5-1992

Relationships among Birds, Willows, and Native Ungulates in and around Northern Yellowstone National Park

Sally Graves Jackson
Utah State University

RELATIONSHIPS AMONG BIRDS, WILLOWS, AND NATIVE UNGULATES IN AND AROUND NORTHERN YELLOWSTONE NATIONAL PARK

by

Sally Graves Jackson

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Wildlife Ecology

Approved:

Major Professor	Committee Member
Committee Member	Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

1992

ACKNOWLEDGMENTS

I am deeply grateful to the Rob and Bessie Welder Wildlife Foundation in Sinton, Texas, for funding this research. I am also grateful to the Utah State University Ecology Center for additional financial support.

John A. Kadlec provided valuable advice throughout this research, and yet still allowed me the latitude to make independent decisions. I also appreciate the generous encouragement and advice of Kim Sullivan and Tom Edwards. Fred Wagner and Charles Kay provided a constant flow of knowledge and literature of the Greater Yellowstone area.

The willing help of numerous individuals associated with Yellowstone National Park, Gallatin National Forest, and Red Rock Lakes National Wildlife Refuge is greatly appreciated. I thank both owner and manager of the B-Bar Ranch in Montana for opening their land for this research.

The field assistance and companionship of Michael Rowell, Beryl Kreuter, Helen Graves, Rob Jackson, and especially JT Stangl were invaluable during this project.

To my parents, sister, and friends, who have provided love and encouragement throughout my academic pursuits, I am forever grateful. To my husband, Rob, I can only look forward to more pursuits in which your love, humor, and faith make such a difference.

Sally Graves Jackson

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (continued)

ABSTRACT

Relationships Among Birds, Willows, and Native
Ungulates in and around northern
Yellowstone National Park

by

Sally Graves Jackson, Master of Science
Utah State University, 1991

Major Professor: Dr. John A. Kadlec
Department: Fisheries and Wildlife

Although the impacts of livestock and human activities on riparian zones and associated wildlife have been well-documented, little is known about the impacts that browsing by large native ungulates such as elk and moose may have. In the northern Yellowstone area, some willow stands experience intense browsing by elk and moose whereas others experience medium or very low amounts of browsing. The objectives of this study were (1) to compare the species and densities of birds among willow stands that have experienced different intensities of browsing by native ungulates, (2) to measure the relationship between five species of birds and aspects of habitat structure, and (3) to develop and evaluate predictive models that relate presence or absence of the five species to habitat characteristics. In 1989 and 1990, I measured densities of nesting songbirds and aspects of habitat structure in eight large willow stands that have experienced different intensities of browsing. The densities of five focal species (Common Yellowthroat, Lincoln's Sparrow, Warbling Vireo, Wilson's Warbler, and Yellow Warbler) varied considerably among sites. Only two sites had all five species and only one species--the Lincoln's Sparrow--was found in all eight sites. The proportion of severely browsed willows in the eight sites ranged from 3.5% to 100%. The nonlinear relationship between total bird densities and frequency of severe browsing suggests that birds have a threshhold of tolerance for browsing, beyond which bird numbers and total numbers of species drop. Principal Components Analysis of 14 habitat variables indicates that the study sites varied in terms of distances between shrubs, shrub heights, height heterogeneity, foliage density at various height intervals, and frequency of severely browsed willows. Browsing does appear to affect the assemblages of breeding birds in these sites, but site- and landscape-level factors such as food abundance, willow species composition, hydrology, type and gradient of adjacent community, and riparian zone width and elevation also play important roles. Such variables should be incorporated into future predictive models to improve model performance. (82 pages)

CHAPTER I

INTRODUCTION

CONCEPTUAL BACKGROUND

An animal's habitat is the conglomerate of physical and biotic factors which characterize the kind of place in which it lives (Partridge 1978). For the purposes of this thesis, habitat is defined more specifically after Hutto (1985:456): "a spatially contiguous vegetation type that appears more or less homogeneous throughout and is physiognomically distinctive from other such types."

Habitat selection by birds involves the choice of particular habitats from available habitats, and results in birds being nonrandomly distributed in space (Partridge 1978). The assemblage of birds at a given site may change considerably if the vegetation component is changing (Lack 1933).

At a region-wide scale (as defined by Wiens et al. 1987), a particular habitat type may vary considerably. Willow-dominated riparian habitat, the object of this study, may vary in terms of site hydrology; temperature regime; elevation; slope; aspect; fire and drought history; species composition and structure of willows; density of willows; vegetation between willows; and the effects of livestock and herbivorous wildlife such as beaver (<u>Castor canadensis</u>), elk (<u>Cervus elaphus</u>), and moose (<u>Alces alces</u>).

The impacts of livestock and native wildlife can be considerable. The impacts of livestock on riparian zones are especially well-documented, and much work has been done to describe the response to these impacts by wildlife in riparian zones (e.g., Cope 1979, Thomas et al. 1979, Mosconi and Hutto 1982, Kauffman and Kreuger 1984, Taylor 1986, Tucker 1987, Knopf et al. 1988).

