests with an oak component contributed to habitat suitability (Robbins 1978).

New York—In mixed stands, deciduous trees were preferred (Kendeigh 1945).

Conclusions

Habitat requirements in the above studies were very consistent and agreed quite

favorably with our results. Throughout their range, red-eyed vireos inhabit a variety of wooded areas. However, they apparently prefer larger forest tracts with pole to mature trees, high and moderately dense canopy, well-developed understory-subcanopy, and sparse ground vegetation. Possibly, forests with an oak component are preferred. In our study, most males (85% of observations) sang from oaks, which were the most common overstory trees.

Male red-eyed vireos apparently required tall trees for song perches. In our study, males usually sang at heights >8 m (81% of observations) from trees 12-20 m tall (70%). The understory-subcanopy layer provides nest sites in shrubs or saplings (Bent 1950, DeGraaf et al. 1980).

Warbling Vireo

Warbling vireos were found in southeastern Missouri bottomland hardwoods, especially in or near forest edge. Habitat around song perches most consistently had intermediate ground vegetation coverage (30-65%, never <25), level terrain (0° slope), and few or no dead stems 2.5-9.9 cm dbh (<50/ha). Other important features included no dead stems 10.0-29.9 cm dbh (0/ha), a low to intermediate number of woody stems <2.5 cm dbh (<2800/ha), an intermediate subcanopy closure (always 30-80%) and a canopy of intermediate closure (40-85%, never <25) and intermediate to great height (>16 m) (Table 24). These characteristics describe forest edge or open pole to mature forest with tall trees and few dead trees.

Summary of Other Studies

Density of Small Woody Stems

Oregon—Several types of Oregon white oak stands with sparse to dense understory provided habitat, but highest populations of warbling vireos were in forests with densest understory of 3500 shrub stems/ha (Anderson 1970).

Utah (isolated valley in UT, AZ, NV)—A prominent feature of habitat as selected by MVA was high shrub density (Whitmore 1977).

Wyoming—Optimum habitat was scrub-meadow and flatland aspen with numerous shrubs, but not willow-sedge with irregular shrub cover (Salt 1957).

Ground Vegetative Cover

Utah—Low ground cover was selected as an important feature (Whitmore 1977).

Wyoming—Several habitat types with numerous forbs and grasses provided suitable habitat (Salt 1957).

Canopy Closure

California—Canopy closure <40% was one of two criteria for optimum

warbling vireo habitat in the Sierra Nevadas (Verner 1980).

Oregon—Highest densities of warbling vireos inhabiting Orgeon white oak stands with canopy closures 44-82% were in the stands with most complete canopy (82%) (Anderson 1970).

Utah—High degree of canopy closure was a key characteristic of habitat (Whitmore 1977).

Canopy Height

California—Optimum habitat contained pole to larger trees >6 m tall in the Sierra Nevadas (Verner 1980).

Oregon—Warbling vireo habitat included several Oregon white oak stands with canopy heights 9-18 m; preferred areas had the tallest trees (>18 m) (Anderson 1970).

Table 24. Important characteristics of warbling vireo habitat in Missouri (N = 30).

	Optimum		*Main*		*Avoided*	
Variable	*Range*	*%*[a]	*Range*	*%*	*Range*	*%*
PRIMARY						
Dead stems 2.5-9.9 cm dbh/ha	0*	57	<50*	83	>100*	3
Ground vegetative cover (%)	55-60*	30	30-65	87	<25 or >70	7
Slope (deg)	0*	90	0*	90	>0*	10
SECONDARY						
All woody stems <2.5 cm dbh/ha	700-1400*	43	<2800	91	>2800	9
Dead stems 10.0-29.9 cm dbh/ha	0*	63	0*	63	>100	0
Subcanopy closure (%)	45-50*	23	30-80	100	<30 or >80	0
Canopy closure (%)	70-80	33	40-85	77	<40 or >85	23
Canopy height (m)	16-20	27	>16	83	<8	0

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

Wyoming—Several habitat types with trees 1.5-21 m tall were occupied, but not willow-sedge swamp with scattered clumps of trees 3.0-3.6 m tall (Salt 1957).

Conclusions

In general, the primary requirements for warbling vireos appear to be tall trees (>8 m) and variable but relatively open canopy (<85%). Nests typically are located 6.1-27.4 m above ground (Harrison 1975). However, even these limited characteristics were not consistent throughout the breeding range. Habitat in the Virgin River Valley (Arizona, Utah and Nevada) had high canopy closure, numerous trees, sparse ground vegetation coverage and great shrub density, as determined from MVA (Whitmore 1977). Values for these variables were not presented. This description of habitat appears contradictory to that found in our study and in others. However, western habitats generally have less vegetation at all levels than eastern habitats.

Warbling vireos usually are associated with large trees in open woodland, forest edge, along river systems, roadsides, and village shade trees (Bent 1950, Fitch 1958, James 1971, DeGraaf et al. 1980). Such areas with little understory were preferred in Kentucky (Mengel 1965). Large trees in riverbottoms and along watercourses provide the principal habitat in many locations (Bent 1950, Hamilton 1962, Mengel 1965, James 1971) as in our study. Absence of slope selected in this study reflects this habitat preference, but probably is not a critical factor of itself in many locations.

Prothonotary Warbler

Prothonotary warblers were observed only on bottomland hardwood study areas in southeastern Missouri. Habitat around song perches was most consistently characterized by level terrain (always 0° slope), a small number of woody stems <2.5 cm dbh (<2800/ha, never >4200), short ground vegetation (<0.20 m, never >0.36), and a high canopy (16-40 m, never <12). Other important features included few dead stems 2.5-9.9 cm dbh (<200/ha, never >250) and an intermediate subcanopy closure (30-80%, never <10 or >90) (Table 25).

Although the above characteristics appear to delineate specific forest habitat, ranges are typical of most mature bottomland hardwoods in southeastern Missouri. Prothonotary warblers were observed on all such study areas.

Summary of Other Studies

Density of Small Woody Stems

Arkansas—Forest areas with sparse understory provided suitable habitat (James 1971).

Presence of Snags

Eastern U.S.—Snags with secondary cavities were required for nesting; their optimum size was 20 cm dbh (Evans and Conner 1979).

Size of Contiguous Habitat

Eastern U.S.—Waterways with a wooded border <30 m wide were avoided (Hardin and Evans 1977); populations were considerably lower in forest areas <100 ha than in larger areas (Robbins 1979).

Proximity of Water

Eastern U.S.—Nests typically were within 6 m of water (Hardin and Evans 1977; DeGraaf et al. 1980).

Michigan—Of 84 nests found, 61 were over water (Harrison 1975).

Table 25. Important characteristics of prothonotary warbler habitat in Missouri (N = 30).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	700-2800*	73	<2800*	97	>2800*	3
Ground vegetative height (m)	.10-.20†	40	.01-.20*	77	>.20	20
Canopy height (m)	16-20	27	16-40	93	<16	7
Slope (degrees)	0*	100	0*	100	>0*	0
SECONDARY						
Dead stems 2.5-9.9 cm dbh/ha	<50*	57	<200	97	>200	3
Subcanopy closure (%)	50-75	47	30-80	90	<30 or >80	10

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

†*P<0.10.*

Conclusions

Prothonotary warblers typically are associated with bottomland and riparian woodland habitat, or other forested areas near water (Bent 1953, Griscom and Sprunt 1957, Mengel 1965). Mature forest stands possibly are preferred (Meanley 1966).

In our study, absence of slope was the principal characteristic delineating bottomland habitat. Absence of slope, in itself, probably was not important but reflected distance to water as the key criterion. Forty percent of song perch plots in our study had standing water in low spots.

Low densities of small woody stems and short ground vegetation, both determined to be primary characteristics in our study, may be linked to distance to water. Bottomland forest in southeastern Missouri typically had sparse understory and low ground vegetation.

Although our results indicated that a high density of small dead stems is undesirable for prothonotary warbler habitat, it is known that this warbler nests in natural or secondary cavities at heights of 0.9-9.8 m (Harrison 1975), and some snags may be essential. A well-developed, but not dense, subcanopy layer was another feature of habitat in our study. This warbler forages in the lower forest layers (Griscom and Sprunt 1957), and a distinct subcanopy layer may provide increased foraging substrate.

The selected characteristics in our study cannot be thoroughly evaluated because of lack of quantitative data in other studies. Possibly, they are not important of themselves but are consistent components of bottomland hardwoods, and thus reflect the most critical feature, proximity of water. Distance to water and possibly forest size should be included in the habitat description.

Cerulean Warbler

Cerulean warblers were observed on moist, wooded slopes and stream valleys in uplands and also on bottomland hardwood study areas. Habitat around song perches was most consistently characterized by a large number of live stems ≥30 cm dbh (50-150) and a high (always >18 m), closed canopy (>85%, never <65). Other important features included an intermediate to closed subcanopy (always >45%), an intermediate number of woody stems <2.5 cm dbh (corrected values 1030-2800/ha, never <1030), and few dead stems 2.5-9.9 cm dbh (always <175/ha) (Table 26).

The above characteristics describe a mature forest with high, dense canopy and well-developed but not dense subcanopy and shrub layers.

Summary of Other Studies

Density of Large Trees

Eastern U.S.—MVA selected many large trees as an important component of cerulean warbler habitat (Robbins 1978).

Ground Cover - Understory Development

Eastern U.S.—Areas with little undergrowth were preferred by cerulean warblers (DeGraaf et al. 1980); low ground cover was a key component of habitat (Robbins 1978).

Canopy Closure and Height

Eastern U.S.—Tall canopy and high degree of canopy closure were prominent habitat features selected by MVA (Robbins 1978).

Tree Species Composition

Eastern U.S.—Sparsity of coniferous trees was a prominent characteristic of cerulean warbler habitat (Robbins 1978).

Table 26. Important characteristics for cerulean warbler habitat in Missouri (N = 13).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Live stems ≥30 cm dbh/ha	100-125*	38	50-150	92	<50 or >150	8
Canopy closure (%)	85-90†	31	>85	69	<65	0
Canopy height (m)	18-20	38	>18	100	<18	0
SECONDARY						
All woody stems <2.5 cm dbh/ha	2100-2800	31	1030-2800†	77	<1030	0
Dead stems 2.5-9.9 cm dbh/ha	50-100	38	<175	100	>175	0
Subcanopy closure (%)	65-70	23	>45	100	<45	0

[a]*Percent of observations.*
**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*
†P<0.10.

Conclusions

In the absence of quantitative data from other studies our data cannot be adequately assessed. Cerulean warblers appear primarily to require numerous, tall trees in mature forest habitat. Multivariate and univariate analysis of habitat data for a Tennessee forest resulted in selection of no variables which consistently described cerulean warbler habitat (Anderson and Shugart 1974).

Cerulean warblers prefer bottomland forest or moist areas of upland forest with tall trees (Bent 1953, Bond 1957, Griscom and Sprunt 1957, Mengel 1965). Except for some measure of habitat moistness, the three primary characteristics in our study describe this habitat. These characteristics are interrelated since the presence of many large trees results in a tall dense canopy. Cerulean warblers forage in the canopy layer (Griscom and Sprunt 1957, K.E. Evans 1978). The upper canopy also provides song perches; most males in our study (77% of observations) sang from heights of 12-24 m. Nests are usually located in the shrub layer (Evans and Kirkman 1981), and the importance of subcanopy closure and small woody stem density in our study may reflect this preference of nest sites. However, in other studies these warblers typically located their nests on the horizontal branch of a tree, 6.1-18.3 m above ground (Harrison 1975).

Yellow-throated Warbler

Yellow-throated warblers were observed only in southeastern Missouri bottomland hardwoods. The most consistent characteristics of habitat around song perches were a high canopy (>24 m, never <20) and level terrain (always 0° slope). Other important features included a small number of dead stems 2.5-10.0 cm dbh (<50/ha, never >225), an intermediate to large number of live stems >30 cm dbh (always >49/ha), and an intermediate to nearly closed canopy (60-95%, never <40) (Table 27). These characteristics describe most mature bottomland hardwoods in southeastern Missouri.

Summary of Other Studies

No suitable quantitative habitat data were found.

Conclusions

In the western portion of its range (including Missouri), the yellow-throated warbler prefers mature bottomland forest and large trees in other forested lowland areas. Large bald cypress and sycamore trees are especially preferred (Bent 1953, Griscom and Sprunt 1957, Mengel 1965). Males in our study usually sang at heights >12 m. The middle and upper canopy layers of large trees also are used for foraging (Griscom and Sprunt 1957, Mengel 1965).

Table 27. Important characteristics of yellow-throated warbler habitat in Missouri (N = 17).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Canopy height (m)	24-28*	59	>24*	88	<24*	12
Slope (degrees)	0*	100	0*	100	>0*	0
SECONDARY						
Live stems ≥30 cm dbh/ha	100-125	24	>49	100	<49	0
Dead stems 2.5-9.9 cm dbh/ha	0*	47	<50*	76	>50	24
Canopy closure (%)	60-95	88	60-95	88	<60 or >95	12

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

The western form was named the sycamore yellow-throated warbler (or sycamore warbler) by early ornithologists who observed that sycamore and bald cypress trees were preferred nesting trees (Bent 1953). Yellow-throated warblers tend to be tree specific and occupy different habitats in other locations. In eastern Kentucky, dry upland forest containing scrub or shortleaf pine were inhabited by yellow-throated warblers. Pine stands apparently were preferred over nearby sycamore stands (Mengel 1965). On the southern slope of the Missouri Ozarks, the warbler inhabited pines on the hilltops as well as sycamores in the bottoms (Widmann 1907).

Except for the low density of dead stems 2.5-9.9 cm dbh, characteristics selected as important in our study provide a quantitative description of habitat consistent with other qualitative descriptions for the western form of the yellow-throated warbler.

Summer Tanager

Summer tanagers were observed primarily in upland hardwoods, although several were also noted in bottomland hardwoods and old fields. Habitat around song perches was most consistently characterized by short ground vegetation (0.01-0.20 m), few woody stems <2.5 cm dbh (corrected values <2800/ha, never

>6300) and an intermediate canopy height (12-20 m). Other important features included a nearly closed canopy (75-95%), an intermediate to large number of live stems ≥30 cm dbh (50-150/ha), and an intermediate number of live stems 2.5-9.9 cm dbh (400-750/ha) (Table 28). These characteristics describe older pole to mature forest habitat with sparse shrub and ground layers.

Table 28. Important characteristics of summer tanager habitat in Missouri (N = 33).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	700-1400†	30	<2800*	85	>2800*	15
Ground vegetative height (m)	.01-.20*	74	.01-.20*	74	<.01 or >.20	26
Canopy height (m)	16-20*	58	12-20	73	<12	0
SECONDARY						
Live stems 2.5-9.9 cm dbh/ha	700-750*	18	400-750	63	<400 or >750	37
Live stems ≥30 cm dbh/ha	125-150*	24	50-150	63	>150	10
Canopy closure (%)	90-95	21	75-95	70	<75 or >95	30

[a]*Percent of observations.*
**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*
†P<0.10.

Summary of Other Studies

Density of Small Woody Stems

Arkansas—Forest edge with a dense understory was preferred over forest areas with sparse understory vegetation (Shugart and James 1973).

Georgia—Habitat of summer tanagers included pine forests with spotty or well-developed understory and pine forest with 23% thicket cover. It did not include grass-scrubland with 10-35% thicket cover or climax oak-hickory with well-developed understory (Johnston and Odum 1956).

Tennessee—Habitat suitability was related positively to density of small trees <8.4 cm dbh (Anderson and Shugart 1974).

Canopy Closure

Arkansas—Summer tanager habitat included forest edge or sub-climax forest with intermediate canopy closure (64%) but not red cedar glades with 47% closure, or climax forest with 74% closure (Shugart and James 1973).

Georgia—Pine forests with canopy closure as low as 33% provided suitable habitat (Johnston and Odum 1956).

Canopy Height

Georgia—Older pine forests with canopy heights 18-27 m provided habitat, but not grass-scrubland with trees <7.5 m tall, or climax forest with canopy height ≥30 m (Johnston and Odum 1956).

Indiana—Upland forests were preferred by summer tanagers, but they occasionally used brushy fields with saplings ≥7 m tall (Nolan 1963).

Size of Contiguous Habitat

Arkansas—Primary habitat consisted of forest edge but not climax forest (Shugart and James 1973).

Eastern U.S.—Contrariwise, forests <100 ha supported considerably sparser populations than larger forest tracts (Robbins 1979).

Tree Species Composition

Georgia—Several pine forests were used, but not climax oak-hickory forests (Johnston and Odum 1956).

Kentucky—In contrast, oak woodlands were possibly preferred (Mengel 1965).

Conclusions

Summer tanagers preferred widely different habitat types in the above studies. They are commonly associated with open, dry forests and forest edge. But they also frequent groves, orchards, roadside trees and residential shade trees (Widmann 1907, Bent 1958, Fitch 1958, Mengel 1965, Harrison 1975).

Several intermediate to large trees possibly fulfill the principal requirements. In our study, canopy height was never <12 m. Males usually sang from tops of trees 12-20 m tall (60% of observations). They sang from oak trees in 77% of the observations, but oaks were the most common overstory species in our study. These tanagers nest in shrubs or trees and forage in trees (Evans and Kirkman 1981).

Summer tanagers selected specific habitat, apparently responding to a number of habitat characteristics in our study. These results agree only moderately with habitat descriptions in other studies, which often contradict one another.

Forest Interior - Pole or Sawtimber, Sparse Understory

Carolina Chickadee

Carolina chickadees were found primarily in southeastern Missouri bottomland hardwoods, although one was also recorded on a central Missouri upland hardwood study area. Habitat around song perches most consistently had short ground vegetation (<0.10 m, never >0.30), no dead stems ≥30 cm dbh (always 0/ha), and level terrain (always 0° slope). Discriminant function analysis selected ground vegetation height as the most important variable differentiating study areas with and without Carolina chickadees.

Other important features included an intermediate to closed canopy (>70%, never <65), intermediate subcanopy closure (40-60%), a large number of live stems 2.5-9.9 cm dbh (>650/ha), few live stems ≥30 cm dbh (<25/ha), and a small to intermediate number of woody stems <2.5 cm dbh (700-3500/ha, never <700) (Table 29).

These characteristics describe reproduction stage bottomland forest with a closed canopy, but relatively sparse shrub and ground layers.

Summary of Other Studies

Ground Vegetative Cover

Eastern U.S.—Scanty ground cover was selected as an important habitat characteristic by MVA (Robbins 1978).

Georgia—Carolina chickadee habitat included several pine forest types with understories ranging from distinct but spotty to continuous and well-developed (Johnston and Odum 1956).

Tennessee—Primary habitat characteristics for Carolina chickadees revealed by MVA were open and sparse understory (Anderson and Shugart 1974).

Canopy Closure

Eastern U.S.—Dense canopy was a basic component of Carolina chickadee habitat (Robbins 1978).

Canopy Height

Georgia—Principal habitat included ≥60-year-old pine stands with trees 18-27 m tall (Johnston and Odum 1956).

Virginia—One- to 7-year-old clearcuts with woody vegetation 0.3-3.5 m tall provided habitat, but not pole or mature deciduous stands with canopy heights >8 m (Conner and Adkisson 1975).

Slope

Southeastern U.S.—Prime habitat appeared to be lowland swamps (with little slope), although habitat at elevations of about 1525 m was also occupied (Bent 1946).

Tree Species Composition

Eastern U.S.—Little conifer cover appeared to be an important habitat feature (Robbins 1978).

Georgia—In contrast, older pine stands were preferred over several deciduous shrublands and oak-hickory climax forest (Johnston and Odum 1956).

Table 29. Important characteristics of Carolina chickadee habitat in Missouri (N = 10).

Variable	*Optimum Range*	*%*[a]	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Dead stems ≥30 cm dbh/ha	0	100	0	100	>0	0
Ground vegetative height (m)	.01-.10†	50	<.10*	70	>.30	0
Slope (degrees)	0*	100	0*	100	>0	0
SECONDARY						
All woody stems <2.5 cm dbh/ha	700-1400*	60	700-3500	90	<700 or >3500	10
Live stems 2.5-9.9 cm dbh/ha	650-700	20	>650	90	<650	10
Live stems ≥30 cm dbh/ha	24*	40	<25	60	>50	30
Subcanopy closure (%)	40-60*	70	40-60*	70	<40 or >60	30
Canopy closure (%)	80-85	30	>70	90	>70	10

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

†P<0.10.

Conclusions

Few quantitative data are available to support or contradict our results. Carolina chickadees often nest in relatively open situations such as young forest, hedgerows, and field borders, especially near older forest stands where they forage (Hardin and Evans 1977). In Illinois, nests were located in portions of the forest with relatively low densities of trees (Brewer 1963). Decaying tree stubs 1.6-2.0 m tall and 11-13 cm diameter at the cavity provided nesting sites (Brewer 1961). In Kentucky, most woodlands and forest types were frequented, including forest edge (Mengel 1965). Prime habitat in the southeastern U.S. appeared to be lowland swamps (Bent 1946).

Our data, based on a small sample, generally support qualitative and the limited quantitative descriptions of habitat available in the above studies. Carolina chickadees apparently prefer young forest habitat with relatively open subcanopy-understory layers. Although ground vegetative coverage was not selected as important in our study, short ground vegetation appeared to be the most critical habitat component. Because of the small sample size and the scarcity of quantitative data from other studies, these conclusions should be viewed with caution.

Wood Thrush

Wood thrushes were observed primarily on central Missouri upland and bottomland hardwood study areas, although several were also noted on southeastern Missouri upland hardwood study areas. Habitat around song perches consistently had a high (16-32 m, never <15), nearly closed to closed canopy (>80%, never <50) and intermediate to closed subcanopy (>60%). Another important feature was an intermediate number of woody stems ≥2.5 cm dbh (1200-1500/ha, never <800 or >2000) (Table 30).

These characteristics describe older pole to mature hardwood forest habitat with great tree densities and associated well-developed canopy and subcanopy.

Summary of Other Studies

Density of Small Woody Stems

Connecticut—Shrub cover 1-3 m tall was positively related to wood thrush populations (Bertin 1977).

Various Localities—Numerous saplings or a well-developed shrub layer were present in occupied habitat (Bent 1949, Martin 1960, DeGraaf et al. 1980).

Density of Trees

Arkansas—Forest habitat with low wood thrush densities had 483 woody stems ≥7.5 cm dbh/ha (Shugart and James 1973).

Delaware—Preferred forest habitats had mean densities of 805-975 stems ≥5 cm dbh/ha (Longcore and Jones 1969).

Eastern U.S.—Wood thrush numbers were related to numbers of trees >52.5 cm dbh (Robbins 1978). The number of trees >39 cm dbh was selected as a key variable for habitat suitability by MVA (Anderson 1979).

New York—Removal of 25-100% of commercial timber by logging had a progressively detrimental effect on wood thrush populations (Webb 1977).

Wisconsin—Woodlands with 680-1000/ha stems >2.5 cm dbh provided suitable habitat (Bond 1957).

Ground Vegetative Cover - Understory Development

Various Localities—Relatively dense ground cover was an important habitat feature or enhanced wood thrush populations (Good and Dambach 1943, Bertin 1977, Anderson 1979). Suitable habitat in the U.S. had a well-developed understory (Bent 1949, Johnston and Odum 1956, DeGraaf et al. 1980).

Canopy Closure

Arkansas—Deciduous forests with canopy closure of 74% provided wood thrush habitat (Shugart and James 1973).

Eastern U.S.—Canopy closure was a key habitat variable (Anderson 1979) and was positively related to wood thrush abundance (Robbins 1978).

Wisconsin—Preferred habitat had 70-80% canopy closure (Bond 1957).

Canopy Height

Connecticut—Some trees >12 m tall were required for wood thrush habitat (Bertin 1977).

Eastern U.S.—Within limits, wood thrush numbers were positively related to canopy heights (Robbins 1978).

Virginia—Pole to mature deciduous forests with canopy heights 8-25 m provided suitable habitat (Conner and Adkisson 1975).

Size of Contiguous Habitat

Eastern U.S.—The critical minimum size of habitat parcels was 4 ha (Robbins 1979).

New Jersey—Wood thrushes were mostly associated with woodlots >2 ha in size (Galli et al. 1976).

Habitat Moistness

U.S.—Damp forest habitat was preferred or required (Bent 1949, Fitch 1958, Bertin 1977, DeGraaf et al. 1980).

Table 30. Important characteristics of wood thrush habitat in Missouri (N = 33).

Variable	*Optimum Range*	*%*[a]	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Subcanopy closure (%)	80-85*	18	>60	85	<60	15
Canopy closure (%)	>95*	32	>80	76	<70	9
Canopy height (m)	16-20	42	16-32	97	<16*	3
SECONDARY						
All woody stems ≥2.5 cm dbh/ha	1300-1500	36	1200-1500	48	<800 or >2000	0

[a]*Percent of observations.*
**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

Conclusions

Habitat requirements in these preceding studies were quite consistent, but different from our results for several characteristics. Wood thrushes primarily appear to require older pole to mature deciduous or mixed forest, indicated by large trees and intermediate to high canopy height (>8 m), a relatively closed canopy (>70%), moderate to dense understory-subcanopy layers, moistness, and woodlot size of at least 2 ha.

Although density of trees ≥30 cm dbh was not selected as important in our study, the component appearing most important (canopy height >16 m) reflects the requirement for larger trees. Preference for relatively tall trees possibly is related to an optimum height of 12 m from which males delivered the evening song (Bertin 1977). Most male wood thrushes (67% of observations) in our study sang (in mornings) at heights <12 m from trees 2.4-23.0 m tall.

Density of small woody stems which contributes to understory-shrub layer development did not appear a prominent feature of habitat in our study as it did in several other investigations. However, subcanopy closure was a primary variable; wood thrushes required relatively dense subcanopy closure. This characteristic is a measure of shrub-sapling density. In several other studies, the ground vegetation-understory layer was well-developed, but in our study ground layer coverage was quite variable. This apparent discrepancy possibly is due to different definitions of ground layer and understory, as well as differing methods of measuring these layers.

A well-developed understory possibly provides nest sites; wood thrushes usually place their nests in saplings or bushes (Bent 1949, Mengel 1965, DeGraaf et al. 1980). Wood thrushes also forage in low, shrubby vegetation or on the ground (Bent 1949, Fitch 1958).

Wood thrushes typically inhabited older deciduous or mixed stands (Kendeigh 1945); population levels were positively correlated with tree diameter in Connecticut (Bertin 1977). These thrushes also were abundant in or near the edge of mature forest habitat in Kentucky (Mengel 1965), Illinois (Karr 1968) and Pennsylvania (Davis and Savidge 1971). MVA delineated distance to forest edge as an important characteristic affecting habitat suitability in the eastern U.S. (Anderson 1979). In our study, 40% of wood thrush observations were on central Missouri bottomland hardwood areas. These study areas, mostly narrow strips near the Missouri River, comprised only 16% of the forest habitat sampled. This suggests a preference for both forest edge where the forest area is large enough, and habitat moistness.

The selected characteristics in our study do not completely describe preferred habitat. Some measure of habitat moistness, area size, and possibly distance to edge must be added to the primary characteristics before these characteristics can be used for assessing potential wood thrust habitat. Additionally, a uniform measure of understory should be included. The importance of the secondary characteristic, woody stems ≥2.5 cm dbh, probably is readily assessed by estimates of canopy and subcanopy closure.

Northern Parula

Northern parulas were observed primarily on southeastern Missouri bottomland hardwood and central Missouri upland hardwood study areas. The most consistent characteristic of habitat around song perches was a high canopy (>20 m, never <14). Discriminant function analysis of upland study areas selected canopy height as the most important variable differentiating study areas where several parulas were found from those lacking parulas. Other important features included an intermediate to large number of live stems ≥30 cm dbh (always >24/ha), a closed canopy (>80%, never <50) and nearly closed to closed subcanopy (>70%, never <35) (Table 31). Song perches were located in older pole to mature forest habitat with dense canopy and subcanopy.

Summary of Other Studies

Canopy Closure

Arkansas—Climax oak-hickory forest with 74% canopy closure was inhabited, but several other younger forest types with closure <65% were not (Shugart and James 1973).

Size of Contiguous Habitat

Eastern U.S.—Density of parulas was low in forest tracts <100 ha (Robbins 1979).

Tree Species Composition

Eastern U.S.—In deciduous forest areas lacking beard mosses or Spanish moss, white oaks and sycamores are preferred tree species (Brooks 1947).

Ontario—Of several coniferous and deciduous types, only hemlock forest provided suitable habitat (Martin 1960).

Various Localities—Many forest types support parula populations, but conifers, especially hemlock, or hardwoods where beard mosses or Spanish moss hangs from trees are often used for nest sites (Brooks 1947, Bent 1953, Griscom and Sprunt 1957, DeGraaf et al. 1980).

Table 31. Important characteristics of northern parula habitat in Missouri (N = 40).

Variable	*Optimum Range*	*%*[a]	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Canopy height (m)	20-24	30	>20*	73	<16	8
SECONDARY						
Live stems ≥30 cm dbh/ha	50-75*	33	>24	100	0	0
Canopy closure (%)	85-90*	33	>80	73	<55	3
Subcanopy closure (%)	75-80†	18	>70	60	<30	0

[a]*Percent of observations.*
**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*
†P<0.10.

Conclusions

Quantitative data on habitat requirements of the northern parula are lacking, but the most consistent features of parula habitat appear to be presence of tall (>20

m), mature trees which provide a high, dense canopy (>70% closure).

These requirements are adequately delineated by the first three characteristics selected in our study. Importance of a well-developed subcanopy was not confirmed in other studies. Where beard mosses or Spanish moss are lacking, nests usually are located at heights of 3.0-12.2 m above ground (Harrison 1975) in shrubs or trees (Evans and Kirkman 1981). This is primarily the subcanopy zone. Ground-understory vegetation probably is not important to parulas because they forage at the tops of foliage in the upper canopy (Morse 1967). Tree species composition should also be considered when assessing parula habitat; hemlocks, sycamores and oaks appear to be preferred. In our study, males often sang from sycamores (44% of observations), which were only moderately abundant on central Missouri study sites.

Habitat requirements vary somewhat from locality to locality, and without supporting quantitative data, the results of our study may have limited application in other areas.

Northern Oriole

Northern orioles were found only on central Missouri bottomland hardwood study areas. Habitat around song perches consistently had a high canopy (20-32 m, never <15), few woody stems <2.5 cm dbh (170-2100/ha, but never <170), level terrain (always 0° slope) and a nearly closed to closed canopy (>80%). Another feature was an intermediate to closed subcanopy (>45%) (Table 32). These characteristics describe mature, bottomland forest habitat with sparse understory.

Summary of Other Studies

Density of Small Woody Stems

Eastern U.S.—A deciduous shrub component was a prominent feature of suburban habitat for northern orioles (Thomas et al. 1977).

Subcanopy Closure

Eastern U.S.—A mid-canopy coniferous and deciduous layer formed an essential component of suburban habitat for northern orioles (Thomas et al. 1977).

Canopy Closure

Various Localities—Most open deciduous woodlands provide suitable habitat (Fitch 1958, Mengel 1965, Anderson 1971, James 1971, DeGraaf et al. 1980).

Canopy Height

Various Localities—Presence of tall trees is required (Bent 1958, Fitch 1958,

Mengel 1965, Anderson 1971, James 1971, DeGraaf et al. 1980).

Size of Contiguous Habitat

New Jersey—Small woodlots (≤0.2 ha) supported higher populations than larger woodlots (Galli et al. 1976).

Table 32. Important characteristics of northern oriole habitat in Missouri (N = 49).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	700-1400*	37	170-2100*	86	>2100	14
Canopy closure (%)	>95*	53	>80	78	<80	22
Canopy height (m)	24-28*	41	20-32*	86	<20*	16
Slope (degrees)	0*	100	0*	100	>0*	0
SECONDARY						
Subcanopy closure (%)	70-95	51	>45	90	<45	10

[a]*Percent of observations.*
**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

Conclusions

Northern orioles occur in most open deciduous woodland habitat with tall trees (Bent 1958, Fitch 1958, Mengel 1965, Anderson 1971, James 1971, DeGraaf et al. 1980). Preference for elm trees (Bent 1958, DeGraaf et al. 1980) probably reflects the requirement of a high, open canopy. These were commonly tall trees in open situations of the eastern U.S.; low woody vegetation provided foraging habitat in these areas (Sibley and Short 1964). In our study, habitat included tall trees forming a closed canopy with a sparse understory but well-developed subcanopy layer. These orioles feed and nest in shrubs or trees (Evans and Kirkman 1981), but nests usually are built 7.6-9.5 m above ground (Harrison 1975).

As in New Jersey, a preference for small woodlots was indicated in our study. Territorial northern orioles were located only on central Missouri bottomland

hardwood study areas which were mostly narrow, forested strips along the Missouri River. Absence of slope may only reflect this fact.

Throughout their range, northern orioles inhabit a variety of areas, requiring primarily the presence of tall trees and possibly smaller forested islands. Our results, therefore, should be cautiously extrapolated to other areas.

Rose-breasted Grosbeak

Rose-breasted grosbeaks were observed primarily in central Missouri bottomland hardwoods, although several were also found in upland hardwoods. The most consistent characteristic of habitat around song perches was an intermediate to large number of live stems 10.0-29.9 cm dbh (150-500/ha, never <125). Other important features included short to intermediate ground vegetation (<0.30 m), few woody stems <2.5 cm dbh (corrected values <2100/ha) and an intermediate to high canopy (12-28 m, never <10) (Table 33). These characteristics describe open, mature forest habitat with numerous pole size trees and sparse shrub and ground layers.

Table 33. Important characteristics of rose-breasted grosbeak habitat in Missouri (N = 22).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Live stems 10.0-29.9 cm dbh/ha	350-400†	18	150-500	86	<150	5
SECONDARY						
All woody stems <2.5 cm dbh/ha	1400-2100*	32	<2100†	71	>2100	29
Ground vegetative height (m)	.01-.10*	39	<.30	95	>.30	5
Canopy height (m)	20-24*	45	12-28	95	<12 or >28	5

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

†*P<0.10.*

Summary of Other Studies

Density of Small Woody Stems

Northeastern U.S.—Forest edge with dense, tall shrubs and thickets provided optimum habitat (DeGraaf et al. 1980).

Understory Vegetation

Nebraska—Along the Platte and Missouri River, this grosbeak breeds most commonly in groves of mature cottonwoods with understory vegetation 2-3 m high, a vegetative formation seemingly favored throughout the range (West 1962).

South Dakota—Riparian vegetation with dense to park-like understory provided suitable habitat (Anderson and Daugherty 1974).

Canopy Closure

New York—Opening of forest stands by removal of varying amounts of commercial timber increased rose-breasted grosbeak populations (Webb 1977).

Ontario—In seeming contrast, a direct relationship existed between grosbeak numbers and canopy closure along roadside transects (Weber and Theberge 1977).

Canopy Height

Northeastern U.S.—Tall trees along forest edge contributed to optimum grosbeak habitat (DeGraaf et al. 1980).

Conclusions

Rose-breasted grosbeaks are associated with various wooded habitats including moist second-growth woods, parkland situations, thickets, and suburban shade trees (Fitch 1958, Bent 1968, Harrison 1975). In the northeastern U.S., the interface between tall forest trees and fields with dense tall shrubs and thickets provides optimum habitat (DeGraaf et al. 1980).

In our study, rose-breasted grosbeaks were found primarily in small forested areas with relatively tall trees, canopy closure typically >70% and never <40%, and sparse understory and ground layers. These grosbeaks forage on the ground and nest in shrubs or small trees (Evans and Kirkman 1981) at heights of 1.8-7.9 m (Harrison 1975). Rose-breasted grosbeaks in New Jersey occurred in large and small forest tracts, exhibiting no preference in area size (Galli et al. 1976). Habitat in South Dakota included riparian vegetation in large and small tracts with dense to park-like understory (Anderson and Daugherty 1974). In the Great Plains, these grosbeaks preferred forest stands of variable structure having a dense understory or ground layer (West 1962).

Rose-breasted grosbeaks appear to be generalists occurring in various wooded habitats in different parts of their breeding range. Thus, our results may not be appropriate to other localities.

Forest Interior - Pole or Sawtimber, Dense Understory

Red-headed Woodpecker

Red-headed woodpeckers were observed primarily on upland hardwood study areas, although several were also noted on central and southeastern Missouri bottomland study areas. Habitat around song perches most consistently had an intermediate to large number of dead stems ≥30 cm dbh (20-80/ha) and an intermediate number of live stems 10.0-29.9 cm dbh (150-350/ha). Other important features included a high canopy (16-32 m, never <13), an intermediate to closed subcanopy (>55%), intermediate to dense ground vegetation (>45%) and an intermediate to large number of dead stems 10.0-29.9 cm dbh (24-75/ha) (Table 34). These characteristics describe pole to mature forest habitat with numerous large snags and a well-developed subcanopy-understory layer.

Table 34. Important characteristics of red-headed woodpecker habitat in Missouri (N = 21).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Live stems 10.0-29.9 cm dbh/ha	200-250	29	150-350	81	<150 or >350	19
Dead stems >30 cm dbh/ha	20-30	38	20-80*	67	0*	33
SECONDARY						
Dead stems 10.0-29.9 cm dbh/ha	24-50	57	24-75	71	0	14
Subcanopy closure (%)	70-75	24	>55	90	<55	10
Ground vegetative cover (%)	60-65*	24	>45	90	<45	10
Canopy height (m)	16-20	33	16-32	86	<13	0

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

Summary of Other Studies

Density of Intermediate-sized and Larger Trees

Virginia—Nesting habitat had high basal area but relatively low density of trees >7 cm dhb (67/ha); the trees were usually large, >20 cm dbh (Conner and Adkisson 1977).

Density of Large Snags

Eastern U.S.—Wooded habitats with numerous snags were preferred (Scott et al. 1977, Graber et al. 1977). To maintain good populations of red-headed woodpeckers, 160-200 snags are needed per 40 ha of habitat; optimum size of snags was 40-60 cm dbh (Evans and Conner 1979).

Ground Vegetative Cover - Understory Development

Arkansas—Suitable red-headed woodpecker habitat had sparse understory (James 1971).

Ohio—Grazed woodlots supported higher red-headed woodpeckers than ungrazed woodlots (Good and Dambach 1943).

U.S.—In contrast, open forest with dense ground vegetation comprised preferred habitat (Scott et al. 1977, DeGraaf et al. 1980).

Virginia—Suitable habitat had sparse understory (Conner and Adkisson 1977).

Relationship To Canopy Openings

Various Localities—Optimum red-headed woodpecker habitat consisted of wooded areas with sparse canopies or numerous canopy openings (James 1971, Conner and Adkisson 1977, Graber et al. 1977, Scott et al. 1977, DeGraaf et al. 1980).

Tree Species Composition

Illinois—Favored feeding substrates were white oaks (48% of observations), followed by snags (15%) (Williams 1975).

Conclusions

Red-headed woodpeckers are usually associated with open forest habitat including forest edge, savannah-like situations, herbicide treated timber stands, farm yards and orchards; they are also found in many other forested areas (Bent 1939, Mengel 1965, Graber et al. 1977, Hardin and Evans 1977, Scott et al. 1977, DeGraaf et al. 1980).

Numerous large snags were consistently present on habitat utilized by red-headed woodpeckers in our study, a result confirmed elsewhere (Graber et al. 1977, Scott et al. 1977). Snags are used for perching, feeding, nesting and roosting;

three snags 40-60 cm dbh are required per territory (Evans and Conner 1979). The numerous snags possibly are significant in opening up the canopy rather than providing foraging substrate (Graber et al. 1977).

Red-headed woodpeckers often forage on the ground or by flycatching (Conner 1976, Conner and Adkisson 1977). Preference for areas with an open canopy or with numerous openings reflects this behavior (Conner and Adkisson 1977, Graber et al. 1977, DeGraaf et al. 1980). Canopy closure in our study was typically >75%, and seldom <55%. The relatively great subcanopy and canopy coverages resulted in a dense overstory in our study, and therefore our results do not support the requirement for an open canopy.

In our study, ground vegetation was also relatively dense. Dense ground vegetation possibly provides increased feeding substrate. However, suitable habitat in Virginia had a sparse understory which was related to the ground-feeding habits (Conner and Adkisson 1977), presumably by allowing greater access to the ground layer.

The characteristics selected as important to red-headed woodpeckers in our study do not adequately describe optimum breeding habitats elsewhere. This optimum habitat consists of a relatively open canopy and numerous large snags. The degree of understory-ground vegetation development varied among studies. Presence of numerous snags was the principal characteristic in our study that was consistent with other studies, although the high tree canopies we observed are consistent with sparsely stocked larger trees noted in some other studies.

Hairy Woodpecker

Hairy woodpeckers were sparsely distributed in central Missouri upland and bottomland hardwoods. Habitat around song perches was most consistently characterized by an intermediate to high canopy (always 15-23 m), an intermediate to great number of woody stems <2.5 cm dbh (corrected values 2100-5600/ha) and an intermediate to great number of live stems ≥30 cm dbh (49-150/ha, never <49). Other important features included intermediate ground vegetation coverage (40-65%), intermediate subcanopy closure (50-75%, never <50) and an intermediate number of live stems 10.0-29.9 cm dbh (100-200/ha, never >375) (Table 35). These characteristics describe older pole to mature forest habitat with well-developed, but not dense, understory and ground layers.

Summary of Other Studies

Density of Small Woody Stems - Understory Development

Georgia—Older forest stands with well-developed understories were preferred over younger stands with less dense understory (Johnston and Odum 1956).

Ohio—Grazed woodlots had smaller populations of hairy woodpeckers than ungrazed woodlots (Good and Dambach 1943).

Ontario—Hemlock stands with little undergrowth supported highest woodpecker populations, but other forest types with dense undergrowth were also used (Martin 1960).

Oregon—Shrub densities averaged 318/ha on grazed Oregon white oak stands that provided primary habitat, vs. 3100/ha on ungrazed stands providing less suitable habitat (Anderson 1970).

Wisconsin—Mesic upland forest stands having less shrub cover supported higher populations than xeric stands with more shrub cover (Bond 1957).

Wyoming—Optimum habitat included several coniferous forest types with a well-developed to sparse shrub understory (Salt 1957).

Density of Small Trees - Subcanopy

Tennessee—UVA and MVA selected numerous small trees as an important component of hairy woodpecker habitat (Anderson and Shugart 1974).

Wyoming—Coniferous forest stands with open subcanopy provided optimum habitat (Salt 1957).

Density of Intermediate-sized Trees

Wisconsin—Preferred habitat had more trees >10 cm dbh (373-380/ha) than did less suitable habitat (Bond 1957).

Density of Large Trees

Georgia—Climax oak-hickory and 100-year-old pine stands with average tree size 32.5-45.0 cm dbh comprised primary hairy woodpecker habitat (Johnston and Odum 1956).

Various Localities—Hairy woodpeckers inhabitat many coniferous or deciduous forest areas with large, mature trees (Bent 1939, Bond 1957, Salt 1957, Fitch 1958, Mengel 1965, Anderson and Shugart 1974, Conner and Adkisson 1975, Graber et al. 1977, DeGraaf et al. 1980, Verner 1980).