The impacts of beaver have also been studied. Hill (1982) asserts that if beaver dams are numerous and well-distributed along a drainage, they hold most precipitation where it falls or melts, thereby keeping the water table high. The water held by dams is released gradually, keeping water in the stream even in dry months (Hill 1982). The ponds benefit fish, as does the riparian vegetation which may be more lush around beaver dams (Medin and Clary 1990). Dams also entrap silt and slow erosion by promoting plant establishment (Hill 1982). Benefits to wildlife include creation of wetland habitat and encouragement of structurally complex vegetation which is then useful to more birds and more species of birds (Medin and Clary 1990).

But while the impacts of livestock and beaver in riparian habitats and riparian wildlife are relatively well-documented, little research has considered the role that native ungulates, especially elk and moose, may have in altering willow-dominated riparian habitat and its associated community of birds. The first chapter of this thesis addresses this gap in our knowledge, focusing on willow stands in and around northern Yellowstone National Park. Willows are now about 50% less abundant in the park than they were at the beginning of this century (Houston 1982). Investigators such as Patten (1968), Chadde and Kay (1988), and Kay (1990) believe that overbrowsing has played a role in this decline, despite the fact the vegetation has coevolved with browsing since the Pleistocene.

Changes within a habitat will almost certainly be accompanied by a change in the assemblage of birds. Although the exact factors influencing habitat selection by birds are not entirely known, most investigators agree that birds are attracted to some combination of plant species and vegetation structure (Hilden 1965, Rotenberry 1985). Birds with all-purpose breeding territories, such as most songbirds, presumably select nesting habitat that provides cover for the nest, perching and singing sites, and enough area to provide the necessary food for the adults and young.

Hutchinson's (1958) concept of the niche as an n-dimensional space provided the foundation for using multivariate techniques to describe relationships between birds and numerous habitat variables. Work by MacArthur and MacArthur (1961) and MacArthur et al. (1962) emphasized the influence of vegetation structure on habitat selection by birds. James (1971) was among the first to use multivariate techniques to ordinate birds along gradients of vegetation structure. Other important investigations which developed the use of multivariate statistics in ecology include those by Anderson and Shugart (1974), Whitmore (1975), Dueser and Shugart (1978), and Dueser and Shugart (1979). Multivariate techniques are now used extensively to describe relationships between animals and their habitats (see Capen 1981).

Multivariate techniques are also used to identify which habitat variables may be most useful as predictors of species presence or abundance (e.g., Bart et al. 1984, Maurer 1986, Lancia et al. 1982, Marcot et al. 1983, Morrison et al. 1987). Numerous discussions of model development, model testing, and modelling pitfalls are found in Verner et al. (1986). The third chapter of this thesis focuses on my attempt to use habitat data from eight willow stands to predict the presence or absence of particular riparian songbirds.

OBJECTIVES AND JUSTIFICATION

The objectives of this research were:

1. To compare the species and densities of birds among willow stands that have experienced different intensities of browsing by elk and moose,
2. To measure the relationship between five species of birds and aspects of habitat structure, and

3. To develop and evaluate predictive models that relate presence or absence of the five species to habitat characteristics.

Little research has focused on the relationships among songbirds, vegetation, and native ungulates in general, or, more specifically, on the response of songbirds to browsing-induced habitat alterations. In the Yellowstone area, the carrying capacity of the northern elk herd as established by the National Park Service may be higher than can be tolerated by the willow-dominated riparian zones. The results of this research will provide additional information for the ongoing controversy surrounding management of the Park's northern herd.

This research will help to define the quality at which willows need to be maintained for normal densities of riparian songbirds. Many of the species that use these stands for breeding and/or feeding are sensitive species which cannot reproduce in any other type of habitat.

Lastly, this study provides an opportunity to develop and evaluate relatively simple predictive models. Five models will be produced, one for each of five species of songbirds which use willow stands for breeding.

STUDY AREA AND STUDY SITES

Yellowstone National Park occupies 8,995 km^2 (2.2 million acres) in the northwest corner of Wyoming and adjacent parts of Montana and Idaho. Seven national forests, two national wildlife refuges, and numerous private holdings surround the Park, creating about 77,700 km^2 (19.2 million acres) of land known as the Greater Yellowstone Ecosystem. This area encompasses four major life zones: foothills (1574-1829 m; 5165-6000 ft), montane (1829-2316 m; 6000-7600 ft), subalpine (2316-timberline, about 3048 m; 7600 ft-timberline, about 10,000 ft), and alpine (timberline-mountain peaks). The highest point is Eagle Peak (3462 m; 11,358 ft) (McEneaney 1988).

Study sites for this research were willow stands larger than 6.0 ha, and were associated with streams in and around the northern portion of the Park (Fig. 1). Six sites were chosen and surveyed in 1989; these and two additional sites were surveyed in 1990. All sites were located in the montane life zone between elevations of 1900 to 2300 m (Table 1).

TABLE 1. Study sites, their elevations, and years surveyed.