Density of Large Snags

Various Localities—For maintenance of hairy woodpecker populations, 160-200 snags per 40 ha are required; optimum size is 30 cm dbh (Evans and Conner 1979). Minimum sized trees for this woodpecker are about 20-25 cm dbh and 4.0-4.6 m tall (Conner et al. 1975, Thomas et al. 1979).

Canopy Closure

California—Optimum habitat in the Sierra Nevadas had <70% canopy closure (Verner 1980).

Oregon—Primary habitat had a closure ≥61% (Anderson 1970).

Wisconsin—Forested areas used by hairy woodpeckers had canopies >50%, but areas with denser canopies supported higher populations (Bond 1957).

U.S.—In contrast, hairy woodpeckers prefer open woodlands for nesting in many parts of their breeding range (Scott et al. 1977).

Canopy Height

California—Mature forests with trees >15 m tall comprised optimum habitat in the Sierra Nevadas (Verner 1980).

Georgia—Hairy woodpecker habitat consisted of 100-year-old pine and climax oak-hickory forests with canopy heights >25.5 m, but seldom younger pine forests or grassland-deciduous shrublands (Johnston and Odum 1956).

Virginia—Preferred habitat was provided by a mature oak stand with canopy height 23-26 m, but a wide range of canopy heights was accepted (Conner and Adkisson 1975, 1977).

Wyoming—Spruce-fir forest with trees >18 m tall was preferred habitat but younger deciduous stands were used to a lesser extent (Salt 1957).

Table 35. Important characteristics of hairy woodpecker habitat in Missouri (N = 14).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	2100-5600*	86	2100-5600*	86	<1400 or >5600	7
Live stems ≥30 cm dbh/ha	50-75	36	49-150	93	<49	0
Canopy height (m)	16-20*	79	15-23	100	<15 or >23	0
SECONDARY						
Live stems 10.0-29.9 cm dbh/ha	100-200*	57	100-200*	57	>300	7
Ground vegetative cover (%)	50-65*	43	40-65	57	<40	7
Subcanopy closure (%)	50-60*	43	50-75	71	<50	0

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

Size of Contiguous Habitat

Eastern U.S.—Forest tracts >4 ha supported considerably higher populations than smaller tracts (Robbins 1979); only large forest tracts provide nesting habitat (Conner et al. 1975).

New Jersey—Woodlots <2 ha were not inhabited by hairy woodpeckers (Galli et al. 1976).

Conclusions

The most consistent feature of habitat in the above studies was presence of large mature trees. Of the three primary characteristics in our study, two describe this critical component (canopy height and density of large trees). Larger forest tracts also appeared important to hairy woodpeckers. Once these criteria were met, forest structure varied considerably from study to study. Hairy woodpeckers in Virginia nested in forest habitat with a wide range of basal areas and stem densities (Conner and Adkisson 1977). None of the habitat variables measured in an Illinois study were significantly correlated with hairy woodpecker abundance (Graber et al. 1977).

Importance of the other selected characteristics in our study were not consistently documented in the literature. These variables described habitat with well-developed ground, understory, and subcanopy layers. The degree of subcanopy closure in older pole-mature forest stands depends on the density of medium sized trees (10.0-29.9 cm dbh) and smaller woody stems; these three variables are closely interrelated.

Large snags are not necessarily required for nesting since nest cavities often are excavated in large, live trees (Lawrence 1967, Hardin and Evans 1977, Scott et al. 1977). However, snags also provide foraging, perching and roosting sites (Evans and Conner 1979). Male hairy woodpeckers foraged both in live and dead trees in New York (Kisiel 1972). In Colorado, 60% of the time spent foraging was on snags (Stallcup 1968).

Foraging habitat may differ from nesting habitat in some localities. Hairy woodpeckers were often observed foraging in clearcuts in Virginia (Conner et al. 1975).

Hairy woodpeckers occur in a variety of forest habitats with variable structures, apparently requiring only larger forest tracts with some large trees.

Downy Woodpecker

Downy woodpeckers were sparsely distributed on most forest study areas in central Missouri. The most consistent characteristic of habitat around song perches was an intermediate canopy height (12-24 m, never <12). Other important features included an intermediate to nearly closed subcanopy (65-90%), a large number of live stems 2.5-9.9 cm dbh (750-1350/ha, never <250) and an intermediate to large

number of dead stems 2.5-9.9 cm dbh (100-250/ha) (Table 36). These characteristics describe pole to mature forest habitat with numerous smaller trees, resulting in a well-developed subcanopy.

Table 36. Important characteristics of downy woodpecker habitat in Missouri (N = 33).

Variable	*Optimum Range*	*%*[a]	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Canopy height (m)	16-20	42	12-24	91	<12 or >24	9
SECONDARY						
Live stems 2.5-9.9 cm dbh/ha	1300-1350*	15	750-1350	73	<750	27
Dead stems 2.5-9.9 cm dbh/ha	150-200*	33	100-250	60	<100*	21
Subcanopy closure (%)	70-75*	21	65-90	63	<25 or >90	6

[a]*Percent of observations.*
**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

Summary of Other Studies

Density of Small Woody Stems

Tennessee—UVA and MVA indicated that presence of numerous saplings was the only characteristic of importance for downy woodpecker habitat (Anderson and Shugart 1974).

Density of Larger Trees

Illinois—Density of trees 25-55 cm dbh was positively related with downy woodpecker abundance, but relative density of trees >55 cm dbh was negatively related to woodpecker abundance in bottomland but not in upland forest (Graber et al. 1977).

Virginia—Forest habitat with trees <38 cm dbh was preferred (Conner et al. 1975).

Density and Size of Snags

Illinois—Downy woodpecker abundance was positively related to numbers of

dead trees in bottomlands, but not in upland woods (Graber et al. 1977).

Various Localities—Approximately 320-400 snags/ha are required to sustain populations of downy woodpeckers; optimum snag size was 20 cm dbh (Evans and Conner 1979). Minimum snag size for nesting downy woodpeckers was 15.2 cm dbh, and 4.6 m tall (Thomas et al. 1979).

Canopy Height

Virginia—Downy woodpecker habitat included mature oak forest with canopy height 23-26 m and 1-year-old clearcuts with woody vegetation 0.3-1.0 m tall (Conner and Adkisson 1975). By MVA, Conner and Adkisson (1977) selected relatively low canopy height as a key feature of habitat.

Size of Contiguous Habitat

New Jersey—Woodlands <1.2 ha did not provide suitable habitat (Galli et al. 1976).

Tree Species Composition

Most published information about tree species used by downy woodpeckers pertains to foraging sites; presumably nesting or drumming sites bear some relationship to them.

Illinois—Downy woodpeckers foraged mostly on white oaks (44% of observations) and snags (19%) (Williams 1975).

New York—Live elms, white oaks, aspen and staghorn sumac stems provided preferred foraging sites (Kisiel 1972).

Northeastern U.S.—Woodlands with elms and oaks provide foraging habitat (DeGraaf et al. 1980).

Pennsylvania—No tree preferences for foraging were present in summer although there were clear preferences for tulip trees, oaks, and box elder in winter (Travis 1977).

Conclusions

Downy woodpeckers are associated with a variety of wooded habitats. In Kansas (Fitch 1958) and Kentucky (Mengel 1965), habitat included areas with at least a few trees and shrubs. Primary habitat in Illinois was forest interior, especially mature bottomland forest (Graber et al. 1977). In other areas, downy woodpeckers prefer interior or edge of open woodland, orchards, shade trees, farm yards and roadside hedges (Bent 1939, Scott et al. 1977, DeGraaf et al. 1980).

Habitat in Oregon included five Oregon white oak stands with widely differing structures. Downy woodpeckers occurred in all five areas about equally even though these areas had canopy closures of 44-82%, trees 9-18+ m tall, tree densities of 110-378/ha and shrub densities of 318-3100/ha (Anderson 1970). Oak forests with

widely different structures also provided suitable habitat in the eastern deciduous forest area (Probst 1979). Our study did not delineate specific habitat of downy woodpeckers; most variables had wide range values.

No consistent preference for dead or live trees for nesting is exhibited by downy woodpeckers throughout their range. In most localities, snags were preferred (Bent 1939, Lawrence 1967, Hardin and Evans 1977, Conner 1978), but in New Hampshire dead tops of live trees were preferred (Kilham 1974). However, snags also provide foraging, perching, and roosting sites (Evans and Conner 1979).

Wintering habitat requirements or proximity of wintering habitat may affect selection of breeding habitat by downy woodpeckers (Kilham 1974). Preferred winter habitat in many localities includes bottomland forest, shrub habitat, forest edge and uplands with large trees (Graber et al. 1977, DeGraaf et al. 1980). Most downy woodpeckers are non-migratory (Bent 1939, Scott et al. 1977), requiring suitable wintering habitat within or near breeding habitat. Proximity of wintering habitat possibly is the most critical requirement that should be evaluated, but a wide variety of habitats will suffice for breeding.

Downy woodpeckers are forest generalists; thus, the characteristics describing habitat in Missouri do not clearly delineate habitat elsewhere.

Black-and-white Warbler

Black-and-white warblers were observed primarily in central Missouri upland hardwoods, although several were also studied in southeastern Missouri bottomland hardwoods. The most consistent characteristics of habitat around song perches were dense ground vegetation (60-95%), an intermediate canopy height (12-20 m, never <10 or >22), a slight to moderate slope (>5°), intermediate to tall ground vegetation (0.20-0.60 m), and a large number of woody stems <2.5 cm dbh (corrected values 2800-7000/ha). Another important feature was a large number of live stems 10.0-29.9 cm dbh (>200/ha, never <70) (Table 37). These characteristics describe pole to mature forests on hillsides, with dense shrub and ground layers.

Summary of Other Studies

Density of Small Woody Stems

Georgia—Mature forest with a well-developed understory supported populations of this warbler, but not grassland-shrub habitat or pine stands with 23-35% shrub cover (Johnston and Odum 1956).

Ground Vegetative Cover - Understory Development

Arkansas—Several wooded tracts with sparse to dense ground-understory cover were used by black-and-white warblers, but not red cedar glades or

shrub-grasslands (Shugart and James 1973).

Georgia—Of several successional stages available, only oak-hickory stands with well-developed understory provided suitable habitat (Johnston and Odum 1956).

Canopy Closure

Arkansas—Preferred habitat had 74% canopy closure, less suitable habitat had 64% closure, and unsuitable habitat had <50% closure (Shugart and James 1973).

New York—In contrast, heavy logging (70-100% of commercial timber removed) resulted in increased black-and-white warbler population levels (Webb 1977).

Canopy Height

Georgia—Habitat consisted of mature deciduous forest with trees >30 m tall;

Table 37. Important characteristics of black-and-white warbler habitat in Missouri (N = 33).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	2800-4200*	36	2800-7000	76	<2800*	21
Ground vegetative cover (%)	75-80*	21	60-95*	82	<45	3
Ground vegetative height (m)	.20-.30†	33	.20-.60	76	<.20*	21
Canopy height (m)	16-20	52	12-20*	88	<8 or >20*	3
Slope (degrees)	5-10*	33	>5	70	0*	18
SECONDARY						
Live stems 10.0-29.9 cm dbh/ha	200-250	21	>200	85	<150	6

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

†P<0.10.

woods with canopy <7 m high were not used by black-and-white warblers (Johnston and Odum 1956).

Virginia—Oak pole stands with canopy height 8-11 m provided suitable habitat, but not mature oak forest with a canopy height 23-25 m (Conner and Adkisson 1975).

Size of Contiguous Habitat

Eastern U.S.—Population density was considerably lower in forests <300 ha than in larger tracts (Robbins 1979).

New Jersey—This warbler was not found in forest tracts <7.5 ha and was not common even in 24 ha tracts (Galli et al. 1976).

Conclusions

Preferred or suitable habitat differed considerably in the referenced studies, and no habitat characteristics were consistently prominent. Black-and-white warblers occur in a variety of woody habitats depending on locality. Habitat in some areas consists mostly of dry portions of wooded swampland (Bent 1953, Griscom and Sprunt 1957). Elsewhere, dry, rocky hillsides with forest cover constitute preferred habitat (Bent 1953). In our study, slope values may only reflect the hilly terrain of most upland forests in central Missouri; however they agree with the preference for hillsides noted by Bent. The two study areas accounting for 45% of the observations of this warbler in our study had dense (77 and 86%), tall (0.32 and 0.45 m) ground vegetation and steep slopes with numerous, rocky outcroppings. This species nests on the ground, typically under the edge of or near fallen debris (Harrison 1975), and a well-developed ground layer may provide concealing cover.

Black-and-white warblers also inhabit mature deciduous forests and dense hemlock and rhododendron habitat on steep slopes in Kentucky (Mengel 1965) and mature or second growth deciduous or mixed woodland in the northeastern U.S. (DeGraaf et al. 1980). These warblers are most commonly associated with forest edge or early seral forests in New York (Kendeigh 1945).

Black-and-white warblers occurred in well-defined forest habitat in our study. The important characteristics selected in our study conform with qualitative descriptions of habitat in some parts of the breeding range, but numerous inconsistencies appear elsewhere.

Worm-eating Warbler

Worm-eating warblers were observed primarily on upland hardwood study areas in central Missouri, although several were also found on upland and bottomland hardwood study areas in southeastern Missouri. Habitat around song perches most consistently had many woody stems <2.5 cm dbh (corrected values 2100-7700/ha, never <500), a slight to moderate slope (>1°) and an intermediate canopy height (12-24 m, never <10) Other important features included an intermedi-

ate to nearly closed subcanopy (50-95%, never <30), an intermediate to large number of live stems 2.5-9.9 cm dbh (600-1150/ha, never <250), few dead stems 10.0-29.9 cm dbh (<25/ha), a low to intermediate number of live stems 10.0-29.9 cm dbh (24-250/ha, never >450), and a low to intermediate number of live stems ≥30 dbh (<75/ha) (Table 38).

Song perches were located in forest habitat on rocky hillsides with many small trees and shrubs, and few larger trees. Degree of canopy closure was variable but subcanopy closure was relatively great.

Summary of Other Studies

Density of Small Woody Stems

Eastern U.S.—Forest areas with an undergrowth of shrubs and small trees supplied preferred habitat (Bent 1953, DeGraaf et al. 1980).

Density of Intermediate-sized Trees

Eastern U.S.—Abundant trees 16-38 cm dbh were an important characteristic of suitable habitat as determined by MVA (Anderson 1979).

Ground Vegetative Cover

Eastern U.S.—Sparse ground cover was selected by MVA as a principal feature of worm-eating warbler habitat (Robbins 1978).

Canopy Closure

Arkansas—Suitable forest habitat had 74% canopy closure; unsuitable habitat had <65% closure (Shugart and James 1973).

Canopy Height

Arkansas—Only climax oak forest provided habitat, not early seral forest stages with smaller trees (Shugart and James 1973).

Eastern U.S.—Intermediate to high canopy height was a critical component of habitat of worm-eating warblers (Robbins 1978, Anderson 1979).

Virginia—In contrast, 7-to 12-year-old clearcuts with woody vegetation 1.5-5.0 m tall were used by worm-eating warblers, but not pole or mature oak stands with canopies >8 m (Conner and Adkisson 1975).

Slope

Various Localities—Slope was selected as a principal feature of habitat (Anderson 1979). Wooded hillsides were preferred habitat (Bent 1953, Mengel 1965, K. E. Evans 1978, DeGraaf et al. 1980).

Size of Contiguous Habitat

Eastern U.S.—Highest population densities were sustained on forest areas >300 ha (Robbins 1979).

Tree Species Composition

Eastern U.S.—Little conifer cover was a prominent characteristic of habitat (Robbins 1978).

Table 38. Important characteristics of worm-eating warbler habitat in Missouri (N = 38).

Variable	*Optimum Range*	*%*[a]	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	4500-5600*	21	2100-7700	89	<2100*	11
Canopy height (m)	12-16*	42	12-24	92	<10 or >24	3
Slope (degrees)	10-15*	26	>1	92	0*	8
SECONDARY						
Live stems 2.5-9.9 cm dbh/ha	750-1150	52	600-1150	73	<600	16
Live stems 10.0-29.9 dbh/ha	200-250	24	24-250	76	>250	24
Live stems ≥30 cm dbh/ha	25-50†	29	<75	76	>75	24
Dead stems 10.0-29.9 cm dbh/ha	0	42	<25†	79	>50	5
Subcanopy closure (%)	75-80*	26	50-95	95	<50	5

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, $P<0.05$).*

†$P<0.10$.

Conclusions

Throughout their range, worm-eating warblers prefer moist wooded hillsides covered with medium-sized trees and an undergrowth of shrubs and small trees (Bent 1953, Mengel 1965, DeGraaf et al. 1980). Worm-eating warblers forage and nest in the ground layer (Evans and Kirkman 1981), and nests usually are concealed in a thick litter of leaves with numerous small woody stems overhead (Harrison 1975). Most of the characteristics describing habitat in our study apparently also delineate habitat in many other parts of the breeding range. Worm-eating warblers appear to respond to moderate slope, intermediate to high canopy, abundance of small trees and shrubs, abundant medium-sized trees, large forest size, and moist habitat.

Ovenbird

Ovenbirds were studied only in central Missouri upland hardwoods. Habitat around song perches most consistently had many woody stems <2.5 cm dbh (corrected values 2800-7000/ha, never <1400), intermediate canopy height (12-20 m, never <10 or >22), and slight to moderate slope (1-15°). Other important features included an intermediate to nearly closed subcanopy (60-90%), intermediate ground vegetation height (always 0.05-0.50 m), an intermediate to closed canopy (>70%), and intermediate to dense ground vegetation (>55%, never <20) (Table 39).

Song perches were located in forest habitat on hillsides with relatively dense vegetation at all layers.

Summary of Other Studies

Density of Trees

U.S.—Important variables delineated by MVA included number of seedlings, and number of trees 8-15 cm dbh and 24-44 cm dbh in Michigan (Anderson 1979), and numerous trees <53 cm dbh in eastern U.S. (Robbins 1978).

Ground Vegetative Cover

Eastern U.S.—Sparse ground coverage was selected as an important habitat feature (Robbins 1978).

Vermont and Pennsylvania—Ovenbird habitat had sparse vegetation below a height of 0.6 m (MacArthur et al. 1962).

Understory Development

Michigan—Nesting habitat of ovenbirds had open understory (Hann 1937).

Ontario—Of several successional stages, forest stands with dense understory were preferred by ovenbirds (Martin 1960).

Pennsylvania—Several forest types with understory vegetation ranging from sparse to dense provided habitat (Davis and Savidge 1971).

Tennessee—Dense understory was selected as an important habitat feature (Anderson and Shugart 1974).

U.S.—Ovenbird habitat consisted of open forests with sparse understory (Bent 1953, Griscom and Sprunt 1957, DeGraaf et al. 1980).

Vermont and Pennsylvania—Forest habitat had sparse to moderate vegetation at heights below 4.5 m (MacArthur et al. 1962).

Subcanopy Closure

Tennessee—Open subcanopy was a prominent feature of habitat as determined by MVA (Anderson and Shugart 1974).

Vermont and Pennsylvania—Ovenbird habitat had dense vegetation at heights >4.5 m (MacArthur et al. 1962).

Canopy Closure

Arkansas—Well-developed, shaded forests provided ovenbird habitat (James 1971). Habitat consisted of mature oak forest with canopy closure 74%, but not other wooded habitats with canopy closure <65% (Shugart and James 1973).

Michigan—Mean canopy depth was an important variable affecting habitat suitability (Anderson 1979); presumably, canopy depth is linked with canopy density.

New York—Ovenbird populations were lower in areas where the canopy was opened by commercial timber removal (Webb 1977).

Tennessee—In contrast, open canopy was selected as a prominent habitat feature (Anderson and Shugart 1974).

U.S.—habitat consisted of open forests (Bent 1953, Griscom and Sprunt 1957, DeGraaf et al. 1980).

Canopy Height

Ontario—Forests with canopy heights 9-30 m supported populations (Martin 1960).

Pennsylvania—Highest populations of ovenbirds were in mature oak hardwoods, but they were also found in younger forests with canopy height 5-7 m (Davis and Savidge 1971).

Tennessee—Large trees were a principal feature of ovenbird habitat (Anderson and Shugart 1974).

Slope

Michigan—Nests were often in sloping terrain (Hann 1937).

Northeastern U.S.—Nests were located on sloping or level ground (DeGraaf et al. 1980).

Size of Contiguous Habitat

Eastern U.S.—Population densities diminished in forests <10 ha (Robbins 1979).

New Jersey—Forests <4 ha did not support ovenbirds (Galli et al. 1976).

Tree Species Composition

Eastern U.S.—Abundance of oaks was a prominent habitat variable (Robbins 1978).

Table 39. Important characteristics of ovenbird habitat in Missouri (N = 33).

Variable	*Optimum Range*	*%*[a]	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	2800-4900*	52	2800-7000*	88	<2800	7
Canopy height (m)	16-20*	52	12-20*	85	<10 or >22	0
Slope (degrees)	1-5*	39	1-15*	76	0*	9
SECONDARY						
Ground vegetative cover (%)	65-70*	21	>55	73	<45	15
Ground vegetative height (m)	.20-.30*	39	.05-.50	100	<.05 or >.50	0
Subcanopy closure (%)	60-65†	18	60-90	73	<45	6
Canopy closure (%)	80-90*	42	>70	85	<60	3

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

†P<0.10.

Conclusions

Ovenbirds are typically associated with mature forest stands (Bent 1957, Mengel 1965, DeGraaf et al. 1980), especially deciduous or mixed stands

(Kendeigh 1945); but vegetative structure of preferred habitat appears to vary considerably with location. Habitat in most parts of the breeding range consisted of open forests with sparse understory-ground layers (Bent 1953, Griscom and Sprunt 1957, DeGraaf et al. 1980). Forest habitat in our study had relatively dense vegetation in all layers.

The only consistent habitat requirement in the above studies was a forest stand with trees >5-7 m tall. Some of the discrepancies possibly are due to confusion of feeding, nesting, and singing habitats. Ovenbirds in Canada appeared to prefer exposed song perches 4-12 m above ground with an unobscured view (Zach and Falls 1978). In contrast, males in our study typically sang from perches <8 m above ground surrounded by relatively dense vegetation at all levels.

Considering the ovenbird's ground nesting and foraging habits (Griscom and Sprunt 1957), one would expect preferred habitat to have a well-developed ground layer. However, areas with little underbrush and an abundance of fallen leaves, logs and rocks are preferred (Griscom and Sprunt 1957). Most nests are placed alongside trails, woodland roads or partically cleared areas (Bent 1953). Litter depth is probably important for ground nesting but was not measured on forest plots.

The characteristics selected as important in our study are only partly consonant with preferred habitat described for other geographical locations.

Kentucky Warbler

Kentucky warblers were observed primarily in central Missouri hardwoods, although several were also studied in southeastern Missouri forests. Habitat around song perches was most consistently characterized by an intermediate canopy height (12-20 m), an intermediate to nearly closed subcanopy (60-95%), and an intermediate to large number of woody stems <2.5 cm dbh (corrected values >1400/ha). Other important features included an intermediate to tall (>0.10 m, never <0.05) and intermediate to dense (>40%, never <30) ground vegetation layer (Table 40).

These characteristics describe pole to mature forests with relatively dense vegetation at all vertical layers, especially the shrub and ground layers. Males usually established territories in dense thickets near forest openings.

Summary of Other Studies

Density of Small Woody Stems

Eastern U.S.—Density of shrub stems was an important variable affecting habitat suitability, as determined by MVA (Anderson 1979).

Various Localities—Forests with dense shrub-understory layer have been described as suitable Kentucky warbler habitat by Johnston and Odum (1956), Griscom and Sprunt (1957), Fitch (1958), Mengel (1965), and James (1971).

Vermont and Pennsylvania—Moderate amounts of vegetation 0.6-4.5 m tall were present in suitable Kentucky warbler habitat (MacArthur et al. 1962).

Ground Vegetative Cover

Eastern U.S.—Ground coverage was selected as an important habitat variable (Anderson 1979).

Ohio—Ungrazed woodlots had greater Kentucky warbler populations than grazed woodlots (Good and Dambach 1943).

Southeastern U.S.—Habitat for this species consisted of mature bottomland forest with dense ground cover (Meanley 1966).

Vermont and Pennsylvania—In contrast to the findings of several other authors, MacArthur et al. (1962) found that Kentucky warbler habitat had sparse to moderate vegetation below 0.6 m.

Subcanopy Closure

Eastern U.S.—Canopy depth (reflecting degree of subcanopy development) was a key habitat variable (Anderson 1979).

Vermont and Pennsylvania—Suitable habitat had dense vegetation at heights >4.5 m (MacArthur et al. 1962).

Canopy Closure

Eastern U.S.—Canopy closure was an important variable affecting habitat suitability (Anderson 1979).

Tennessee—Relatively open overstory was a prominent habitat feature (Anderson and Shugart 1974).

Canopy Height

Eastern U.S.—Presence of large trees (Robbins 1978) and stand age (Anderson 1979) were selected as prominent habitat features by MVA.

Georgia—Climax oak-hickory forest with canopy height 30+ m provided Kentucky warbler habitat, but not wooded tracts with canopy height <7.5 m (Johnston and Odum 1956).

Virginia—Habitat included 7-year-old clearcuts with woody vegetation 1.5-3.5 m tall, but not pole to mature forest with trees ≥8 m tall (Conner and Adkisson 1975).

Litter Cover and Depth

Kansas—Areas with abundant leaf litter were preferred (Fitch 1958).

Size of Contiguous Habitat

Eastern U.S.—Population densities were considerably higher in areas ≥30 ha than in smaller areas (Robbins 1979).

Tree Species Composition

Eastern U.S.—Presence of few conifers was a principal feature of Kentucky warbler habitat (Robbins 1978).

Table 40. Important chracteristics of Kentucky warbler habitat in Missouri (N = 44).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	4900-5600*	25	>1400	93	<1400*	7
Subcanopy closure (%)	60-80	52	60-95	78	<55	18
Canopy height (m)	12-20†	73	12-20†	73	<12 or >24	10
SECONDARY						
Ground vegetative cover (%)	90-95†	14	>40	98	<40	2
Ground vegetative height (m)	.10-.20	25	>.10	95	<.10*	5

[a]*Percent of observations.*
**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*
†P<0.10.

Conclusions

In other studies, Kentucky warblers were consistently found in pole to mature forests with well-developed subcanopy and understory layers. The primary characteristics in our study readily describe this preferred habitat, but the importance of the ground layer in our study was not consistently confirmed by other studies. A well-developed subcanopy-shrub layer would provide foraging habitat for this mid-level forager (Evans and Kirkman 1981), and dense ground-understory vegetation would provide cover for the nest which is typically placed on the ground or low in a shrub (Harrison 1975).

Other researchers identified several habitat variables that appeared important but were not measured in our study, including number of tree species, presence of small understory plants, and distance to edge (Anderson 1979).

Scarlet Tanager

Scarlet tanagers were observed primarily on upland hardwood study areas in central Missouri, although several were also found on upland and bottomland

hardwood study areas in southeastern Missouri. The most consistent characteristics of habitat around song perches were many woody stems <2.5 cm dbh (corrected values >2800/ha, never <700), a slight to moderate slope (1-15°) and many live stems ≥30 cm dbh (>75/ha). Slope values possibly reflect the hilly terrain of most upland forests in central Missouri rather than habitat requirements of the scarlet tanager.

Other important features included an intermediate number of live stems 10.0-29.9 cm dbh (150-300/ha, never <50 or >550), an intermediate to large number of woody stems ≥2.5 cm dbh (1200-1900/ha, never <900), an intermediate to large number of live stems 2.5-9.9 cm dbh (always >450/ha), an intermediate canopy height (16-24 m), and an intermediate to closed subcanopy (>55%, never <20) (Table 41). These characteristics describe habitat in mature, dense upland forests on hillsides, with well-developed understory.

Table 41. Important characteristics of scarlet tanager habitat in Missouri (N = 23).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	4200-5600*	35	>2800	91	<2800*	9
Live stems ≥30 cm dbh/ha	100-125*	35	>75	74	<75	26
Slope (degrees)	5-10*	43	1-15*	83	0*	13
SECONDARY						
All woody stems ≥2.5 cm dbh/ha	1400-1500	22	1200-1900	83	<900 or >1900	4
Live stems 2.5-9.9 cm dbh/ha	800-850	13	>450	100	<450	0
Live stems 10.0-29.9 cm dbh/ha	250-300*	30	150-300	74	<150 or >350	17
Subcanopy closure (%)	65-70†	22	>55	87	<50	9
Canopy height (m)	16-20	52	16-24	74	<12 or >24	13

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, $P<0.05$).*

†$P<0.10$.

Summary of Other Studies

Density of Small Woody Stems

Eastern U.S.—Density and size of shrub stems was selected by MVA as an important variable affecting habitat suitability for scarlet tanagers (Anderson 1979).

Ground Vegetative Cover

Eastern U.S.—Sparse ground cover was selected by MVA as a principal characteristic of habitat (Robbins 1978).

Canopy Closure

Eastern U.S.—Dense canopy cover was selected as a key component of habitat (Robbins 1978).

Canopy Height

Eastern U.S.—A high canopy was a prominent feature of scarlet tanager habitat (Robbins 1978).

Virginia—Primary habitat consisted of oak pole forest with canopy height 8-11 m, followed in preference by canopy 23-25 m high (Conner and Adkisson 1975).

Size of Contiguous Habitat

Eastern U.S.—Forests smaller than 100 ha had considerably lower densities of scarlet tanagers than larger forests (Robbins 1979).

New Jersey—This species did not occur in woodlands <10 ha and was not common in woodlands <24 ha (Galli et al. 1976).

Tree Species Composition

Eastern U.S.—Presence of numerous oaks was a prominent feature of habitat (Robbins 1978).

Pennsylvania—Nineteen of 29 nests were in oaks (Harrison 1975).

Conclusions

Scarlet tanagers occur in moderately open forest (Mengel 1965), mature deciduous and mixed woodlands (DeGraaf et al. 1980), roadside trees, groves, parks, and orchards (Harrison 1975). In Pennsylvania, habitat included mature oak hardwoods, dense red pine stands, grass shrublands, and forest edge (Davis and Savidge 1971).

The most consistent characteristics of scarlet tanager habitat appear to be a relatively large forest area and presence of intermediate to large oaks. Forbush (cited in Bent 1958) attributed this affinity for oaks to the larger number of insects found

on oak trees. However, scarlet tanagers forage in the ground layer in other localities (Evans and Kirkman 1981). Scarlet tanagers possibly respond primarily to the presence of oaks in woodlands (for whatever reason) and only secondarily to other characteristics. Most of 16 oak forests of varying structure supported scarlet tanager populations (Probst 1979). Male scarlet tanagers sang from a variety of tree species in our study, but 61% sang from oaks.

Presence of intermediate to large trees is important for providing nesting sites. Of 29 nests in Pennsylvania, 19 (66%) were >10.5 m above ground (Harrison 1975).

Although scarlet tanagers appeared to respond to specific forest habitat in our study, our conclusions were not entirely supported by other studies.

Forest Interior - Open Tree Reproduction

Black-capped Chickadee

Black-capped chickadees were sparsely distributed on forest study areas in central Missouri; several were also observed in old fields. Habitat around song perches was most consistently characterized by few live stems ≥30 cm dbh (<50/ha, never >100), no dead stems ≥30 cm dbh (always 0/ha), and intermediate to tall ground vegetation (0.20-0.60 m). Other important features included intermediate to dense ground vegetation (>55%), a low to intermediate canopy (4-16 m), and an intermediate number of live stems 2.5-9.9 cm dbh (350-850/ha) (Table 42).

These characteristics describe an open reproduction forest stand with a dense ground layer. The forest study area with the most black-capped chickadee observations had a low, relatively open canopy and relatively dense, tall ground vegetation.

Summary of Other Studies

Density of Small Woody Stems

Tennessee—Presence of small understory trees was the only habitat component appearing important in MVA (Anderson and Shugart 1974).

Washington—Shrub cover was a key habitat variable selected by MVA (Sturman 1968).

Density of Large Trees

Eastern U.S.—Absence of large trees >53 cm dbh and presence of numerous small trees <53 cm dbh were selected by MVA as prominent components of chickadee habitat (Robbins 1978).

New York—Young forest was often part of the territory of chickadees (Odum 1941).

Ontario—Primary habitat consisted of older hemlock forest with large trees,

and to a lesser extent other forest types with variously sized trees. Populations were lowest in the youngest forest type (Martin 1960).

Oregon—Oak savannah with intermediate sized trees was preferred, but more mature forest was also used (Anderson 1970).

Pennsylvania—Forest edge provided principal habitat of black-capped chickadees, but they also used grass-shrublands to mature oak forests (Davis and Savidge 1971).

Size of Snags

Oregon—Minimum size of snags used by this chickadee was 1.8 m tall and 10.2 cm dbh (Thomas et al. 1979).

U.S.—Dead stubs, typically 1.6-2.0 m tall and 11-13 cm dbh were required for nesting (Hardin and Evans 1977).

Ground Vegetative Cover

Eastern U.S.—Dense ground cover was a consistent feature of habitat (Robbins 1978).

Canopy Closure

Washington—Upper canopy volume was selected as an important variable affecting habitat suitability (Sturman 1968).

Canopy Height

Ontario—Preferred habitat had hemlock trees 22.5 m tall, but other acceptable areas had trees 9-30 m tall; populations were lowest in young forest with trees 6 m tall (Martin 1960).

Oregon—Preferred habitat was oak savannah with trees 9-18 m tall, but mature forest with trees >18 also tall were used (Anderson 1970).

Pennsylvania—Habitat consisted primarily of forest edge, but also included various wooded habitats with trees at least 5-7 m tall (Davis and Savidge 1971).

Tree Species Composition

Eastern U.S.—Important characteristics of suburban habitats for chickadees included presence of coniferous vegetation at 6.3-7.5 m heights and deciduous vegetation at 9.3-10.5 m heights (Thomas et al. 1977). In rural areas, many conifers and few oaks were prominent features of habitat (Robbins 1978).

U.S.—Short-lived tree species that produce snags and decaying stubs are preferred for nesting (Scott et al. 1977).

Conclusions

Black-capped chickadees inhabit most wooded types from heavily forested to residential areas, but prefer mixed woodlands (DeGraaf et al. 1980). As a result, no

Table 42. Important characteristics of black-capped chickadee habitat in Missouri (N = 18).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Live stems ≥30 cm dbh/ha	0*	39	<50	83	>50	17
Dead stems ≥30 cm dbh/ha	0†	100	0†	100	>0†	0
Ground vegetative height (m)	.30-.40†	33	.20-.60†	78	<.20*	17
SECONDARY						
Live stems 2.5-9.9 cm dbh/ha	600-700	33	350-850	72	<350 or >850	28
Ground vegetative cover (%)	60-65	28	>55	90	<55	10
Canopy height (m)	8-12*	33	4-16	62	>16	38

[a]*Percent of observations.*
**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*
†P<0.10.

characteristics appeared in the published studies that consistently delineated habitat.

A preference for younger, more open forest possibly exists in some areas, as was apparent in our study. Territories in New York often included deep forest, together with either young forest or other more open types; this species nested in open situations and foraged in the denser forest (Odum 1941). In southern Illinois, nest sites also were situated in rather open portions of the forest (Brewer 1963). Preferred habitat in Kansas was forest near its edge (Fitch 1958). The apparent discrepancies in habitat selection may, in part, be explained by the differences between nesting and foraging habitat. But published information about these preferences consists mainly of qualitative habitat descriptions; therefore our results cannot be thoroughly assessed against published quantitative findings.

White-eyed Vireo

White-eyed vireos were observed primarily in old field-forest edge habitat adjacent to southeastern Missouri bottomland study areas. Several were also studied in central Missouri upland old field-forest edge habitat. Habitat around song perches

most consistently had an intermediate to large number of woody stems <2.5 cm dbh (1400-5950/ha), an intermediate number of woody stems ≥2.5 cm dbh (900-1700/ha), intermediate subcanopy closure (30-70%), an intermediate canopy height (8-22 m), and intermediate ground vegetation coverage (40-80%) (Table 43).

These characteristics describe late seral old field or forest edge habitat with a few large trees and numerous small trees and shrubs. These conditions are accompanied by an open but variable canopy and well-developed, but not dense, subcanopy and ground layers.

Table 43. Important characteristics of white-eyed vireo habitat in Missouri (N = 38).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	2800-3150*	18	1400-5950	84	<1400*	5
All woody stems ≥2.5 cm dbh/ha	1000-1100*	13	900-1700	60	<300*	3
Ground vegetative cover (%)	60-65*	18	40-80*	6	<20 or >90*	10
Subcanopy closure (%)	45-70*	55	30-70*	76	<15*	3
Canopy height (m)	12-14*	24	8-22*	73	<8*	11
SECONDARY						
NONE						

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

Summary of Other Studies

Density of Small Woody Stems

Arkansas—Shrubs and low trees were an important part of white-eyed vireo habitat, as determined by MVA (James 1971).

Georgia—Prime habitat included late seral shrubland and young pine forest with 23-35% shrub cover. Grassland-shrub types with 10% shrub cover, nearly mature pine forest, and climax oak-hickory forests were not used by this species (Johnston and Odum 1956).

Indiana—Fields with blackberry thickets and numerous groups of small trees, or brushy fields with ≥50% woody coverage were vireo habitat. Early stage old fields with less woody vegetation were not used (Nolan 1963).

Vermont and Pennsylvania—White-eyed vireo habitat had moderate to dense vegetation at heights of 0.6-4.5 m (MacArthur et al. 1962).

Ground Vegetative Cover

Vermont and Pennsylvania—Habitat was in sparse to moderate vegetation at heights <0.6 m (MacArthur et al. 1962).

Canopy Height

Georgia—Shrubland and forests with trees ≤18 m tall provided suitable habitat, but not wooded areas with trees <2 m or >22.5 m tall (Johnston and Odum 1956).

Indiana—Habitat was provided by old fields with numerous stands of trees 1-7+ m tall, but not old fields with numerous trees 0.3-5.0 m tall (Nolan 1963).

Northeastern U. S.—Preferred habitat was in close-growing stands of trees 2.4-7.6 m tall (DeGraaf et al. 1980).

Virginia—Seven-year-old clearcuts with trees 1.5-3.5 m tall were inhabited by white-eyed vireos; younger clearcuts with woody vegetation <1.5 m tall and pole oak stands with trees 8-11 m tall were not used (Conner and Adkisson 1975).

Conclusions

White-eyed vireos occur in a variety of shrubby habitats including thickets in mature bottomland forest, open forest, old fields and clearings, other shrubland habitat, and forest edge (Bent 1950, Fitch 1958, Barlow 1962, Hamilton 1962, Mengel 1965, Meanley 1966, DeGraaf et al. 1980). The primary requirement is a dense shrub-small tree layer.

Low shrubby vegetation provides foraging (Hamilton 1962) and nesting substrates (Mengel 1965, Evans and Kirkman 1981). White-eyed vireos typically feed at heights of 1.5-6.0 m in the southeastern U.S. (Meanley 1966) and 0.6-7.6 m in Louisiana (Dickson and Noble 1978). The nest site is usually in a small tree or shrub 0.3-2.4 m above ground (Harrison 1975). Male white-eyed vireos typically sing from perches 1-8 m above ground, but they were in larger trees 4-12 m tall in our study.

The well-developed subcanopy layer, important to this species in our study, partially results from the presence of numerous small trees and shrubs. Other studies did not describe subcanopy closure in white-eyed vireo habitat nor ground vegetation coverage. Otherwise, the selected characteristics in our study appear consistent with habitat descriptions in other studies. Throughout their range, white-eyed vireos apparently require relatively dense, low growing (2-7 m tall), woody vegetation. They inhabit a wide range of wooded habitats if this requirement is met.

Louisiana Waterthrush

Louisiana waterthrushes were observed primarily in central Missouri upland hardwoods, although several were studied in southeastern Missouri bottomland hardwoods. The most consistent measured characteristics of habitat around song perches were an intermediate number of live stems 2.5-9.9 cm dbh (525-850/ha, never <525), an intermediate number of woody stems ≥2.5 cm dbh (always 1000-1800/ha) and a low to intermediate number of live stems ≥30 cm dbh (<75/ha). Other important features included an intermediate to high canopy (always >15 m), a small number of dead stems 10.0-29.9 cm dbh (<25/ha), an intermediate number of woody stems <2.5 cm dbh (corrected values 1400-5600/ha, never <295 or >5600), and intermediate to tall ground vegetation (>0.10 m) (Table 44). These characteristics describe pole to mature forest habitat with few large trees but numerous small trees and shrubs.

Table 44. Important characteristics of Louisiana waterthrush habitat in Missouri (N = 13).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
All woody stems ≥2.5 cm dbh/ha	1000-1100*	29	1000-1800	100	<1000 or >1800	0
Live stems 2.5-9.9 cm dbh/ha	750-800*	23	525-850	79	<525	0
Live stems ≥30 cm dbh/ha	<75*	86	<75*	86	>75	14
SECONDARY						
All woody stems <2.5 cm dbh/ha	2100-2800	31	1400-5600	92	<1400 or >5600	8
Dead stems 10.0-29.9 cm dbh/ha	0	50	<25†	86	>25	14
Ground vegetative height (m)	.10-.40	64	>.10	93	<.10	7
Canopy height (m)	16-20	54	>15	100	<15	0

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

†*P<0.10.*

Summary of Other Studies

Density of Small Woody Stems

Northeastern U.S.—Preferred habitat consisted of bottomland forest with a dense understory (DeGraaf et al. 1980).

Density of Large Trees

Eastern U.S.—Presence of many large trees was selected as a key habitat component by MVA (Robbins 1978).

Canopy Height

Eastern U.S.—High canopy was a prominent feature of waterthrush habitat (Robbins 1978).

Size of Contiguous Habitat

Eastern U.S.—Forests ≥100 ha supported higher population densities than smaller tracts (Robbins 1979).

Proximity of Water

Throughout Range—Nearby water is required (Bent 1953, Griscom and Sprunt 1957, Mengel 1965, DeGraaf et al. 1980).

Conclusions

Preferred habitat of Louisiana waterthrushes typically consists of wooded streams with swiftly flowing water, but they are also found near slow-moving or still water in wooded lowlands (Bent 1953, Griscom and Sprunt 1957, Mengel 1965, DeGraaf et al. 1980). Most investigators did not describe the type of forest habitat preferred by this species, but mentioned only the presence of water, preferably flowing. Habitat in the northeastern U.S. often consisted of bottomland forest with a dense understory and an abundance of moss-covered logs (DeGraaf et al. 1980).

Published quantitative data on habitat requirements of Louisiana waterthrushes are insufficient to assess the results of our study. Distance to water, especially small streams, was perhaps the most important variable in our study, as it averaged 6 m and was always <25 m. Because we did not measure distance to water for most other species, we have no standard for comparison. Of 14 nests in Pennsylvania, 13 were located next to streams (Harrison 1975).