Site	Elevation (m)	Years Surveyed
Slough Creek	1900	1990
Tom Miner Creek	2000	1989, 1990
Cougar Creek	2010	1989, 1990
Red Rock Creek	2023	1989, 1990
Lamar Valley	2050	1990
Gallatin River	2200	1989, 1990
Obsidian Creek	2250	1989, 1990
Soda Butte Creek	2300	1989, 1990

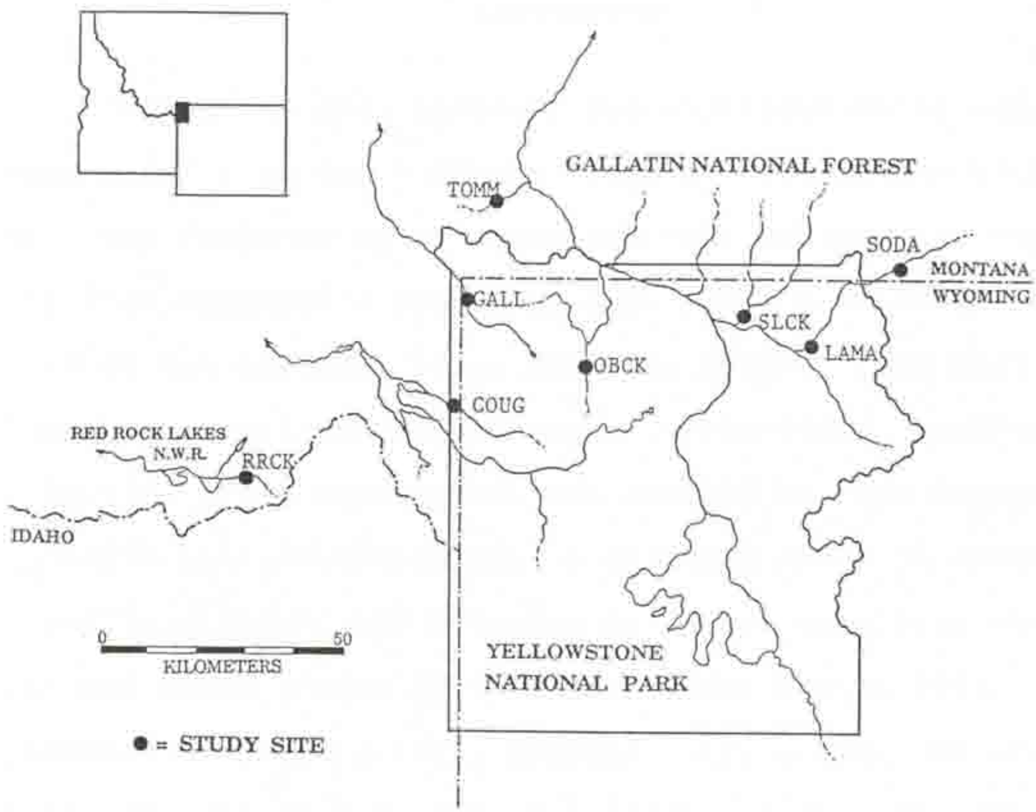

FIGURE 1. Locations of eight study sites in and around northern Yellowstone National Park. (COUG=Cougar Creek, GALL=Gallatin River, OBCK=Obsidian Creek, RRCK=Red Rock Creek, SODA=Soda Butte Creek, TOMM=Tom Miner Creek, LAMA=Lamar Valley, SLCK=Slough Creek).

CHAPTER 2

THE EFFECT OF BROWSING BY ELK AND MOOSE ON THE BREEDING BIRD COMMUNITY OF WILLOW STANDS IN AND AROUND NORTHERN YELLOWSTONE NATIONAL PARK

BACKGROUND

During the past century, the distribution of willows (Salix spp.) on the northern range of Yellowstone National Park has declined by an estimated 50%; willows and other riparian vegetation now cover only about 0.4% of the total area of the northern range (Houston 1982). This decline has been associated with drought in the 1930s, herbivory by a beetle, plant succession, the effects of fire suppression on soil-water relationships, a climatic shift to warmer, drier conditions, and browsing by native ungulates such as elk and moose (Grimm 1939, Patten 1968, Beetle 1974, Olmsted 1979, Tyers 1981, Houston 1982, Despain et al. 1986, Chadde and Kay 1988, Kay 1990). Such a decline could have a major impact on the many species of wildlife, including birds, which use riparian zones for foraging, breeding, cover, and other purposes.

Browse utilization rates higher than 90% were reported in the 1970s for willows in northern Yellowstone (Houston 1982). Kay (1990) does not believe that these rates have decreased, although Singer et al. (1990) reported rates of

27-48% in certain study areas of the northern range. Patten (1968) speculated that increased willow mortality occurred along the Gallatin River in Yellowstone as a result of browsing.

Intense browsing by elk and moose may alter not only the distribution of willows at the scale of the landscape (e.g., Hanley and Taber 1980), but it may also change individual willow plants. Patten (1968) found that willows which were commonly more than 1 m tall were stunted by browsing to less than 1 m. Houston (1982) noted that willows within browsing exclosures in the Park had greater height and canopy cover than willows outside, although there was no significant difference in the number of plants inside and outside. Chadde and Kay (1988) found that tall-growing species of willow along Slough Creek did not reach heights above 1-1.5 m because of repeated browsing by ungulates. Kay (1990) reported that browsing virtually eliminated seed production by willows outside browsing exclosures.