This species appeared to select very specific habitat in our study, but characteristics of this habitat possibly only represent the vegetation types found along wooded streams on our study areas. Louisiana waterthrushes possibly inhabit most forest types if flowing water is present. However, this ground-nesting and

foraging species also may require well-developed foraging substrates (Evans and Kirkman 1981).

Forest Edge

Brown Thrasher

Brown thrashers were observed primarily in old fields, although several were also found in grasslands and central Missouri forests. The most consistent characteristic of habitat around song perches was intermediate litter depth (1.0-2.0 cm). Other important features included an intermediate to large number of woody stems <2.5 cm dbh (350-2450/ha, never <120), intermediate to dense litter coverage (55-95%, never <30), a low to intermediate canopy (4-18 m, but never <4), and a small to intermediate number of woody stems ≥2.5 cm dbh (24-2100/ha, never 0) (Table 45). These characteristics describe forest edge or overgrown grassland-old field habitat with a well-developed litter layer.

Table 45. Important characteristics of brown thrasher habitat in Missouri (N = 17).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Litter depth (cm)	1.0-2.0*	69	1.0-.2.0*	69	<1.0 or >2.0	31
SECONDARY						
All woody stems <2.5 cm dbh/ha	350-1400*	47	350-2450	59	<350*	6
All woody stems ≥2.5 cm dbh/ha	24-1300	68	24-2100	100	0*	0
Canopy height (m)	4-12	53	4-18	88	<4*	0
Litter cover (%)	85-90*	32	55-95	92	<55 or >95	8

[a]*Percent of observations.*

**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*

Summary of Other Studies

Density of Small Woody Stems

Eastern U.S.—The most important characteristics of suburban brown thrasher

habitat was the presence of a deciduous shrub and small tree layer (Thomas et al. 1977).

Michigan—Nest sites were usually associated with dense shrubby vegetation of forest edge (Gates and Gysel 1978).

Density of Trees

Arkansas—Presence of few trees was a prominent habitat feature, as determined by MVA (James 1971).

Ground Vegetative Cover

Arkansas—Dense ground cover was delineated as a key habitat component (James 1971).

Canopy Height

Eastern U.S.—Canopies >6 m high decreased the attractiveness of suburban brown thrasher habitat (Thomas et al. 1977).

Virginia—Brown thrasher habitat consisted of 3-year-old clearcuts with numerous small trees 1-2 m tall and a few large uncut trees. Older clearcuts or forest stands with trees >3 m tall were not good thrasher habitat (Conner and Adkisson 1975).

Conclusions

Brown thrashers occur in a wide variety of habitats, requiring mainly the presence of shrubby vegetation. These include brushy pastures, old fields, hedgerows, shrubbery in residential areas, overgrown clearings, and forest edge (Bent 1948, Mengel 1965, Graber et al. 1970, DeGraaf et al. 1980).

Results of our study appear consistent with those from other studies, but the most prominent feature of brown thrasher habitat in our study was a well-developed litter layer which was not reported elsewhere. Brown thrashers nest and feed on the ground in some localities (DeGraaf et al. 1980); hence, an abundance of litter possibly provides nesting and foraging substrates.

Habitat in our study had a well developed shrub-small tree layer. This appears to be the most important feature of habitat throughout the breeding range. Brown thrashers often build their nests at heights of 0.6-2.1 m in low, dense woody vegetation (DeGraaf et al. 1980). Shrubby vegetation also provides a foraging substrate. In a Louisiana forest, brown thrashers were observed primarily at heights of 0.6-7.6 m but were common at all other heights (Dickson and Noble 1978).

A few tall trees were consistently present in the song perch habitat of our study, and apparently they are needed, for males sing from tops of tall trees (Bent 1948). In our study, most males sang from trees 4-18 m tall, at heights of 1-16 m above ground.

Brown thrashers apparently require numerous small woody stems and a few tall trees; beyond that, detailed assessment of our results is not possible.

Blue-winged Warbler

Blue-winged warblers were observed on old field study sites and one upland hardwood site. The characteristics most consistently describing habitat around song perches were an intermediate number of woody stems <2.5 cm dbh (420-4200/ha, never <420), an intermediate number of live stems 2.5-9.9 cm dbh (150-650/ha, never 0), and an intermediate number of woody stems ≥2.5 cm dbh (200-1000/ha, never 0). Other important features included intermediate canopy closure (10-70%), dense ground vegetation (>85%, never <65) of intermediate to great height (0.40-0.90 m, never <0.15), and an intermediate canopy height (6-20 m) (Table 46).

The habitat utilized by these warblers on the upland hardwood study area was a large opening with much woody invasion. This site had a relatively open canopy (x = 65%), and relatively dense (x = 86%), tall (x = 0.45 m) ground vegetation for forest habitat.

Other song perches were located in old fields in very late seral stages, or forest edges with dense ground vegetation.

Table 46. Important characteristics of blue-winged warbler habitat in Missouri (N = 30).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	1400-1750*	23	420-4200	93	<420*	0
All woody stems ≥2.5 cm dbh/ha	400-500*	17	200-1000*	86	<200 or >1700	3
Live stems 2.5-9.9 cm dbh/ha	250-300*	13	150-650*	73	<150*	3
SECONDARY						
Ground vegetative cover (%)	>95	77	>85	97	<85	3
Ground vegetative height (m)	.40-.50	27	.40-.90	77	<.40	20
Canopy closure (%)	20-25*	17	10-70	87	0* or >70	7
Canopy height (m)	6-8†	33	6-20*	83	<6*	17

[a]*Percent of observations.*

**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*

†*P<0.10.*

Summary of Other Studies

Density of Small Woody Stems

Arkansas—Forest edge with dense understory provided prime blue-winged warbler habitat, and to a lesser extent, old fields with numerous shrubs and small trees were used. Areas with sparse woody vegetation, cedar glades, and forests were not used (Shugart and James 1973).

Eastern U.S.—Blue-winged warbler territories consisted of overgrown fields with many shrubs and small trees (Ficken and Ficken 1968).

Massachusetts—Habitat included edges of forest and old fields with dense woody vegetation throughout (Meyerriecks and Baird 1968).

Canopy Closure

Arkansas—Habitat consisted primarily of forest edge, followed by old fields with 17% canopy closure, but not woody habitats with ≥25% closure or grassland with less woody vegetation (Shugart and James 1973).

Canopy Height

Eastern U.S.—Overgrown fields with trees <6 m tall and bordered by taller deciduous trees provided suitable habitat (Ficken and Ficken 1968).

Massachusetts—Blue-winged warbler habitat consisted of forest edge and old fields bordered by trees 6.0-7.5 m tall (Meyerriecks and Baird 1968).

Virginia—Three- to 7-year-old clearcuts with trees 1.5-5.0 m tall and a few larger uncut trees were used by this species. Older clearcuts and forest types with trees >5 m tall were not used (Conner and Adkisson 1975).

Conclusions

In published studies, the primary requirements of blue-winged warblers appeared to be abundant shrubs and small trees (<6 m tall) in relatively open areas surrounded by taller trees (>6 m tall) or with a few scattered taller trees within the area. Nests typically were placed at or in woodland edge (Ficken and Ficken 1968). Important characteristics in our study, with the exception of dense, tall ground vegetation, describe habitat fulfilling the above requirements.

A well-developed ground layer provides nesting cover and material for this ground-nesting species (DeGraaf et al. 1980), low woody vegetation provides a foraging substrate, and taller woody vegetation provides song perches (Ficken and Ficken 1968, Meyerriecks and Baird 1968). Therefore, the selected characteristics in our study appear to describe preferred habitat in most parts of the breeding range.

Indigo Bunting

Indigo buntings were observed in old fields, grasslands, and clearings in central Missouri forest. This species has adapted to a variety of habitats; therefore,

values for most variables covered broad ranges, and only two secondary variables appeared important. Ground vegetation was intermediate to tall (>0.40 m) and the number of woody stems <2.5 cm dbh was intermediate to great (24-4200/ha) (Table 47). These characteristics describe most brushy grassland-old field or forest edge habitat. Woody invasion was greatest on the only two grassland study areas utilized by indigo buntings.

Table 47. Important characteristics of indigo bunting habitat in Missouri (N = 81).

Variable	*Optimum* *Range*	*%*[a]	*Main* *Range*	*%*	*Avoided* *Range*	*%*
PRIMARY						
(none)						
SECONDARY						
All woody stems <2.5 cm dbh/ha	24-350	12	24-4200	86	0*	1
Ground vegetative height (m)	.40-.50	20	>.40	73	<.40	27

[a]*Percent of observations.*
**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*

Summary of Other Studies

Density of Small Woody Stems

Arkansas—Primary habitat consisted of forest edge with a dense understory and oak subclimax forest, but not grasslands with few small trees (Shugart and James 1973).

Eastern U.S.—Presence of few small trees was selected as an important habitat feature by MVA (Robbins 1978).

Indiana—Habitat of indigo buntings included scrublands with little woody vegetation and brushy fields with fairly dense woody vegetation (Nolan 1963). Fields with scattered clumps of shrubs and small saplings, as well as older seral stages with dense stands of small trees, provided suitable habitat (Carey and Nolan 1979).

Utah (isolated valley in UT, AZ, NV)—MVA identified relatively low shrub density as a critical feature of indigo bunting habitat (Whitmore 1977).

Density of Large Trees

Utah—Low densities of large trees were a prominent habitat feature (Whitmore 1977).

Ground Vegetative Cover

Arkansas—Forest edge with dense understory and subclimax forest with sparse ground cover supported indigo bunting populations (Shugart and James 1973).

Indiana—Indigo buntings occupied habitat ranging from old fields with dense ground cover to those with little ground cover and large eroded areas (Carey and Nolan 1979).

Michigan—Forest edge met all requirements including a well-developed ground layer (Gates and Gysel 1978).

Ohio—Ungrazed woodlots supported higher densities of indigo buntings than grazed woodlots (Good and Dambach 1943).

Utah—Dense ground cover was a key habitat component (Whitmore 1977).

Canopy Closure

Arkansas—Various wooded types with canopy closures 17-64% supported bunting populations, but not areas with less woody vegetation or >64% canopy closure (Shugart and James 1973).

Indiana—Areas ranging from those with little woody cover to brushy fields with 50% canopy coverage provided bunting habitat (Nolan 1963).

Michigan—An open canopy was required (Gates and Gysel 1978).

Canopy Height

Arkansas—Wooded habitats with some trees ≥ 13 m tall supported populations, but not climax forest (Shugart and James 1973).

Indiana—Habitat ranged from old fields with little woody vegetation to brushy fields with trees ≥7 m tall (Nolan 1963).

Virginia—One- to 12-year-old clearcuts with woody vegetation 1.0-7.5 m tall provided habitat, but not pole stands and mature forest with trees 8-25 m tall (Conner and Adkisson 1975).

Proximity of Edge

Michigan—Forest edge itself provided all habitat components (Gates and Gysel 1978).

North Dakota and Montana—Nesting occurred near forest edge (Kroodsma 1975).

Ontario—The amount of forest edge and numbers of indigo buntings were closely related (Weber and Theberge 1977).

Size of Contiguous Habitat

Eastern U.S.—Small area size was identified by MVA as an important habitat feature (Robbins 1978).

Conclusions

Indigo buntings inhabit a wide variety of open and semi-open situations with brushy vegetation such as forest edge, overgrown old fields, roadside brush, hedgerows and old burns, but they avoid deep forest (Fitch 1958, Mengel 1965, Bent 1968, DeGraaf et al. 1980).

Males require high, open perches for singing and females require dense, tall ground vegetation for nesting (Bent 1968). In our study, male indigo buntings usually sang from the tops of woody vegetation 1-16 m tall. Nests typically are placed in low, dense woody vegetation 0.6-3.7 m above ground (Harrison 1975). In Michigan, indigo buntings required an open canopy, high singing perches, and well-developed ground vegetation for nesting and feeding. These requirements were met by forest edge habitat (Gates and Gysel 1978).

Indigo buntings are generalists, apparently requiring only a few relatively tall song perches and some low, dense woody vegetation for nesting. These requirements are met by a variety of habitat types with greatly different vegetative structure.

Rufous-sided Towhee

Rufous-sided towhees were observed primarily in old field and upland forest edge habitat, although several were also noted on grassland study areas. The most consistent characteristics of habitat around song perches were a litter layer of intermediate depth (1.0-3.0 cm, never <0.5) and dense litter coverage (70-95%, never <25). Other important features included a low to intermediate number of woody stems <2.5 cm dbh (350-5950/ha, but never <225), a few woody stems ≥2.5 cm dbh (24-2100/ha), and intermediate to dense ground vegetation coverage (>60%) (Table 48). Woody invasion was greatest on the two grassland study areas utilized by rufous-sided towhees.

These characteristics embrace a wide variety of habitats, from brushy grasslands or old fields to forest edge and open woodland.

Summary of Other Studies

Density of Small Woody Stems

Arkansas—Well-developed shrub-understory layer was an important habitat feature (Shugart and James 1973).

Indiana—Brushy habitats with numerous shrubs and small trees supported rufous-sided towhee populations (Nolan 1963).

Pennsylvania—A variety of wooded habitats with well-developed shrub understory layers provided suitable towhee habitat (Davis and Savidge 1971).

Density of Trees

Eastern U.S.—Small basal area and few small trees were selected by MVA as prominent habitat components (Robbins 1978).

Canopy Closure

Arkansas—Forest edge, grasslands with numerous shrubs or small tree stems, and old fields with 17-25% canopy provided suitable towhee habitat. Hayfields without woody vegetation, or climax oak forest with 74% canopy closure did not (Shugart and James 1973).

Eastern U.S.—Sparse canopy cover was an important habitat feature (Robbins 1978).

Indiana—Brushy habitats with canopy coverage up to 50% provided habitat (Nolan 1963).

Oregon—Stands of Oregon white oak with canopy closures of 44-61% supported larger numbers of rufous-sided towhees than oak stands with canopy closures of 80-82% (Anderson 1970).

Canopy Height

Eastern U.S.—A low canopy was an important characteristic of habitat (Robbins 1978).

Indiana—Old fields with trees 1-7 m tall and brushy fields with trees ≥ 7 m tall supported towhee populations (Nolan 1963).

Virginia—Towhee habitat consisted of 7- to 12-year-old clearcuts with trees 1.5-5.0 m tall, but not clearcuts with woody vegetation <1 m tall or pole to mature oak forest with trees 8-25 m tall (Conner and Adkisson 1975).

Litter Cover

Southeastern U.S.—Towhee habitat consisted of mature bottomland forest with a well-developed litter layer (Meanley 1966).

Conclusions

A wide variety of brushy habitats support rufous-sided towhees, including brushy old fields, pastures and clearings, hedgerows, roadside thickets, woodland edge, slashings, open groves, forests, and swamps (Mengel 1965, Bent 1968, DeGraaf et al. 1980); but they typically are associated with dense brushy vegetation in these areas (Mengel 1965, DeGraaf et al. 1980). In Pennsylvania, towhees were most numerous in forest edge and grass-scrublands. However, they were also common in mature oak hardwoods, dense red pine, dense spruce, young aspen, and locust stands (Davis and Savidge 1971).

The litter layer, although not described in most studies, possibly fulfills the only critical habitat requirement other than brushy cover. Litter provides a substrate

Table 48. Important characteristics of rufous-sided towhee habitat in Missouri (N = 50).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
Litter cover (%)	80-85*	21	70-95*	71	<50	8
Litter depth (cm)	1.0-2.0*	50	1.0-3.0*	70	<1.0†	17
SECONDARY						
All woody stems <2.5 cm dbh/ha	350-2450	46	350-5950	90	<350*	4
All woody stems ≥2.5 cm dbh/ha	24-100	14	24-2100	96	0*	2
Ground vegetative cover (%)	>95	42	>60	96	<60	4

[a]*Percent of observations.*
**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*
†P<0.10.

for foods of this species which forage by kicking leaf litter to the side (Bent 1968). Additionally, nests are located on the ground or in low brushy vegetation (Harrison 1975); thus, low, dense woody vegetation and ground vegetation provide nesting cover. In a Louisiana forest, towhees were observed primarily at heights <0.6 m above ground (Dickson and Noble 1978).

The primary habitat requirements of rufous-sided towhees apparently are a relatively dense understory-ground layer and well-developed litter layer. Published quantitative data are few and the results of our study cannot be adequately assessed without further research in other locations.

Disturbed Land

Horned Lark

Horned larks were observed only on agricultural land adjacent to the central Missouri bottomland hardwood study areas. Habitat at singing locations was consistently characterized by shallow litter (always <0.4 cm), short ground vegetation (<0.10 m), and no woody stems (always 0/ha). Other important features included sparse litter coverage (always <25%) and ground vegetation (<20%) (Table 49). These characteristics describe recently disturbed areas with little vegetation and sparse litter layer.

Table 49. Important characteristics of horned lark habitat in Missouri (N = 9).

Variable	Optimum Range	%[a]	Main Range	%	Avoided Range	%
PRIMARY						
All woody stems <2.5 cm dbh/ha	0*	100	0*	100	>0	0
All woody stems ≥2.5 cm dbh/ha	0*	100	0*	100	>0	0
Ground vegetative height (m)	0*	67	<.10*	89	>.10*	11
Litter depth (cm)	0*	56	<0.4*	100	>0.4	0
SECONDARY						
Ground vegetative cover (%)	5-10	33	<20	78	>20	22
Litter cover (%)	0*	56	<25	100	>25	0

[a]*Percent of observations.*
**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*

Summary of Other Studies

Density of Small Woody Stems

Arkansas—Mowed hayfields without woody vegetation provided habitat, but not burned grassland with a few dead sassafras trees or grasslands and old fields with woody invasion (Shugart and James 1973).

Colorado—Habitat occupied by horned larks had only 33% as many woody stems as unoccupied areas (Wiens 1973a).

Illinois—Habitat consisted of barren areas lacking woody vegetation; even areas with as little as 36% shrub coverage were not used (Karr 1968).

Ground Vegetative Cover

Illinois—Herbaceous vegetative coverage was only 8% on suitable lark habitat; unsuitable plots had 72% or more herbaceous coverage (Karr 1968).

Missouri—Grass coverage averaged 63% and forb coverage 6% at 1 cm in suitable habitat. Coverage by both grasses and forbs at greater heights was negligible in occupied horned lark habitat (Skinner et al. 1984).

North America—Grasslands supporting lark populations had sparser vegetation than grasslands without larks (Cody 1968).

Ground Vegetative Height

Central and Western U.S.—Grazed areas supported the highest populations of horned larks; there was a steady decrease in population density through a continuum of types as vegetation became taller and more heterogeneous (Wiens 1977).

Missouri—Horned larks were common only on plots in very short grasslands, usually heavily grazed pastures; mean coverage by grasses was 63% at 1 cm, but only 3% at 25 cm, forb coverage was 6% at 1 cm, 2% at 25 cm (Skinner et al. 1984).

North America—Grasslands supporting horned larks had vegetation averaging 0.23 m tall, which was shorter than areas without larks (Cody 1968).

Litter Cover

Colorado—Horned lark habitat had 23% litter coverage which was not different from uninhabited areas (Wiens 1973a).

Illinois—Areas with 76% bare ground provided suitable habitat, but not areas with 15% or less bare ground (Karr 1968).

Litter Depth

Colorado—Occupied habitat had a litter depth of 0.3 cm, which was not different from unoccupied areas (Wiens 1973a).

Plant Species Composition

Colorado—Occupied habitat had only 33% as many forb plants as unoccupied habitat (Wiens 1973a).

Conclusions

Horned larks are associated with recently disturbed lands or other areas with low vegetative cover and much bare ground, including plowed fields, recently hayed fields, golf courses, athletic fields, cemeteries, and airports (Fitch 1958, DeGraaf et al. 1980). The principal requirements are bare ground for nest depressions and open areas for aerial displays (Bent 1942). Preferred habitats in Illinois were stubble fields, plowed ground, and fall-planted fields (Beason and Franks 1974).

Habitat with sparse vegetation at all levels and sparse litter accumulation is required by horned larks. The selected characteristics in our study appear to reflect preferred horned lark habitat adequately. However, ranges of several of the variables in our study were narrower than those reported elsewhere.

DISCUSSION

Alternative Analyses Explored

After considering several methods of analysis, we judged that frequency distribution analysis best reflected habitat selection by the bird species we studied. Alternative methods of analysis are evaluated below, and reasons for our choice are presented. More detailed explanations, with examples, are given in Kahl et al. (1981).

Suitability Index Curves. For the suitability index curve analysis (Schamberger and Farmer 1978), individual and all species curves were constructed and compared as in the frequency distribution analysis. The interval with the greatest number of observations (the optimum interval) was assigned a value of one. All other intervals were assigned values equal to the number of observations in that interval divided by the number in the optimum interval. This method relies upon transformed data and conceals some of the differences between the individual and all species curves. When the two curves have the same optimum interval, both are assigned the value of one. However, the untransformed values for the two optimum intervals can be vastly different. For example, 78% of hairy woodpecker observations were within the optimum level for canopy height, 16-20 m, but only 38% of all species observations fell within this interval. These significantly different values in individual and all species frequency distributions at the optimum interval are biologically important, but they are not detectable in the suitability curves.

Coefficients of Variation (CV). For another analysis we selected habitat variables having the smallest coefficients of variation (Barr et al. 1976). This procedure does not adequately accommodate large natural variability or variability due to differing characteristics of the study areas. For example, small woody stem densities varied more than canopy closure on forest study areas, and this simple fact would be reflected in the CV's regardless of any selection exercised by a bird species. Additionally, distinct threshold values for certain variables were apparent in frequency distributions, but these variables appeared unimportant in CV analysis. As another example, numbers of small woody stems above 2800/ha are important components of ovenbird habitat. Below this threshold, there were few observations; above it, there were numerous observations but values were quite variable. Coefficients of variation for these data were large, and thus did not reflect the degree of importance of small woody stems.

Discriminant Function Analysis (DFA). In discriminant function analysis (Barr et al. 1976), mean values of each habitat variable for all bird species were compared for two groups of study areas, those with three or more observations of a target species and those with none. DFA selects the variables that maximize the difference between the two groups of study areas. For purposes of this study, DFA was inappropriate partly because it left little opportunity for biological judgments. Species were excluded from some study areas for reasons not perceived in DFA. Limiting factors apparently differed among study areas unsuitable for a given species, and this phenomenon was not detectable with DFA. Additionally, this

application of DFA did not distinguish habitat used by a species from unused habitat on suitable study areas.

Means and Standard Deviations. The mean and standard deviation of data for important variables could have provided a uniform, objective description of optimum and main ranges in the species accounts. However, many of the variables have non-normal distribution not adequately described by the mean and standard deviation. Several outlying points would shift the mean from the true center of abundance. Even without distant outliers, the mean often did not describe the optimum range.

Frequency Distribution Analysis. This procedure lacked most of the disadvantages of the alternative methods of analysis described above, permitted biological judgment, and provided a basis for statistical evaluation of differences between habitat data for the target species and for all forest or grassland-old field species. Frequency distribution analysis was, therefore, the method of choice.

Limitations of Data and Analyses

The method of measuring habitat characteristics and the difficulty of estimating certain characteristics in the field should be considered prior to applying these results in the field or comparing them to other studies. For example, canopy and subcanopy closures were measured precisely with an ocular tube fitted with cross-pieces. Readings for canopy and subcanopy closure embraced not only relatively large openings in these layers left by snags, but also openings between branches and leaves of individual trees. As a result, biologists estimating closure in the field without the ocular tube would probably overestimate closures, and their results would not be strictly comparable with ours.

It is important to keep definitions clearly in mind. For example, the term "subcanopy" is interpretable in different ways. In our study, canopy was defined as the foliage and branches of the dominant overstory trees. Subcanopy consisted of all vegetation above the observer's head but below the canopy layer. Ellis et al. (1979), in examining several methods of habitat evaluation, found that some habitat characteristics were much more difficult to assess than others because of intrinsic properties of the characteristics, especially if criteria were subjectively worded in field instructions.

Conclusions about habitat requirements of bird species in this study were affected by limitations of resources and several inherent limitations of methodology. Data were collected from only three localities in Missouri and the range of habitats was therefore limited. Prime habitat for some species possibly was not encountered.

Determination of optimum habitat would require estimation of breeding densities, and comparison of those results to results of other studies. Adequate estimation of breeding densities depends upon either extensive observation or marking of individuals, both beyond the scope of this study. Relying on the "spot-map" method (Williams 1936, Robbins 1970) to delineate territories, a logical extension of the bird-location techniques used in this study, can lead to erroneous results even by able avian ecologists (Best 1975). The spot-map method enhances

observer bias due to identification abilities, observation conditions, and the screening effect of different habitats (Best 1975).

There are weaknesses in any short-term study of *r*-selected species. Populations may fluctuate, and during years of high population levels, individuals are often dispersed in marginal or sub-optimal habitat (Balda 1975). Additionally, weather can affect foliage densities so that the appearance of prime habitat varies from year to year.

The oak-hickory forest section of the eastern deciduous forest ecoregion described by Bailey (1978) includes central and southern Missouri. Habitat characteristics for most species encountered in this study are probably similar throughout the ecoregion. However, our findings should be extrapolated to other geographic regions with caution. Some species utilize distinctly different habitats depending upon geographic locality and habitat availability. For example, northern parulas in the eastern U.S. nest primarily in forested areas with beard mosses or Spanish moss which provide preferred nesting sites (Bent 1953, DeGraaf et al. 1980). These plants do not occur in Missouri, yet 40 parula song perches were studied.

Obtaining large sample sizes for many species required a method based upon habitat used by singing males, which are relatively easy to locate and identify. However, the breeding status of males is usually not known. Unmated males of some species sing much more frequently than mated males (Frankel and Baskett 1961, Samson 1979), and habitats used by unmated and mated males could differ. Studies of yellow warblers (Ficken and Ficken 1966) and redstarts (Ficken and Ficken 1967, Morse 1973) showed that unmated or yearling males used peripheral or marginal habitat. The alternatives to the methodology employed in this study are measuring vegetation only on song-perch plots of known breeding males or at nest sites. Either alternative would have yielded but few data on few species.

Another problem inherent in our methodology was that song-perch habitat does not always represent feeding or nesting habitat, especially on open lands (James 1971). Prairie warblers (Nolan 1978), blue-winged warblers (Ficken and Ficken 1968), and Swainson's warblers (Meanley 1971) often placed nests at the periphery of song territories. Male blue-winged (Murray and Gill 1976) and male Swainson's warblers (Meanley 1971) avoided the nest area after initiation of incubation. Although blue-winged warbler territories in New York and Maryland usually consisted of overgrown fields bordered by deciduous trees, nests were always located in the field-woodland edge (Ficken and Ficken 1968). In contrast, nine ovenbird nests were all within the 90% equal-frequency ellipse of song centers (Zach and Falls 1978). Ovenbird males sometimes shifted the center of singing nearer the nest (Hann 1937). Factors other than nest sites are probably important to selection of habitat by a species and assessing them may be equally desirable. These include song perches, shelter or protection from predation, terrain and general habitat structure, water, nesting materials, feeding perches, and others (Verner 1975). Although song perch habitat possibly does not include nesting or feeding habitat, specific song perches are required by many species and could be the determining factor in habitat selection.

Finally, important habitat requirements for certain species probably were not assessed by the variables measured in this study. For example, habitat patchiness or heterogeneity can affect bird species diversity, especially in shrublands (Roth 1976). Bell's vireos (Barlow 1962) and yellow-breasted chats (Thompson and Nolan 1973) are usually found nesting in dense thickets. Size of contiguous habitat, in particular forest-tract size, was not investigated in this study, as most forest study sites were on the edge of or in extensive forest. Forest size can strongly influence habitat use by several deep forest species (summarized by Robbins 1979). Similar conclusions have been drawn for certain grassland bird species in Missouri (Samson 1980).

Despite possible flaws in our data, as discussed above, it is comforting that our quantitative habitat descriptions for 33 of 49 species in this report resemble published qualitative descriptions (Bent 1939, 1942, 1946, 1948, 1949, 1950, 1953, 1958, 1968, DeGraaf et al. 1980, and others). There were some discrepancies between our data and *quantitative* data from other published studies. Differing methods of habitat measurement, regional ecology, and mixing the published data about foraging, nesting, and singing habitat may be accountable. Further, many of the bird species may be able to adapt to subtle variations in habitat components as long as certain basic requirements are met.

Our results probably do reflect selection of breeding habitat by many target species if specific habitat was required. Frequency distributions of data for habitat utilized by breeding males should encompass a narrow range for any important variable, and probably would differ from the all species distribution. In contrast, the frequency distribution for unmated males or mated pairs during years of high populations in peripheral or marginal habitat should be spread over wider ranges. Thus, by emphasizing the optimum range of frequency distributions and the differences between the individual and all species distribution, we have probably removed from consideration many males that were in peripheral habitat.

Although quantitative data on habitat requirements of nongame birds have been collected in numerous studies, many of these data are unpublished and often sample bases are small. This report provided quantitative data from a large sample of singing males, and should be useful to biologists engaged in habitat evaluation and habitat modeling as a basis for land management or land acquisition. Any evaluation scheme or predictive model developed from these data should be field-tested before being put in use. Field checking of these data is needed to determine correlations with actual abundance of the birds.

Habitat Modeling

The main potential use of our data is for habitat modeling. Models should include a weighting scheme reflecting the relative importance of variables to be assessed and critical values of these variables. As described in methods, relative importance of the selected habitat characteristics in our study is indicated by (1) classification into primary or secondary variables, (2) statistically significant differences between the values for individual target species and the all species distributions, and (3) the percentage of observations in optimum and main value

ranges for individual species. This information for 49 target species is summarized in Tables 1-49.

The species accounts and their accompanying tables outline only the most important or special habitat characteristics for the individual species, based largely on the departure of values from the all species frequency distributions. Therefore, they do not completely describe suitable habitat. For example, degree of canopy closure was not selected as an important variable for several forest species obviously requiring some canopy closure, because it did not differ markedly from the forest bird all species distribution in these instances. The Kentucky warbler is a good case in point. Most song perches of this species (86%) were in forest habitat with >65% canopy closure. Similarly, 78% of forest bird all species observations were in plots with >65% canopy closure, and this characteristic did not appear to distinguish Kentucky warbler habitat from that of other forest species. It was not identified as a primary or secondary variable. Nevertheless, canopy closure, based on forest bird all species distributions should be included in Kentucky warbler habitat models.

To meet this type of problem and thus to aid in modeling, we have provided all species optimum and main ranges of all habitat variables measured, both for grassland-old field birds (Table 50) and forest species (Table 51). These ranges can be used as adjuncts to those in the bird species accounts at the discretion of the modeler.

Table 50. Optimum and main ranges of habitat characteristics for grassland-old field bird all species distributions, and perntages of total observations falling within the specified intervals. (For definitions of optimum and main ranges, see Methods.)

Variable	*Optimum range*	*Percent of observations*	*Main range*	*Percent of observations*
All woody stems <2.5 cm dbh/ha	*0*	*29*	*<1400*	*66*
All woody stems ≥2.5 cm dbh/ha	*0*	*41*	*<50*	*55*
Live stems 2.5-9.9 cm dbh/ha	*0*	*51*	*<100*	*67*
Live stems 10.0-29.9 cm dbh/ha	*0*	*64*	*<50*	*79*
Live stems ≥30.0 cm dbh/ha	*0*	*87*	*0*	*87*
Dead stems 2.5-9.9 cm dbh/ha	*0*	*81*	*0*	*81*
Dead stems 10.0-29.9 cm dbh/ha	*0*	*90*	*0*	*90*
Dead stems ≥30.0 cm dbh/ha	*0*	*98*	*0*	*98*
Ground vegetative cover (%)	*95-100*	*71*	*>90*	*85*
Ground vegetative height (m)	*0.2-0.4*	*41*	*0.1-0.7*	*87*
Subcanopy closure (%)	*0*	*78*	*0*	*78*
Canopy closure (%)	*0*	*56*	*<25*	*82*
Canopy height (m)	*1-2*	*31*	*0-8*	*85*
Litter coverage (%)	*95-100*	*20*	*>50*	*73*
Litter depth (cm)	*0.1-1.0*	*36*	*0.1-2.0*	*65*

Table 51. Optimum and main ranges of habitat characteristics for forest bird all species distributions, and percentages of total observations falling within the specified intervals. (For definitions of optimum and main ranges, see Methods.)

Variable	*Optimum range*	*Percent of observations*	*Main range*	*Percent of observations*
All woody stems <2.5 cm dbh/ha	*700-1400*	*17*	*24-5600*	*88*
All woody stems ≥2.5 cm dbh/ha	*1200-1500*	*29*	*800-1900*	*82*
Live stems 2.5-9.9 cm dbh/ha	*300-1100*	*74*	*300-1100*	*74*
Live stems 10.0-29.9 cm dbh/ha	*200-250*	*17*	*50-400*	*79*
Live stems ≥30 cm dbh/ha	*25-75*	*34*	*0-150*	*88*
Dead stems 2.5-9.9 cm dbh/ha	*24-100*	*36*	*0-250*	*81*
Dead stems 10.0-29.9 cm dbh/ha	*0*	*33*	*<50*	*76*
Dead stems ≥30.0 cm dbh/ha	*0*	*78*	*<30*	*95*
Ground vegetative cover (%)	*60-70*	*14*	*>20*	*88*
Ground vegetative height (m)	*0.1-0.2*	*25*	*0.01-0.5*	*86*
Subcanopy closure (%)	*50-90*	*64*	*40-95*	*80*
Canopy closure (%)	*95-100*	*17*	*>60*	*85*
Canopy height (m)	*16-20*	*38*	*12-28*	*89*
Slope (degrees)	*0*	*53*	*<10*	*87*

SUMMARY

Habitat characteristics at song perches of male birds were measured during late spring and early summer of 1977 and 1978 on 31 forest and 22 nonforest study areas (1.7-12.8 ha). Data on habitats surrounding nine or more song perch plots are reported for 49 bird species for which there were no sampling peculiarities or other limitations.

The objective of the study was to identify measurable components that consistently describe habitats of certain species, thus providing quantitative bases for habitat evaluation and habitat modeling.

In the principal analysis, habitat characteristics important to a species were determined by comparing frequency distributions for the individual species to all species distributions. Species accounts were prepared that outlined specific habitat characteristics, if any, for each species. These specific requirements must be coupled with information about more general requirements for construction of habitat models. These general requirements are revealed by data on habitat characteristics for which frequency distributions of individual species did not differ substantially from the all species distributions in either grassland-old field or forest situations.

Alternative methods of analysis explored included suitability index curves, coefficients of variation, discriminant function analysis, means and standard deviations, and cluster analysis using mean values for habitat characteristics. Reasons for rejecting these methods were discussed.

Despite several limitations of the data and analysis, the quantitative habitat descriptions for 33 of 49 species in this report accord with published qualitative descriptions. This report provides quantitative habitat data from many observations of singing males of 49 bird species and should be useful to biologists engaged in habitat evaluation and modeling, land management, or land acquisition. Data are also provided for an additional 11 species; because of sampling problems or their great adaptability, we were unable to draw firm conclusions about their habitat requirements.

LITERATURE CITED

Anderson, B. W. 1971. Man's influence on hybridization in two avian species in South Dakota. Condor 73:342-347.

———, and R. J. Daugherty. 1974. Characteristics and reproductive biology of grosbeaks (*Pheucticus*) in the hybrid zone in South Dakota. Wilson Bull. 86:1-11.

Anderson, S. H. 1970. The avifaunal composition of Oregon white oak stands. Condor 72:417-423.

———. 1979. Habitat assessment for breeding bird populations. Trans. North Am. Wildl. Nat. Resour. Conf. 44:431-445.

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

Bailey, R. G. 1978. Description of the ecoregions of the United States. USDA For. Serv. Intermtn. Reg., Ogden, UT. 77pp.

Balda, R. P. 1975. Vegetation structure and breeding bird diversity. Pages 59-80 *in* D. R. Smith, Tech. Coord. Symposium on management of forest and range habitats for nongame birds. U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. WO-1.

Barlow, J. C. 1962. Natural history of the Bell's vireo, *Vireo bellii* Audubon. Univ. Kansas Publ., Mus. Nat. Hist. 12:241-296.

———, and J. C. Rice. 1977. Aspects of the comparative behavior of red-eyed and Philadelphia vireos. Can. J. Zool. 55:528-542.

Barr, A. J., J. H. Goodnight, J. P. Sall, and T. T. Helwig. 1976. A user's guide to SAS76. Sparks Press, Raleigh, NC. 329pp.

Baskett, T. S., D. A. Darrow, D. L. Hallett, M. J. Armbruster, J. A. Ellis, B. F. Sparrowe, and P. A. Korte, eds. 1980. A handbook for terrestrial habitat evaluation in central Missouri. U.S. Fish and Wildl. Serv. Resour. Publ. 133. 155pp.

Beason, R. C., and E. C. Franks. 1974. Breeding behavior of the horned lark. Auk 91:65-74.

Bent, A. C. 1939. Life histories of North American woodpeckers. U.S. Natl. Mus. Bull. 174. 334pp.

———. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. U.S. Natl. Mus. Bull. 179. 555pp.

———. 1946. Life histories of North American jays, crows, and titmice, Part II. U.S. Natl. Mus. Bull. 191. 495pp.

———. 1948. Life histories of North American nuthatches, wrens, thrashers, and their allies. U.S. Natl. Mus. Bull. 195. 475pp.

———. 1949. Life histories of North American thrushes, kinglets and their allies. U.S. Natl. Mus. Bull. 196. 454pp.

———. 1950. Life histories of North American wagtails, shrikes, vireos, and their allies. U.S. Natl. Mus. Bull. 197. 411pp.

———. 1953. Life histories of North American wood warblers. U.S. Natl. Mus. Bull. 203. 734pp.

———. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U.S. Natl. Mus. Bull. 211. 549pp.

———. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Natl. Mus. Bull. 237. 1889pp.

Berger, A. J. 1968. Clutch size, incubation period, and nestling period of the American goldfinch. Auk 85:494-498.

———, and D. F. Parmelee. 1952. The alder flycatcher in Washtenaw County, Michigan: breeding distribution and cowbird parasitism. Wilson Bull. 64:33-38.

Bertin, R. I. 1977. Breeding habitats of the wood thrush and veery. Condor 79:303-311.

Best, L. B. 1975. Interpretational errors in the "mapping method" as a census technique. Auk 92:452-460.

———. 1977. Territory quality and mating success in the field sparrow (Spizella pusilla). Condor 79:192-204.

———. 1978. Field sparrow reproductive success and nesting ecology. Auk 95:9-22.

Bond, R. R. 1957. Ecological distribution of breeding birds in the upland forests of southern Wisconsin. Ecol. Monogr. 27:351-384.

Brawn, J. D. 1979. The relationship of cavity nesting birds to snags in the oak-hickory forest. M.S. Thesis. Univ. Mo., Columbia. 150pp.

Brewer, R. 1961. Comparative notes on the life history of the Carolina chickadee. Wilson Bull. 73:348-373.

———. 1963. Ecological and reproductive relationships of black-capped and Carolina chickadees. Auk 80:9-47.

Brooks, M. 1947. Breeding habitats of certain wood warblers in the unglaciated Appalachian region. Auk 64:291-295.

Bull, E. L., and E. C. Meslow. 1977. Habitat requirements of the pileated woodpecker in northeastern Oregon. J. Forestry 75:335-337.

———, A. D. Twombly, and T. M. Quigley. 1980. Perpetuating snags in managed mixed conifer forests of the Blue Mountains, Oregon. Pages 325-336 *in* R. M. DeGraaf and N. G. Tilghman, eds. Workshop Proc., Management of western forests and grasslands for nongame birds. U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. INT-86.

Carey, M., and V. Nolan, Jr. 1979. Population dynamics of indigo buntings and the evolution of avian polygyny. Evolution 33:1180-1192.

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

Conner, R. N. 1976. Nesting habitat for red-headed woodpeckers in southwestern Virginia. Bird-banding 47:40-43.

_____. 1978. Snag management for cavity nesting birds. Pages 120-128 *in* R. M. DeGraaf ed. Workshop Proc., Management of southern forests for nongame birds. U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. SE-14.

_____, and C. S. Adkisson. 1975. Effects of clearcutting on the diversity of breeding birds. J. Forestry 73:781-785.

_____, and _____. 1977. Principal component analysis of woodpecker nesting habitat. Wilson Bull. 89:122-129.

_____, R. G. Hooper, H. S. Crawford, and H. S. Mosby. 1975. Woodpecker nesting habitat in cut and uncut woodlands in Virginia. J. Wildl. Manage. 39:144-150.

Crooks, M. P., and G. O. Hendrickson. 1953. Field sparrow life history in central Iowa. Iowa Bird Life 23:10-13.

Daniel, C., and R. Lamaire. 1974. Evaluating effects of water resource developments on wildlife habitat. Wildl. Soc. Bull. 2:114-118.

Davis, D. E., and I. R. Savidge. 1971. Distribution of certain birds in various types of vegetation. Bird-banding 42:264-268.

DeGraaf, R. M., G. M. Witman, J. W. Lanier, B. J. Hill, and J. M. Keniston. 1980. Forest habitat for birds of the northeast. Northeast. For. Exp. Sta. Eastern Reg. U.S. Dep. Agric., For. Serv. 598pp.

Dennis, J. V. 1958. Some aspects of the breeding ecology of the yellow-breasted chat (*Icteria virens*). Bird-banding 29:169-183.

Dickson, J. G., and R. E. Noble. 1978. Vertical distribution of birds in a Louisiana bottomland hardwood forest. Wilson Bull. 90:19-30.

Ellis, J. A., J. N. Burroughs, M. J. Armbruster, D. L. Hallett, P. A. Korte, and T. S. Baskett. 1979. Appraising four field methods of terrestrial habitat evaluation. Trans. North Am. Wildl. Nat. Resour. Conf. 44:369-379.

Erickson, P. A., B. P. Holcomb, and G. Camougis. 1980. Investigation of the relationship between land use and wildlife abundance, Vol. I, Literature survey. U.S. Army Engineer. Inst. Water Resour., Ft. Belvoir, VA. Contract Rep. 80-C2. 146pp.

Evans, E. W. 1978. Nesting responses of field sparrows (*Spizella pusilla*) to plant succession on a Michigan old field. Condor 80:34-40.

Evans, K. E. 1978. Oak-pine and oak-hickory forest bird communities and management options. Pages 76-89 *in* R. M. DeGraaf, ed. Workshop Proc., Management of southern forests for nongame birds. U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. SE-14.

_____, and R. N. Conner. 1979. Snag management. Pages 214-225 *in* R. M. DeGraaf and K. E. Evans, compilers. Workshop Proc., Management of north central and northeastern forests for nongame birds. U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. NC-51.

_____, and R. A. Kirkman. 1981. Guide to bird habitats of the Ozark Plateau. U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. NC-68. 79pp.

Ficken, M. S., and R. W. Ficken. 1966. Notes on mate and habitat selection in the yellow warbler. Wilson Bull. 78:232-233.

_____, and _____. 1967. Age-specific differences in the breeding behavior and ecology of the American redstart. Wilson Bull. 79:188-199.