The effect of browsing on shrubs varies depending on the season or seasons during which browsing occurs (Willard and McKell 1978). During a short-term study in Alaska, Wolff (1978) noted that willows which had been browsed most heavily in winter produced the greatest amount of new growth the following spring. However, they acknowledged that continuous heavy winter browsing could eventually cause a decline in productivity; such browsing removes twigs grown during the previous growing season, and may cause shrubs to develop a stunted, clubbed appearance.

Elk include forbs, graminoids, and browse in their diet throughout the year (Marcum 1979, Houston 1982), but they consume proportionately more browse as winter progresses (Hobbs et al. 1979). Houston (1982) described the northern Yellowstone elk's winter diet as 17% browse, 80% grasses, and 3% forbs, but the proportion of browse can be much higher during severe winters (Singer et al. 1990). More than 90% of the winter diet of the moose in Yellowstone is browse, much of which comes from willows (Peek 1974, Houston 1982). However, there are only about 200 moose in the park (Despain et al. 1986), whereas the northern elk herd numbered more than 20,000 as recently as 1988.

The history of management of the northern elk herd and related controversies are detailed by Tyers (1981) and Kay (1990); only a brief summary is presented here.

After Yellowstone was founded in 1872, a primary goal of the Park's early wildlife managers was to enhance populations of its native ungulates. Consequently, hay was provided in the Park during winter months for the benefit of elk, mule deer (Odocoileus hemionus), white-tailed deer (Odocoileus virginianus), bison (Bison bison), bighorn sheep (Ovis canadensis), and pronghorn antelope

(Antilocapra americana) (Kay 1990). Systematic predator control was initiated to reduce the numbers of large predators.

By the late 1920s, all wolves (Canis lupus) and most mountain lions (Profelis concolor) had been eliminated from the park (Kay 1990). Historic park records indicate that the northern elk herd irrupted to approximately 35,000 animals during the first two decades of the 1900s, and then crashed to fewer than 15,000 animals following a series of severe winters. The National Park Service began to think that without predators, the northern elk herd had become larger than the carrying capacity of its winter range. Grimm (1939) noted the effects of continued heavy use of the winter range, including nudation, stunting of preferred forage plants, soil erosion, invasion by non-native plant species, and high elk mortality due to winter malnutrition.

A program of live-trapping and translocating elk to Montana and Wyoming was initiated, and, in the late 1940s, National Park Service personnel began to further control elk numbers in the park by shooting them. Under such management the northern herd declined to fewer than 5000 animals in the late 1960s.

Also in the 1960s, a national controversy developed over the Park's elk-culling program. Leopold (1963) argued that such direct control was necessary to compensate for the Park's lost predator component, but in 1967, the

National Park Service discontinued both killing and translocating Yellowstone's elk and adopted a new management policy which is still in use today.

The new policy, called "natural regulation," was based in part on the ideas of Caughley (1970), and was summarized by Cole (1971) and Houston (1982). Its main points are that (1) the native ungulates in an ecologically complete habitat do not have the capacity to progressively deplete food supplies that limit their own densities, (2) the numbers of these ungulates are depressed by density-influenced intraspecific competition and the partially density-independent effects of periodic severe weather, and (3) large predators are not essential in limiting ungulate populations. The validity of this management policy has been argued extensively, particularly in terms of its effect on the condition of Yellowstone's northern range (e.g., Beetle 1974, Peek 1980, Caughley 1981, Peek 1981, Chase 1986). The National Park Service maintains that since "willows have evolved with browsing by elk and moose in the Yellowstone area for many centuries . . . , any decline in willows must be related to either a) a change in ungulate abundance or b) a change in willow growth or establishment conditions" (Singer et al. 1988:3).

The importance of riparian zones to land birds and other wildlife has been documented convincingly by numerous investigators and has been the focus of several symposia and publications (e.g., Johnson and Jones 1977, Johnson et al. 1985, Warner and Hendrix 1984). Carothers et al. (1974) showed that breeding bird diversity is greater in riparian habitat than in most other terrestrial habitats. Thomas et al. (1979) noted that of the 363 terrestrial species of vertebrates known to occur in the Great Basin of southeastern Oregon, 288 (79.3%) are either directly dependent on riparian zones or utilize them more than other habitats. In western Montana, 59% of 151 species of land birds use riparian habitats for breeding purposes and 36% of those breed only in riparian areas (Mosconi and Hutto 1982). At least 144 species of birds include the northern Yellowstone area in their breeding ranges (McEneaney 1988), and more than 50 of these are tied in some way to riparian habitat during the breeding season.

Thus, riparian zones may be a critical source of diversity at the scale of the landscape. The disproportionate use of riparian zones by birds and other wildlife is especially significant given that these zones generally constitute less than 0.5% of the total land area in the western United States (Anderson and Ohmart 1986).