_____, and _____. 1968. Territorial relationships of blue-winged warblers, golden-winged warblers, and their hybrids. Wilson Bull. 80:442-451.

Fitch, H. S. 1958. Home ranges, territories, and seasonal movements of vertebrates of the National History Reservation. Univ. Kansas, Mus. Nat. Hist. Publ. 11:63-326.

Flood, B. S., M. E. Sangster, R. D. Sparrowe, and T. S. Baskett. 1977. A handbook for habitat evaluation procedures. U.S. Fish and Wildl. Serv. Resour. Publ. 132. 77pp.

Frankel, A. I., and T. S. Baskett. 1961. The effect of pairing on cooing of penned mourning doves. J. Wildl. Manage. 25:372-384.

Galli, A. E., C. F. Leck, and R. T. T. Forman. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. Auk 93:356-364.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59:871-883.

Good, E. E., and C. A. Dambach. 1943. Effect of land use practices on breeding bird populations in Ohio. J. Wildl. Manage. 7:291-297.

Graber, J. W., R. R. Graber, and E. L. Kirk. 1977. Illinois birds: Picidae. Ill. Nat. His. Survey Biol. Note 102. 73pp.

Graber, R. R., J. W. Graber, and E. L. Kirk. 1970. Illinois birds: Mimidae. Ill. Nat. Hist. Survey Biol. Note 68. 38pp.

_____, _____, and _____. 1974. Illinois birds: Tyrannidae. Ill. Nat. Hist. Survey Biol. Note 86. 56pp.

Griscom, L., and A. Sprunt, Jr. 1957. The warblers of America. Devin-Adair Co., New York. 356pp.

Hamilton, T. H. 1962. Species relationships and adaptations for sympatry in the avian genus *Vireo*. Condor 64:40-68.

Hann, H. W. 1937. Life history of the oven-bird in southern Michigan. Wilson Bull. 49:145-237.

Hardin, K. I., and K. E. Evans. 1977. Cavity nesting bird habitat in the oak-hickory forest—a review. U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. NC-30. 23pp.

Harmeson, J. P. 1974. Breeding ecology of the dickcissel. Auk 91:348-359.

Harrison, H. H. 1975. A field guide to birds' nests. Houghton Mifflin Co., Boston. 257pp.

Harrison, K. G. 1977. Perch height selection of grassland birds. Wilson Bull. 89:486-487.

Hespenheide, H. A. 1971. Flycatcher habitat selection in the eastern deciduous forest. Auk 88:61-74.

Hilden, O. 1965. Habitat selection in birds. Ann. Zool. Fenn. 2:53-75.

Jackson, J. A. 1976. A comparison of some aspects of the breeding ecology of red-headed and red-bellied woodpeckers in Kansas. Condor 78:67-76.

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

_____. 1978. On understanding quantitative surveys of vegetation. Am. Birds 32:18-21.

_____, and H. H. Shugart Jr. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727-736.

Johnston, D. W., and E. P. Odum. 1956. Breeding bird populations in relation to plant succession on the Piedmont of Georgia. Ecology 37:50-62.

Kahl, R. B., T. S. Baskett, J. A. Ellis, and J. N. Burroughs. 1981. Habitat characteristics of selected nongame birds breeding in Missouri. Report to Habitat Evaluation Procedures Group, U.S. Fish and Wildl. Serv., Fort Collins, CO. 341pp. (Available from Mo. Coop. Wildl. Res. Unit, Univ. Mo., Columbia.)

Karr, J. R. 1968. Habitat and avian diversity on strip-mined land in east-central Illinois. Condor 70:348-357.

Kendeigh, S. C. 1945. Community selection by birds on the Helderberg Plateau of New York. Auk 62:418-436.

Kilham, L. 1974. Early breeding season behavior of downy woodpeckers. Wilson Bull. 86:407-418.

King, J. R. 1955. Notes on the life history of Traill's flycatcher (*Empidonax traillii*) in southeastern Washington. Auk 72:148-173.

Kisiel, D. S. 1972. Foraging behavior of *Dendrocopos villosus* and *D. pubescens* in eastern New York state. Condor 74:393-398.

Kroodsma, R. L. 1975. Hybridization in buntings (*Passerina*) in North Dakota and eastern Montana. Auk 92:66-80.

Lawrence, L. 1953. Nesting life and behavior of the red-eyed vireo. Can. Field Nat. 67:47-77.

_____. 1967. A comparative life-history study of four species of woodpeckers. Ornithol. Monogr. 5. 156pp.

Longcore, J. R., and R. E. Jones. 1969. Reproductive success of the wood thrush in a Delaware woodlot. Wilson Bull. 81:396-406.

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

_____, _____, and J. Preer. 1962. On bird species diversity. II. Prediction of bird census from habitat measurements. Am. Nat. 96:167-174.

Martin, N. D. 1960. An analysis of bird populations in relation to forest succession in Algonquin Provincial Park, Ontario. Ecology 41:126-140.

McEllin, S. M. 1979. Nest sites and population demographies of white-breasted and pigmy nuthatches in Colorado. Condor 81:348-352.

Meanley, B. 1952. Notes on nesting Traill's flycatcher in eastern Arkansas. Wilson Bull. 64:111-112.

_____. 1963. Nesting ecology and habits of the dickcissel on the Arkansas Grand Prairie. Wilson Bull. 75:280.

_____. 1966. Some observations on habitats of the Swainson's warbler. Living Bird 5:151-165.

_____. 1971. Natural history of the Swainson's warbler. U.S. Bur. Sport Fish. and Wildl., North Am. Fauna 69. 90pp.

Mengel, R. M. 1965. The birds of Kentucky. Ornithol. Monogr. 3. 581pp.

Meyerriecks, A. J., and J. Baird. 1968. Agonistic interactions between blue-winged and "Brewster's" warblers. Wilson Bull. 80:150-160.

Moore, M. C. 1980. Habitat structure in relation to population density and timing of breeding in prairie warblers. Wilson Bull. 92:177-187.

Morse, D. H. 1967. Competitive relationships between parula warblers and other species during the breeding season. Auk 84:490-502.

_____. 1973. The foraging of small populations of yellow warblers and American redstarts. Ecology 54:346-355.

Mumford, R. E. 1952. Bell's vireo in Indiana. Wilson Bull. 64:224-233.

Murray, B. G., Jr., and F. B. Gill. 1976. Behavioral interactions of blue-winged and golden-winged warblers. Wilson Bull. 88:231-254.

Nickell, W. P. 1951. Studies of habitats, territory, and nests of the eastern goldfinch. Auk 68:447-470.

Nolan, V., Jr. 1963. Reproductive success of birds in a deciduous scrub habitat. Ecology 44:305-313.

_____. 1978. The ecology and behavior of the prairie warbler *Dendroica discolor*. Ornithol. Monogr. 26. 595pp.

Odum, E. P. 1941. Annual cycle of the black-capped chickadee. Auk 58:314-333.

Overmire, T. G. 1962. Nesting of the dickcissel in Oklahoma. Auk 79:115-116.

Pitelka, F. A., and E. J. Koestner. 1942. Breeding behavior of Bell's vireo in Illinois. Wilson Bull. 54:97-106.

Probst, J. R. 1979. Oak forest bird communities. Pages 80-88 *in* R. M. DeGraaf and K. E. Evans, compilers. Workshop Proc., Management of north central and northeastern forests for nongame birds. U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. NC-51.

Reller, A. W. 1972. Aspects of behavioral ecology of red-headed and red-bellied woodpeckers. Am. Midl. Nat. 88:270-290.

Robbins, C. S. 1970. Recommendations for an international standard for a mapping method in bird census work. Audubon Field Notes 24:723-726.

_____. 1978. Determining habitat requirements of nongame species. Trans. North Am. Wildl. Nat. Resour. Conf. 43:57-68.

_____. 1979. Effect of forest fragmentation on bird populations. Pages 198-212 *in* R. M. DeGraaf and K. E. Evans, compilers. Workshop Proc., Management of north central and northeastern forests for nongame birds. U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. NC-51.

Robins, J. D. 1971. A study of Henslow's sparrow in Michigan. Wilson Bull. 83:39-48.

Roseberry, J. L., and W. D. Klimstra. 1970. The nesting ecology and reproductive performance of the eastern meadowlark. Wilson Bull. 82:243-267.

Roth, R. R. 1976. Spatial heterogeneity and bird species diversity. Ecology 57:773-782.

Salt, G. W. 1957. An analysis of avifaunas in the Teton Mountains and Jackson Hole, Wyoming. Condor 59:373-393.

Samson, F. B. 1979. Lowland hardwood bird communities. Pages 49-66 *in* R. M. DeGraaf and K. E. Evans, compilers. Workshop Proc., Management of north central and northeastern forests for nongame birds. U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. NC-51.

_____. 1980. Island biogeography and the conservation of prairie birds. Proc. North Am. Prairie Conf. 7:293-305.

Schamberger, M., and A. Farmer. 1978. The habitat evaluation procedures: their application in project planning and impact evaluation. Trans. North Am. Wildl. and Nat. Resour. Conf. 43:274-283.

Scott, V. E., K. E. Evans, D. R. Patton, and C. P. Stone. 1977. Cavity-nesting birds of North American forests. U.S. Dep. Agric. Handbook 511. 112pp.

Shugart, H. H., Jr., and D. James. 1973. Ecological succession of breeding bird populations in northwestern Arkansas. Auk 90:62-77.

Skinner, R. M., T. S. Baskett, and M. D. Blenden. 1984. Bird habitat on Missouri prairies. Mo. Dep. Conserv., Terrest. Ser. 14. 37pp.

Sibley, C. G., and L. L. Short, Jr. 1964. Hybridization in the orioles of the Great Plains. Condor 66:130-150.

Smith, R. L. 1963. Some ecological notes on the grasshopper sparrow. Wilson Bull. 75:159-165.

Stallcup, P. L. 1968. Spatio-temporal relationships of nuthatches and woodpeckers in ponderosa pine forests of Colorado. Ecology 49:831-843.

Stein, R. C. 1958. The behavioral, ecological and morphological characteristics of two populations of the alder flycatcher, *Empidonax trailii* (Audubon). N. Y. State Mus. Bull. 371:1-63.

Stewart, R. E. 1953. A life history study of the common yellow-throat. Wilson Bull. 65:99-115.

Stokes, A. W. 1950. Breeding behavior of the goldfinch. Wilson Bull. 62:107-127.

Sturman, W. A. 1968. Description and analysis of breeding habitats of the chickadees, *Parus atricapillus* and *P. rufescens*. Ecology 49:418-431.

Thomas, J. W., R. G. Anderson, C. Maser, and E. L. Bull. 1979. Snags. Pages 60-77 *in* J. W. Thomas, Ed. Wildlife habitats in managed forests, the Blue Mountains of Oregon and Washington. U.S. Dep. Agric. Handbook No. 553.

————, R. M. DeGraaf, and J. C. Mawson. 1977. Determination of habitat requirements for birds in suburban areas. U.S. Dep. Agric., For. Serv. Res. Pap. NE357. 15pp.

Thompson, C. F., and V. Nolan, Jr. 1973. Population biology of the yellow-breasted chat (*Icteria virens* L.) in southern Indiana. Ecol. Monogr. 43:145-171.

Travis, J. 1977. Seasonal foraging in a downy woodpecker population. Condor 79:371-375.

U.S. Fish and Wildlife Service. 1980a. Habitat as a basis for environmental assessment: ESM101. Div. Ecol. Serv., Washington, D.C. (Pages unnumbered.)

U.S. Fish and Wildlife Service. 1980b. Habitat evaluation procedures (HEP): ESM102. Div. Ecol. Serv., Washington, D.C. (Pages unnumbered.)

Verner, J. 1975. Avian behavior and habitat management. Pages 39-58 *in* D. R. Smith, Tech. Coord. Symposium on management of forest and range habitats for nongame birds. U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. WO-1.

————. 1980. Bird communities of mixed-conifer forests of the Sierra Nevada. Pages 198-223 *in* R. M. DeGraaf and N. G. Tilghman, eds. Workshop Proc., Management of western forests and grasslands for nongame birds. U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. INT-86.

Von Steen, D. A. 1965. A study of nesting dickcissels in Nebraska. Neb. Bird Rev. 33:22-24.

Walkinshaw, L. H. 1966. Summer biology of Traill's flycatcher. Wilson Bull. 78:31-46.

Webb, W. L. 1977. Songbird management in a northern hardwood forest. Trans. North Am. Wildl. Nat. Resour. Conf. 42:438-448.

Weber, W. C., and J. B. Theberge. 1977. Breeding bird survey counts as related to habitat and date. Wilson Bull. 89:543-561.

West, D. A. 1962. Hybridization in grosbeaks (*Pheucticus*) of the Great Plains. Auk 79:399-424.

Whitaker, G. A., E. R. Roach, and R. H. McCuen. 1976. Inventorying habitats and rating their value for wildlife species. Proc. Southeast Assoc. Game Fish Comm. 30:590-601.

Whitmore, R. C. 1975. Habitat ordination of passerine birds of the Virgin River Valley, southwestern Utah. Wilson Bull. 87:65-74.

————. 1977. Habitat partitioning in a community of passerine birds. Wilson Bull. 89:253-265.

————. 1979. Short-term change in vegetation structure and its effect on grasshopper sparrows in West Virginia. Auk 96:621-625.

Widmann, O. 1907. A preliminary catalogue of the birds of Missouri. Trans. Acad. Sci. St. Louis 17(1):1-288.

Wiens, J. A. 1973a. Pattern and process in grassland bird communities. Ecol. Monogr. 43:237-270.

_____. 1973b. Interterritorial habitat variation in grasshopper and savannah sparrows. Ecology 54:877-884.

_____. 1977. Model estimation of energy flow in North American grassland bird communities. Oecologia 31:135-151.

Williams, A. B. 1936. The composition and dynamics of a beech-maple climax community. Ecol. Monogr. 6:317-408.

Williams, J. B. 1975. Habitat utilization by four species of woodpeckers in a central Illinois woodland. Am. Midl. Nat. 93:354-367.

Williamson, P. 1971. Feeding ecology of the red-eyed vireo (*Vireo olivaceus*) and associated foliage-gleaning birds. Ecol. Monogr. 41:129-152.

Winkworth, R. E., and D. W. Goodall. 1962. A crosswise sighting tube for point quadrat analysis. Ecology 43:342-343.

Zach, R., and J. B. Falls. 1978. Bivariate normal song territories in ovenbirds. Can. J. Zool. 56:2088-2092.

Zimmerman, J. L. 1966. Polygyny in the dickcissel. Auk 83:534-546.

APPENDIX I

*Common and Scientific Names of Plants Mentioned in Text**

Usnaceae
Beard Mosses (*Usnea* spp.)

Polypodiaceae
Ferns (many genera)

Pinaceae
Pines (*Pinus* spp.)
Red pine (*Pinus resinosa*)
Jack pine (*Pinus banksiana*)
Shortleaf pine (*Pinus echinata*)
Scrub pine (*Pinus virginiana*)
Spruces (*Picea* spp.)
Black spruce (*Picea mariana*)
Hemlock (*Tsuga canadensis*)
Firs (*Abies* spp.)

Taxodiaceae
Bald cypress (*Taxodium distichum*)

Cupressaceae
Red cedar (*Juniperus virginiana*)

Graminae
Brome grasses (*Bromus* spp.)
Fescues (*Festuca* spp.)
Orchard grass (*Dactylis glomerata*)
Timothy (*Phleum pratense*)
Muhly grasses (*Muhlenbergia* spp.)
Prairie dropseed
(*Sporobolus heterolepis*)
Bluestems (*Andropogon* spp.)

Cyperaceae
Sedges (*Carex* spp.)

Bromeliaceae
Spanish moss (*Tillandsia usneoides*)

Saururaceae
Lizard's tail (*Saururus cernuus*)

Juglandaceae
Hickories (*Carya* spp.)
Black hickory (*Carya texana*)

Salicaceae
Willows (*Salix* spp.)
Black willow (*Salix nigra*)
Aspen (*Populus* sp.)
Cottonwood (*Populus deltoides*)

Corylaceae
Hop hornbeam (*Ostrya virginiana*)
Birches (*Betula* spp.)

Fagaceae
Oaks (*Quercus* spp.)
White oak (*Quercus alba*)
Overcup oak (*Quercus lyrata*)
Oregon white oak (*Quercus garryana*)
Bur oak (*Quercus macrocarpa*)
Chinquapin oak (*Quercus prinoides*)
Willow oak (*Quercus phellos*)
Black oak (*Quercus velutina*)
Shumard oak (*Quercus shumardii*)
Pin oak (*Quercus palustris*)
Red oak (*Quercus rubra*)

Ulmaceae
Elms (*Ulmus* spp.)
Slippery elm (*Ulmus rubra*)
Hackberry (*Celtis occidentalis*)

Moraceae
Red Mulberry (*Morus rubra*)

Urticaceae
Wood nettle (*Laportea canadensis*)

Aristolochiaceae
Wild ginger (*Asarum canadense*)

**Authority for names of plants occurring in Missouri: Steyermark, J. A. 1963. Flora of Missouri. Iowa State University Press, Ames. 1728pp.*

Magnoliaceae
Tulip tree (*Liriodendron tulipifera*)

Annonaceae
Pawpaw (*Asimina triloba*)

Ranunculaceae
Golden seal (*Hydrastis canadensis*)
Black cohosh (*Cimicifuga racemosa*)

Lauraceae
Sassafras (*Sassafras albidum*)

Hamamelidaceae
Sweet gum (*Liquidambar Styraciflua*)

Plantanaceae
Sycamore (*Platanus occidentalis*)

Rosaceae
Shadbush (*Amelanchier arborea*)
Hawthorns (*Crataegus* spp.)
Blackberries (*Rubus* spp.)
Roses (*Rosa* spp.)
Multiflora rose (*Rosa multiflora*)
Plums (*Prunus* spp.)
Black cherry (*Prunus serotina*)

Leguminosae
Kentucky coffee tree
(*Gymnocladus dioicus*)
Honey locust (*Gleditsia triacanthos*)
Eastern redbud (*Cercis canadensis*)
Red clover (*Trifolium pratense*)
Alfalfa (*Medicago sativa*)
Tick trefoils (*Desmodium* spp.)
Lespedezas (*Lespedeza* spp.)

Anacardiaceae
Staghorn sumac (*Rhus typhina*)
Smooth sumac (*Rhus glabra*)
Dwarf sumac (*Rhus copallina*)
Fragrant sumac (*Rhus aromatica*)
Poison ivy (*Rhus radicans*)

Aqiofoliaceae
Possum haw (*Ilex decidua*)

Aceraceae
Sugar maple (*Acer saccharum*)
Black maple (*Acer nigrum*)
Red maple (*Acer rubrum*)
Silver maple (*Acer saccharinum*)
Box elder (*Acer negundo*)

Hippocastanaceae
Ohio buckeye (*Aesculus glabra*)

Balsaminaceae
Pale touch-me-not (*Impatiens pallida*)

Vitaceae
Virginia creeper
(*Parthenocissus quinquefolia*)

Tamaricaceae
Tamarix (*Tamarix pentandra*)

Cornaceae
Dogwoods (*Cornus* spp.)
Flowering dogwood (*Cornus florida*)
Rough-leaved dogwood
(*Cornus drummondi*)
Swamp dogwood (*Cornus obliqua*)

Ericaceae
Rhododendron (*Rhododendron* sp.)

Ebenaceae
Persimmon (*Diospyros virginiana*)

Oleaceae
Ashes (*Fraxinus* spp.)
White ash (*Fraxinus americana*)

Labiatae
Slender mountain mint
(*Pycnanthemum tenuifolium*)

Scrophulariaceae
False pimpernel
(*Lindernia anagallidea*)

Bignoniaceae
Trumpet creeper (*Campsis radicans*)

Rubiaceae
Bedstraws (*Galium* spp.)

Caprifoliaceae
Coral berry
(*Symphoricarpos orbiculatus*)

Compositae
Daisy fleabane (*Erigeron strigosus*)
Goldenrods (*Solidago* spp.)
Ashy sunflower (*Helianthus mollis*)
Beggar ticks (*Bidens* sp.)