In comparisons among riparian habitats in various conditions, relatively pristine or lightly disturbed riparian zones usually have more species of birds in higher densities than comparable areas that have been severely disturbed. In riparian corridors in Oregon, for example, Taylor (1986) found 11 to 13 times more birds and 10 times greater shrub volumes in undisturbed willows than in willows altered by cattle and nearby dredging. Casey and Hein (1983) found that 12 species of birds which were present in deciduous forest with normal deer densities were not found inside a large wildlife research preserve with high densities of deer, elk, and mouflon sheep. Other investigators have found similar differences in comparisons of birds among disturbed and undisturbed riparian zones, whether the alteration is due to livestock (e.g., Tucker 1987, Knopf et al. 1988), recreation (Blakesley 1986), or other human activities. Thus, I hypothesized that habitat alteration due to overbrowsing by elk and moose might have serious effects on birds.

The numbers and species of birds change with habitat alteration for essentially the same reason that they change with habitat succession; that is, a species of bird occupies only those habitats which provide suitable nesting requirements and meet the "proximate" (Hilden 1965) or "psychological" (Lack 1933) needs of that species. Attempts to describe the habitat requirements of various species by measuring the habitat they select indicate that birds base choices on a wide range of factors, including but not limited to vegetation structure, plant species composition, food abundance, habitat patch size, and competition with other birds (MacArthur et al. 1962, Willson 1974, Balda 1975, Rotenberry and Wiens 1980, Cody 1981, Hutto 1985, Rotenberry 1985, and many others).

The objectives of this segment of the research were (1) to compare the breeding bird assemblages among willow stands that have experienced different intensities of browsing by elk and moose, and (2) to clarify the habitat relationships of five species of birds in terms of vegetation and browsing.

METHODS

In May 1989, I established a 600-m transect through the center of each of six large willow stands, following the general direction of the stream channel. At each of twelve 50-m intervals along the transect was a perpendicular "branch" of a random length. These branches alternated direction relative to the transect line, their lengths did not extend beyond the boundary of the riparian corridor, and their endpoints became sampling points. The average distance between sampling points was 80 meters. This arrangement was adapted from Knopf et al. (1988). I established transects in two additional sites in May 1990.

1. Bird censuses. Censuses of birds in the study sites were conducted using a variable circular-plot technique similar to that used by Knopf et al. (1988). During June and July, which encompassed the weeks of peak singing by territorial male songbirds, I conducted four censuses at six of the eight sites in 1989. All eight sites were surveyed in 1990, although I conducted only three censuses at the Lamar and Soda Butte sites that year because of bad weather and flooded streams. The average number of days between censuses at a given site was ten.

Censuses were conducted from 15 minutes before sunrise to approximately 09:00 hours. Censuses at a given site varied in both starting point and direction of travel. At each of the 12 sampling points, I stood motionless for one minute (as per Reynolds et al. 1980) and then recorded all birds detected by sight or sound for eight minutes. For each bird detected, I recorded species, sex if known, distance and direction from sampling point, and behavior. Also recorded were locations or supposed locations of nests. Censuses were not conducted in inclement weather.

As five "focal" species I chose the Common Yellowthroat (Geothlypis trichas), Lincoln's Sparrow (Melospiza lincolnii), Warbling Vireo (Vireo gilvus), Wilson's Warbler (Wilsonia pusilla), and Yellow Warbler (Dendroica petechia). These species appear to require riparian habitat for nesting, and were numerous enough to provide valid density estimates. Following the method of Reynolds et al. (1980), I calculated the "effective detection distance," or EDD, for each focal species. The number of sightings used in the calculation of each EDD ranged from 33 (Warbling Vireo) to 167 (Lincoln's Sparrow).

Densities of the five focal birds were then calculated from the following formula:

$$D = \frac{2\ (M)}{12\ (\pi\ EDD^2)\ ha}$$

in which D=Density in birds/ha, M=Maximum number of singing males detected within the EDD, 12=the number of sampling points per census, and EDD=the effective detection distance.

2. Vegetation data. In each site, I took identical vegetation measurements in two types of shrub-centered 0.04-ha (radius=11.3m) circular plots: randomly-located and bird-centered (from James and Shugart 1970). Bird-centered plots were located around points recorded during censuses and were believed to be well within nesting territories of the five focal species. While I am aware that the censuses generated bird-centered points more often associated with perch-sites than with nest-sites, and that this may introduce problems brought up by Petit et al. (1988), I believe that the technique was the best possible for this study. Nest-sites of Yellow Warblers and Warbling Vireos were easily located, but searches for nest-sites of Common Yellowthroats, Lincoln's Sparrows, and Wilson's Warblers were consistently fruitless.

The final sample sizes were 172 plots in 1989 and 227 plots in 1990, for a total of 399 plots. The distribution of these plots in random and bird-centered categories varied among sites (Table 2). Vegetation measurements began in late June when willows were fully leafed-out, and ended in late August at the onset of leaf-dropping.

TABLE 2. Distribution of random and bird-centered plots among six sites in 1989 and eight sites in 1990. (RAND=Random, COYE=Common Yellowthroat, LISP=Lincoln's Sparrow, WAVI=Warbling Vireo, WIWA=Wilson's Warbler, YEWA=Yellow Warbler).

	Sample Type						
Site	RAND	COYE	LISP	WAVI	WIWA	YEWA	TOTAL
Cougar Creek	22	11	8	7	11	15	74
Gallatin River	22	13	15		6	2	58
Obsidian Creek	22	14	12		15	8	71
Red Rock Creek	22	1	2	2		14	41
Soda Butte Creek	22		9		9		40
Tom Miner Creek	22	12	11	22	4	12	83
Lamar Valley	10	2	2				14
Slough Creek	10	6	2				18
Total	152	59	61	31	45	51	399

The circular plots were defined by four randomly-oriented, orthogonal radii, and habitat variables were measured in relation to these radii. Vertical structure was measured by holding a metal rod (diameter=5 mm) vertically at five points along each of the radii, and recording the type of basal hit (water, mud, gravel, litter, Carex, forb and grass, live willow, dead willow) and contacts by vegetation type (Carex, forb and grass, live willow, dead willow) within 0.4-m intervals along the rod. The water depth and maximum height of vegetation at each placement of the rod was also recorded. Percent cover by type was calculated from basal hits and, if applicable, from hits along the rod.

The shrub characteristics measured were shrub height, shrub diameter at base, category of browsing experienced (low, medium, or intense), and, in 1990 only, shrub species. These data were recorded for the center shrub and the closest shrub in each of the quarter-circles defined by the orthogonal radii. The browsing category was assigned according to how many branches had been bitten and how severely. Habitat patchiness was measured as the distances between the center shrub and the closest shrub in each quarter-circle at a height of 1.5 meters. These distances were measured between foliage edges.

Values for all variables measured in the circular plots were averaged to single values for further analyses. The frequencies of eleven species of willow were calculated for the eight sites surveyed in 1990. It was assumed for the six sites surveyed both years that willow species composition did not vary between years. The frequency of intensely browsed willows was summarized for all sites, with two years of data combined for the six sites surveyed both years.

The 1989 and 1990 vegetation measurements generated 38 variables. Those variables which did not vary among sites (according to Kruskal-Wallis tests and sequential

Bonferroni tests as described by Rice (1989)) were discarded. The remaining variables were tested for normality and transformed using natural log or arcsin-square-root if necessary. From each pair of highly correlated variables (Pearson product-moment correlation > 0.75), one variable was discarded. One observation considered to be an outlier was also discarded, according to the recommendation of Harner and Whitmore (1981). The remaining 14 variables are explained in Table 3.

Principal Components Analysis (PCA) of the random data from both years was used to reduce the 14 original variables to new, uncorrelated variables called principal components (PCs). I retained PCs with eigenvalues greater than 1.00. The ecological interpretation of each PC was based on those variables which had loadings (eigenvectors) greater than $0.5/(\text{eigenvalue})^{.5}$, as recommended by Afifi and Clark (1984). All analyses were conducted using PC/SAS Version 6.03 (SAS Institute, Inc. 1988).

The eigenvectors of the PCs were used as coefficients to score the original data. These scores were plotted along the four principal component axes. Scores of the random data were plotted by site to show available habitat at each site, and scores of bird-centered data were plotted by species to show the habitat selected by each of the five focal species.

TABLE 3. Explanations of the 14 habitat variables retained for Principal Components Analysis.

Acronym	Description
CVMAXHT	Coefficient of variation of maximum vegetation heights
SHRUBHT	Mean shrub height (m)
SDSHHT	Standard deviation of five shrub heights
SL0040	Frequency of _Salix_ leaves/live branches within 0-0.4m
SD0040	Frequency of dead _Salix_ branches at 0-0.4m
SL4080	Frequency of _Salix_ leaves/live branches at 0.4m-0.8m
SD4080	Frequency of dead _Salix_ branches within 0.4-0.8m
SL80120	Frequency of _Salix_ leaves/live branches at 0.8-1.2m
SL120160	Frequency of _Salix_ leaves/live branches at 1.2-1.6m
UTIL3	Frequency of shrubs in the "intensely browsed" category
PFORB	Mean percent cover by forbs and grasses
PLITT	Mean percent cover by leaf litter
PCAREX	Mean percent cover by _Carex_ spp.
DCTR	Mean distance between center and four adjacent shrubs (m)

RESULTS

1. Bird Data. The censuses generated a species list for each site for each year; these lists were combined for this report, since they varied little between years (Table 4; see also Appendix 1). The list does not include waterfowl, swallows, and raptors, nor does it indicate relative abundances. Densities of nonfocal bird species were not calculated because the numbers of sightings were generally small.

The effective detection distance for all focal species was 40 m. The densities of the five focal species of birds varied considerably among sites (Figs. 2a and 2b). Only two sites--Cougar Creek and Tom Miner Basin--had all five species present. Only one species--the Lincoln's Sparrow--occupied all eight sites. The Warbling Vireo was present in three sites in 1989 and in only two sites in 1990.

In the six sites that were sampled both years, the densities of some species varied between years. Wilson's Warblers decreased at Cougar Creek and Tom Miner Basin; Yellow Warblers decreased at Obsidian Creek; and at Red Rock Creek, Lincoln's Sparrows decreased and Warbling Vireos disappeared altogether.