APPENDIX II

*Common and Scientific Names of Bird Species Mentioned in Text**

Galliformes

Phasianidae

Greater Prairie-chicken (*Tympanuchus cupido*)

Cuculiformes

Cuculidae

Yellow-billed Cuckoo (*Coccyzus americanus*)

Piciformes

Picidae

Red-headed Woodpecker (*Melanerpes erythrocephalus*)
Red-bellied Woodpecker (*Melanerpes carolinus*)
Downy Woodpecker (*Picoides pubescens*)
Hairy Woodpecker (*Picoides villosus*)
Pileated Woodpecker (*Dryocopus pileatus*)

Passeriformes

Tyrannidae

Eastern Wood-Pewee (*Contopus virens*)
Acadian Flycatcher (*Empidonax flaviventris*)
Willow Flycatcher (*Empidonax traillii*)
Great Crested Flycatcher (*Myiarchus crinitus*)
Eastern Kingbird (*Tyrannus tyrannus*)

Alaudidae

Horned Lark (*Eremophila alpestris*)

Corvidae

Blue Jay (*Cyanocitta cristata*)

Paridae

Black-capped Chickadee (*Parus atricapillus*)
Carolina Chickadee (*Parus carolinensis*)
Tufted Titmouse (*Parus bicolor*)

Sittidae

White-breasted Nuthatch (*Sitta carolinensis*)

Troglodytidae

Carolina Wren (*Thryothorus ludovicianus*)
House Wren (*Troglodytes aedon*)

**Authority for names of birds: American Ornithologists' Union 1983. Check-list of North American Birds, 6th edit. American Ornithologists' Union. 877pp.*

Muscicapidae (Sylviinae)
Blue-gray Gnatcatcher (*Polioptila caerulea*)

Muscicapidae (Turdinae)
Wood Thrush (*Hylocichla mustelina*)

Mimidae
Gray Catbird (*Dumetella carolinensis*)
Brown Thrasher (*Toxostoma rufum*)

Vireonidae
White-eyed Vireo (*Vireo griseus*)
Bell's Vireo (*Vireo bellii*)
Yellow-throated Vireo (*Vireo flavifrons*)
Warbling Vireo (*Vireo gilvus*)
Red-eyed Vireo (*Vireo olivaceus*)

Emberizidae (Parulinae)
Blue-winged Warbler (*Vermivora pinus*)
Northern Parula (*Parula americana*)
Yellow Warbler (*Dendroica petechia*)
Yellow-throated Warbler (*Dendroica dominica*)
Prairie Warbler (*Dendroica discolor*)
Cerulean Warbler (*Dendroica cerulea*)
Black-and-white Warbler (*Mniotilta varia*)
American Redstart (*Setophaga ruticilla*)
Prothonotary Warbler (*Protonotaria citrea*)
Worm-eating Warbler (*Helmitheros vermivorus*)
Swainson's Warbler (*Limnothlypis swainsonii*)
Ovenbird (*Seiurus aurocapillus*)
Louisiana Waterthrush (*Seiurus motacilla*)
Kentucky Warbler (*Oporornis formosus*)
Common Yellowthroat (*Geothlypis trichas*)
Yellow-breasted Chat (*Icteria virens*)

Emberizidae (Thraupinae)
Summer Tanager (*Piranga rubra*)
Scarlet Tanager (*Piranga olivacea*)

Emberizidae (Cardinalinae)
Northern Cardinal (*Cardinalis cardinalis*)
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)
Blue Grosbeak (*Guiraca caerulea*)
Indigo Bunting (*Passerina cyanea*)
Dickcissel (*Spiza americana*)

Emberezidae (Emberizinae)
Rufous-sided Towhee (*Pipilo erythrophthalmus*)
Field Sparrow (*Spizella pusilla*)
Lark Sparrow (*Chondestes grammacus*)
Grasshopper Sparrow (*Ammodramus savannarum*)
Henslow's Sparrow (*Ammodramus henslowii*)

Emberizidae (Icterinae)

Red-winged Blackbird (*Agelaius phoeniceus*)
Eastern Meadowlark (*Sturnella magna*)
Brown-headed Cowbird (*Molothrus Ater*)
Orchard Oriole (*Icterus spurius*)
Northern Oriole (*Icterus galbula*)

Fringillidae

American Goldfinch (*Carduelis tristis*)

APPENDIX III

Supplementary Accounts for 11 Species of Birds

These abbreviated supplementary accounts are relegated to an appendix because we had substantial data for most of the 11 species involved, but there were sampling peculiarities for some, or the species are so adaptable (generalists) that our habitat data analysis for them may be misleading. Specific reasons for relegation to the appendix are:

Greater prairie-chicken. The only non-passerine species studied. The data are based on flushings with no reference to sex, breeding status, or time of day. Prairie chickens require several different habitat types in close proximity for different activities.

Red-winged blackbird. Typically a wetland species; our data are mostly from upland sites, where it is a generalist.

Blue grosbeak. Small sample sizes; our data are difficult to explain in terms of the bird's life history.

Gray catbird, yellow-billed cuckoo, blue-gray gnatcatcher, blue jay, Carolina wren, house wren, northern cardinal, brown-headed cowbird. All generalists.

Accounts of these species are organized according to their placement in the cluster analysis (Fig. 3).

Grassland - Managed

Greater Prairie-chicken

Greater prairie-chickens were found only on southwestern Missouri grassland study areas located in large prairie tracts. Habitat at flushing sites was consistently characterized by an absence of woody stems ≥2.5 cm dbh (always 0/ha), an absence of woody stems <2.5 cm dbh (0/ha, never >125), and dense ground vegetation (always >95%) of intermediate height (always 0.10-0.40 m) (Table A).

These characteristics describe managed grasslands with little or no woody vegetation. Distance to the lek is a critical factor of nesting and brood rearing habitat. In Wisconsin, 9 of 25 nests were within 0.8 km of the lek and most were within 1.6 km (Harrison 1975).

Table A. Important characteristics of greater prairie-chicken habitat in Missouri (N = 15).

Variable	*Optimum* *Range*	*%*[a]	*Main* *Range*	*%*	*Avoided* *Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	0*	93	0*	93	>0	7
All woody stems ≥2.5 cm dbh/ha	0*	100	0*	100	>0	0
Ground vegetative cover (%)	>95*	100	>95*	100	<95	0
Ground vegetative height (m)	.30-.40*	47	.10-.40*	100	<.10 or >.40	0
SECONDARY						
(none)						

[a]*Percent of observations.*

**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*

Grassland - Unmanaged

Red-winged Blackbird

Red-winged blackbirds were found on grassland and old field study areas. Habitat around song perches was most consistently characterized by tall ground vegetation (0.40-0.90 m). Other important features included a low to intermediate number of woody stems <2.5 cm dbh (24-2100/ha) and a low canopy (4-8 m, never >8) (Table B).

These characteristics describe brushy grassland-old field habitat with tall ground vegetation. Red-winged blackbirds are usually associated with emergent vegetation in marshes and other wetlands, but readily adapt to upland habitat (Bent 1958, DeGraaf et al. 1980).

Table B. Important characteristics of red-winged blackbird habitat in Missouri (N = 23).

	Optimum		*Main*		*Avoided*	
Variable	*Range*	*%*[a]	*Range*	*%*	*Range*	*%*
PRIMARY						
Ground vegetative height (m)	.40-.50	30	.40-.90*	87	<.40*	13
SECONDARY						
All woody stems <2.5 cm dbh/ha	24-350*	39	24-2100	69	0†	9
Canopy height (m)	4-6*	35	4-8*	65	<4 or >8	35

[a]*Percent of observations.*
**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*
†P<0.10.

Blue Grosbeak

Blue grosbeaks were observed in grassland, old field, and bottomland forest habitats. The most consistent characteristics of habitat around song perches were shallow litter (always <1.0 cm) and dense ground vegetation (>95%). Other important features included a small number of woody stems <2.5 cm dbh (24-1750/ha) and a small number of woody stems ≥2.5 cm dbh (24-300/ha) (Table C).

These characteristics describe overgrown grassland-old field, forest edge, or open forest habitat with sparse litter accumulation. Significance of shallow litter is difficult to explain in relation to the other selected features of blue grosbeak habitat or blue grosbeak life history. Litter was measured only on six plots. This grosbeak inhabits a variety of brushy, openland habitats (Harrison 1975).

Table C. Important characteristics of blue grosbeak habitat in Missouri (N = 10).

	Optimum		*Main*		*Avoided*	
Variable	*Range*	*%*[a]	*Range*	*%*	*Range*	*%*
PRIMARY						
Ground vegetative cover (%)	>95	80	>95	80	<95	20
Litter depth (cm)	0.1-1.0*	83	*<1.0†*	*100*	*>1.0**	*0*
SECONDARY						
All woody stems <2.5 cm dbh/ha	*24-350*	*30*	*24-1750*	*70*	*0*	*10*
All woody stems >2.5 cm dbh/ha	*24-100*	*40*	*24-300*	*60*	*0*	*20*

[a]*Percent of observations.*

**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P≤05).*

†P<0.10.

Old Field - Overgrown Grassland

Gray Catbird

Gray catbirds were observed primarily in grasslands and old fields, although several were also noted in bottomland forests. Habitat around song perches was most consistently characterized by a small to intermediate number of woody stems ≥2.5 cm dbh (24-1400/ha, never 0) and a low to intermediate canopy (2-12 m, never <2). Another important feature was a small to intermediate number of woody stems <2.5 cm dbh (24-2800/ha, never 0) (Table D).

These characteristics describe most brushy grasslands or old fields, thickets, or forest edge.

Table D. Important characteristics of gray catbird habitat in Missouri (N = 26).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
All woody stems ≥2.5 cm dbh/ha	24-100	31	24-1400	92	0*	0
Canopy height (m)	6-8	31	2-12	85	<2*	0
SECONDARY						
All woody stems <2.5 cm dbh/ha	24-1050	35	24-2800	62	0*	0

[a]*Percent of observations.*

**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*

Forest Interior - Forest with Some Large Trees

Yellow-billed Cuckoo

Yellow-billed cuckoos were found primarily in central Missouri upland hardwoods, although several were also observed in all other habitat types (N = 74). Habitat utilized by this species was similar to that of most other forest birds. As a result, no variables appeared crucial to this generalist species.

Blue-gray Gnatcatcher

Blue-gray gnatcatchers were observed in all forest habitats except central Missouri bottomlands (N = 47). Several were also noted in old fields. The distribution of values for most variables appeared random or uniform; thus, no variables were selected as important to this generalist species.

Forest Interior - Pole or Sawtimber, Sparse Understory

Blue Jay

Blue jays were common on bottomland and upland hardwood study areas in central Missouri. Habitat around song perches most consistently had a high canopy (16-28 m). Other important features included an intermediate to closed canopy (>70%), an intermediate to large number of dead stems 2.5-9.9 cm dbh (100-300/ha, never <24), and a small number of woody stems <2.5 cm dbh (corrected values <2100/ha) (Table E).

These characteristics describe an older pole to mature forest with a well-developed canopy and a sparse shrub layer. However, blue jays also are often associated with open, wooded habitat as such found in cities, parks, farms, etc. (Harrison 1975). Four of the central Missouri bottomland study areas were narrow, forested strips along the Missouri River, and accounted for almost 50% of blue jay observations. This possibly reflects a preference for open woodland habitat or small forested islands.

Table E. Important characteristics of blue jay habitat in Missouri (N = 62).

	Optimum		*Main*		*Avoided*	
Variable	*Range*	*%*[a]	*Range*	*%*	*Range*	*%*
PRIMARY						
Canopy height (m)	20-24†	29	16-28	77	<12	0
SECONDARY						
All woody stems <2.5 cm dbh/ha	700-1400*	29	<2100	65	>2100	35
Dead stems 2,5-9.9 cm dbh/ha	100-150	18	100-300	58	<100*	21
Canopy closure (%)	>95*	32	>70	74	<65	20

[a]*Percent of observations.*
**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*
†P<0.10.

Carolina Wren

Although Carolina wrens were found almost exclusively in central Missouri bottomland hardwoods, values of only three variables consistently described habitat around song perches. Carolina wrens utilized areas with a large number of dead stems 2.5-9.9 cm dbh (250-650/ha), a large number of dead stems 10.0-29.9 cm dbh (always 24-225/ha), and a small to intermediate number of woody stems <2.5 cm dbh (700-2100/ha) (Table F).

These characteristics describe a wooded habitat with an unusually large number of snags. Other variables important to this species probably were not measured in this study, although the small sample size precludes adequate delineation of habitat.

Natural cavities or old woodpecker holes and brushy tangles serve as nest sites (Harrison 1975). In addition to the numerous dead trees indicated above, flood drift piles were common on the bottomland study areas. Brushy tangles and log piles in various wooded habitats, but especially near water or in other moist places, are prime habitat for Carolina wrens (Bent 1948, DeGraaf et al. 1980).

Table F. Important characteristics of Carolina wren habitat in Missouri (N = 9).

	Optimum		*Main*		*Avoided*	
Variable	*Range*	*%*[a]	*Range*	*%*	*Range*	*%*
PRIMARY						
Dead stems 2.5-9.9 cm dbh/ha	250-600	67	250-650.	78	<250	22
SECONDARY						
All woody stems <2.5 cm dbh/ha	700-2100†	67	700-2100†	67	<700 or >2100	33
Dead stems 10.0-29.9 cm dbh/ha	24-100	78	24-225	100	0†	0

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

†P<0.10.

Forest Interior - Open Tree Reproduction

House Wren

House wrens were found primarily in central Missouri bottomland hardwoods, although several were also noted in dense thickets on grasslands. Habitat around song perches most consistently had tall ground vegetation (0.40-0.80 m), level terrain (<5° slope, never >10), a small to intermediate number of woody stems <2.5 cm dbh (always 24-3500/ha), and dense ground vegetation (>80%). Other important features included a small number of live stems 2.5-9.9 cm dbh (<750/ha) and a low number of woody stems ≥2.5 cm dbh (<1400/ha) (Table G). Although slope possibly is not important of itself, it reflects the flatness of the bottomland study areas which apparently provided suitable habitat for house wrens because of other characteristics inherent in this bottomland habitat.

The above characteristics describe an open forest with dense ground vegetation. House wrens are also associated with farms, parks, and suburban shrubbery (Harrison 1975).

Table G. Important characteristics of house wren habitat in Missouri (N = 17).

Variable	*Optimum Range*	*%[a]*	*Main Range*	*%*	*Avoided Range*	*%*
PRIMARY						
All woody stems <2.5 cm dbh/ha	24-2800	83	24-3500	100	>3500	0
Ground vegetative cover (%)	>95*	35	>80	71	<80	29
Ground vegetative height (m)	.60-.70*	35	.40-.80*	82	<.40*	18
Slope (degrees)	0†	76	<5	94	>5	6
SECONDARY						
All woody stems ≥2.5 cm dbh/ha	1000-1100*	29	<1400	82	>1400	18
Live stems 2.5-9.9 cm dbh/ha	500-550*	24	<750	88	>750	12

[a]*Percent of observations.*
**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*
†P<0.10.

Northern Cardinal

Northern cardinals were observed primarily in central Missouri forest and old field habitat, although several were also found in all other habitat types. Habitat around song perches was consistently characterized by an absence or low number of live stems ≥30 cm dbh (<75/ha, never >150). Other important features included an intermediate to tall (>0.10 m) and intermediate to dense (>55%, never <20) ground vegetation layer (Table H).

These characteristics do not describe a particular habitat, but imply that northern cardinals avoid mature forests. Northern cardinals are found in a wide variety of habitats except deep forests unless thickets are present (Harrison 1975, DeGraaf et al. 1980).

Table H. Important characteristics of northern cardinal habitat in Missouri (N = 83).

	Optimum		*Main*		*Avoided*	
Variable	*Range*	*%*[a]	*Range*	*%*	*Range*	*%*
PRIMARY						
Live stems ≥30 cm dbh/ha	0*	25	<75*	83	>75	17
SECONDARY						
Ground vegetative height (m)	.20-.30	25	>.10	94	<.10	6
Ground vegetative cover (%)	>95*	19	>55	80	<55	20

[a]*Percent of observations.*

**Significantly different from expected value when compared to forest all species frequency distribution (chi-square, P<0.05).*

Forest Edge

Brown-headed Cowbird

Brown-headed cowbirds were seen almost as frequently in forest habitat (47% of observations) as grassland-old field habitat (53%). Cowbirds probably used forest habitat to a greater extent but were not found as often due to decreased visibility in forest stands. Habitat around song perches was characterized only by a minimum canopy height (>4 m), a minimum number of woody stems <2.5 cm dbh (>700/ha), and a minimum number of woody stems ≥2.5 cm dbh (>24/ha) (Table I). Cowbirds also tended to use areas with snags more often than most other species. Snags are used by cowbirds for watching other bird species that will be parasitized (Robbins 1979).

Cowbirds inhabited a variety of vegetational types and only appeared to require some woody vegetation.

Table I. Important characteristics of brown-headed cowbird habitat in Missouri (N = 51).

	Optimum		*Main*		*Avoided*	
Variable	*Range*	*%*[a]	*Range*	*%*	*Range*	*%*
PRIMARY						
(none)						
SECONDARY						
All woody stems <2.5 cm dbh/ha	700-1050*	18	>700	80	<700*	20
All woody stems ≥2.5 cm dbh/ha	24-50	18	>24	98	0*	2
Canopy height (m)	6-20	68	>4	92	<2*	0

[a]*Percent of observations.*

**Significantly different from expected value when compared to grassland-old field all species frequency distribution (chi-square, P<0.05).*

Figure 1. Locations of Study Areas in Missouri.

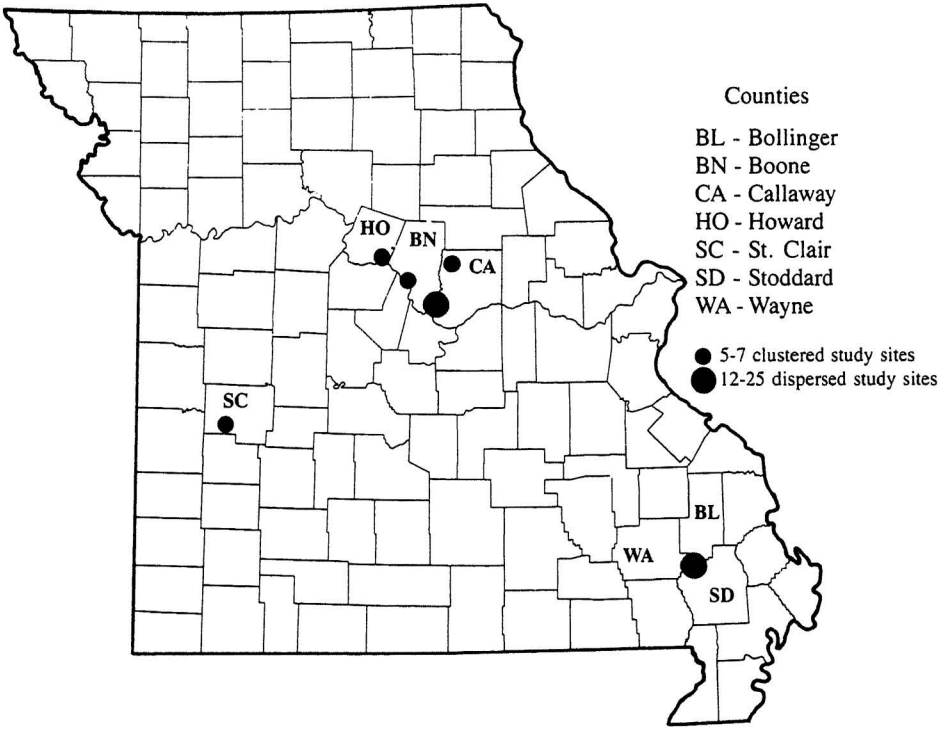
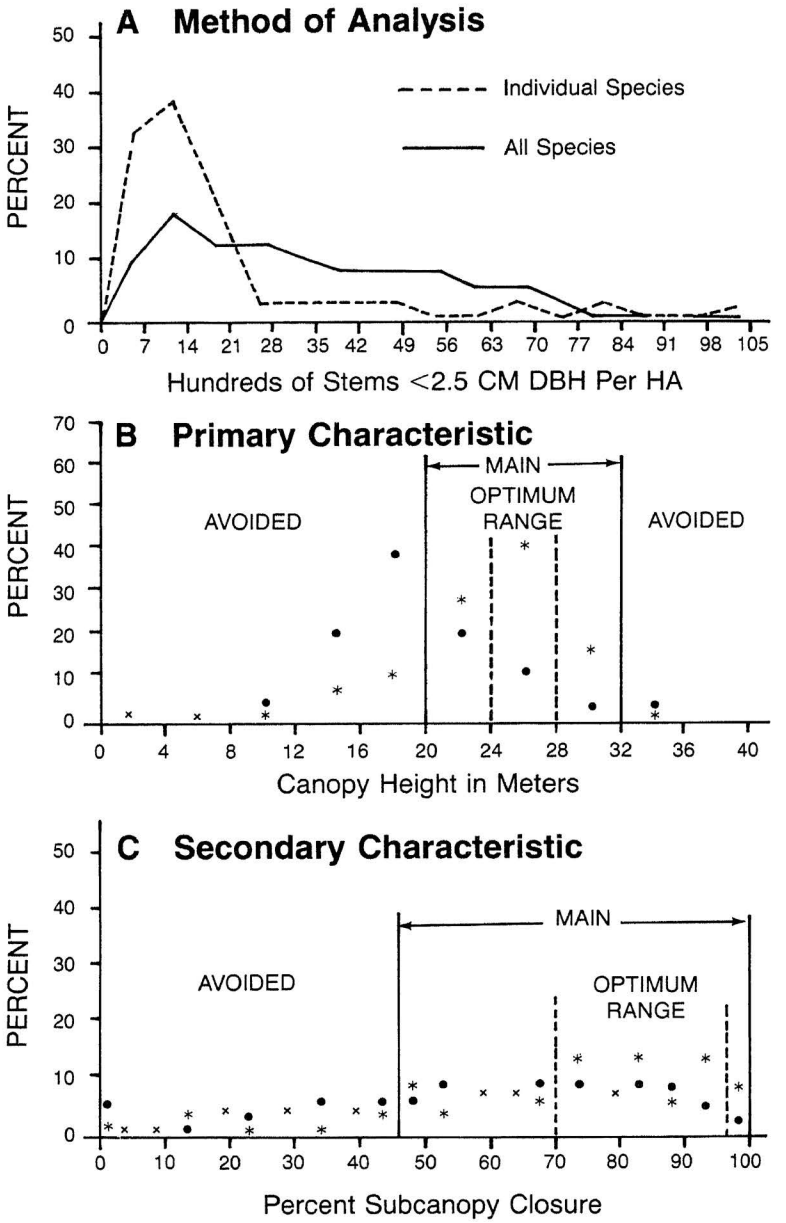


Figure 2. Frequency Distribution for the Northern Oriole Illustrating Method of analysis (A) and Terms Used in the Text (B, C).



* Values for individual species
● All species
x Both

Figure 3. Phenogram of Habitat Similarities for 60 Bird Species, Calculated From Median Values of Habitat Characteristics.