2. Vegetation Data. The frequency of 11 species of willows varied considerably among the eight sites (Fig. 3). While the Cougar Creek and Obsidian Creek sites were dominated by Geyer's willow (S. geyeriana), the Red Rock

TABLE 4. Bird species detected in each site. Data were combined from 1989 and 1990 censuses. (COU=Cougar Creek, GAL=Gallatin River, OBC=Obsidian Creek, RRC=Red Rock Creek, SOD=Soda Butte Creek, TOM=Tom Miner Creek, LAM=Lamar Valley, SLC=Slough Creek, "•"=presence).

	Site							
Species	COU	GAL	OBC	RRC	SOD	TOM	LAM	SLC
American Robin	•	•	•	•	•	•		
Belted Kingfisher	•		•		•	•		
Black-billed Magpie				•				
Brewer's Blackbird							•	•
Brown-headed cowbird	•	•	•	•		•	•	•
Common snipe	•	•	•	•		•	•	•
Common Yellowthroat	•	•	•	•		•	•	•
Fox Sparrow	•			•				
Lazuli Bunting		•				•		
Lincoln's Sparrow	•	•	•	•	•	•	•	•
MacGillivray's Warbler	•			•				
Northern Waterthrush	•							
Red-winged Blackbird			•	•		•	•	
Rufous Hummingbird	•	•			•	•		
Sandhill Crane		•	•	•		•		
Savannah Sparrow		•	•	•		•	•	
Song Sparrow	•			•		•		•
Sora			•			•	•	
Spotted Sandpiper	•		•	•	•	•	•	•
Warbling Vireo	•			•		•		
White-crowned Sparrow	•	•	•	•	•	•		
Willow Flycatcher	•							
Wilson's Warbler	•	•	•		•	•		
Yellow Warbler	•	•	•	•		•		•
Yellow-bellied Sapsucker	•			•		•		
Yellow-headed Blackbird				•				•
TOTAL #SPECIES	18	12	14	18	7	19	9	9

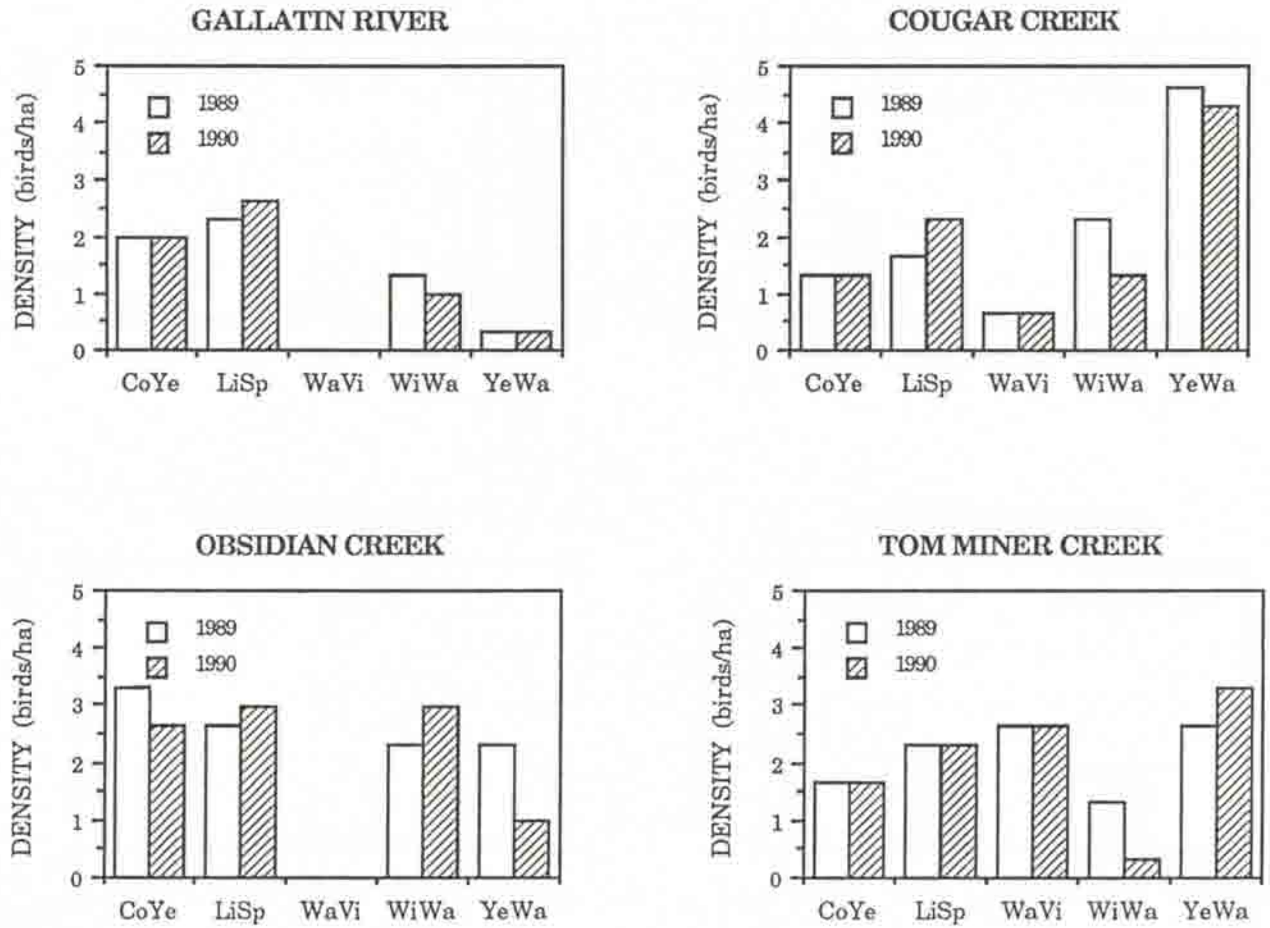

FIGURE 2a. Densities (birds/ha) of the five focal species of birds in four of eight sites sampled. (CoYe=Common Yellowthroat, LiSp=Lincoln's Sparrow, WaVi=Warbling Vireo, WiWa=Wilson's Warbler, YeWa=Yellow Warbler).

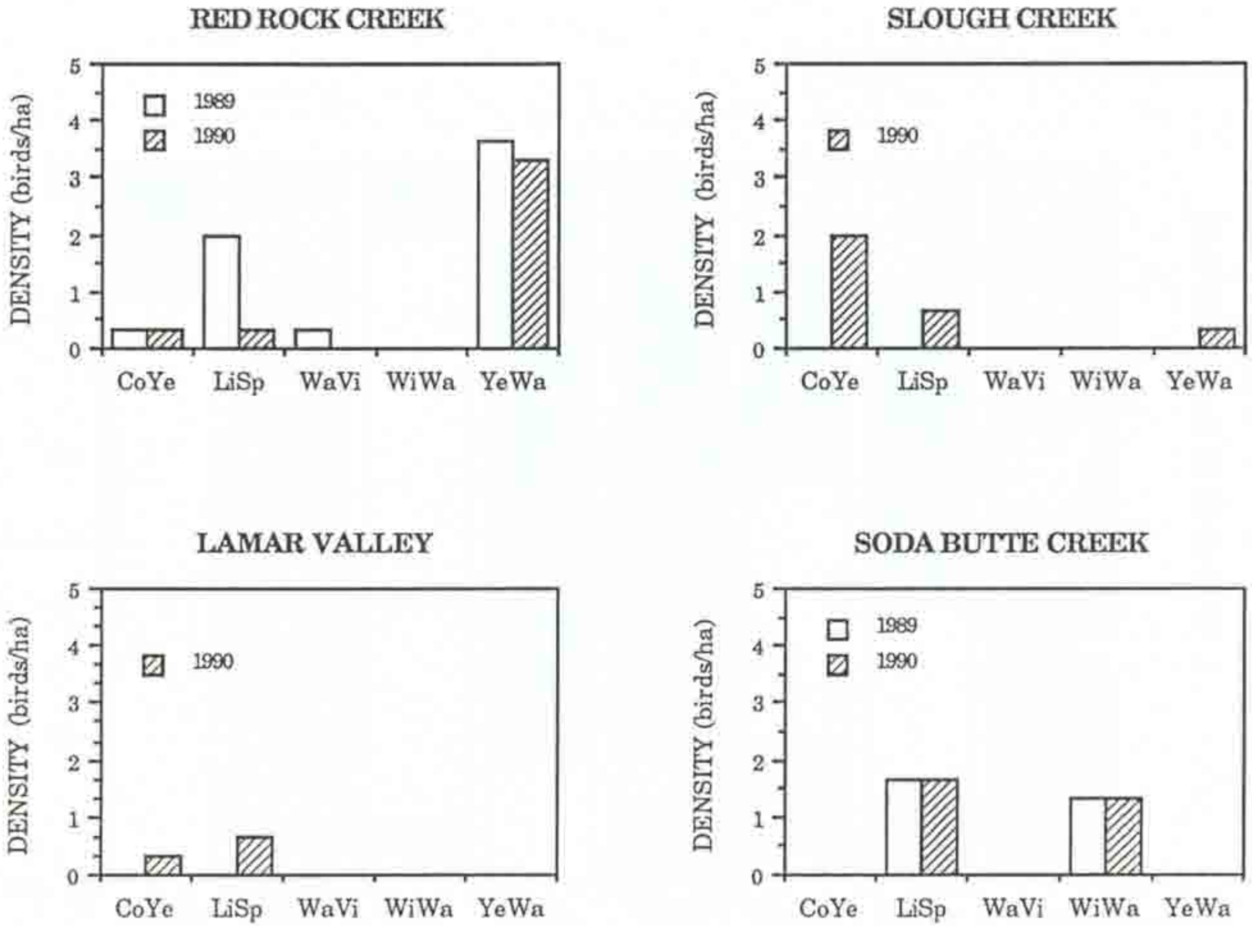

FIGURE 2b. Densities (birds/ha) of the five focal species of birds in four of eight sites sampled. (CoYe=Common Yellowthroat, LiSp=Lincoln's Sparrow, WaVi=Warbling Vireo, WiWa=Wilson's Warbler, YeWa=Yellow Warbler).

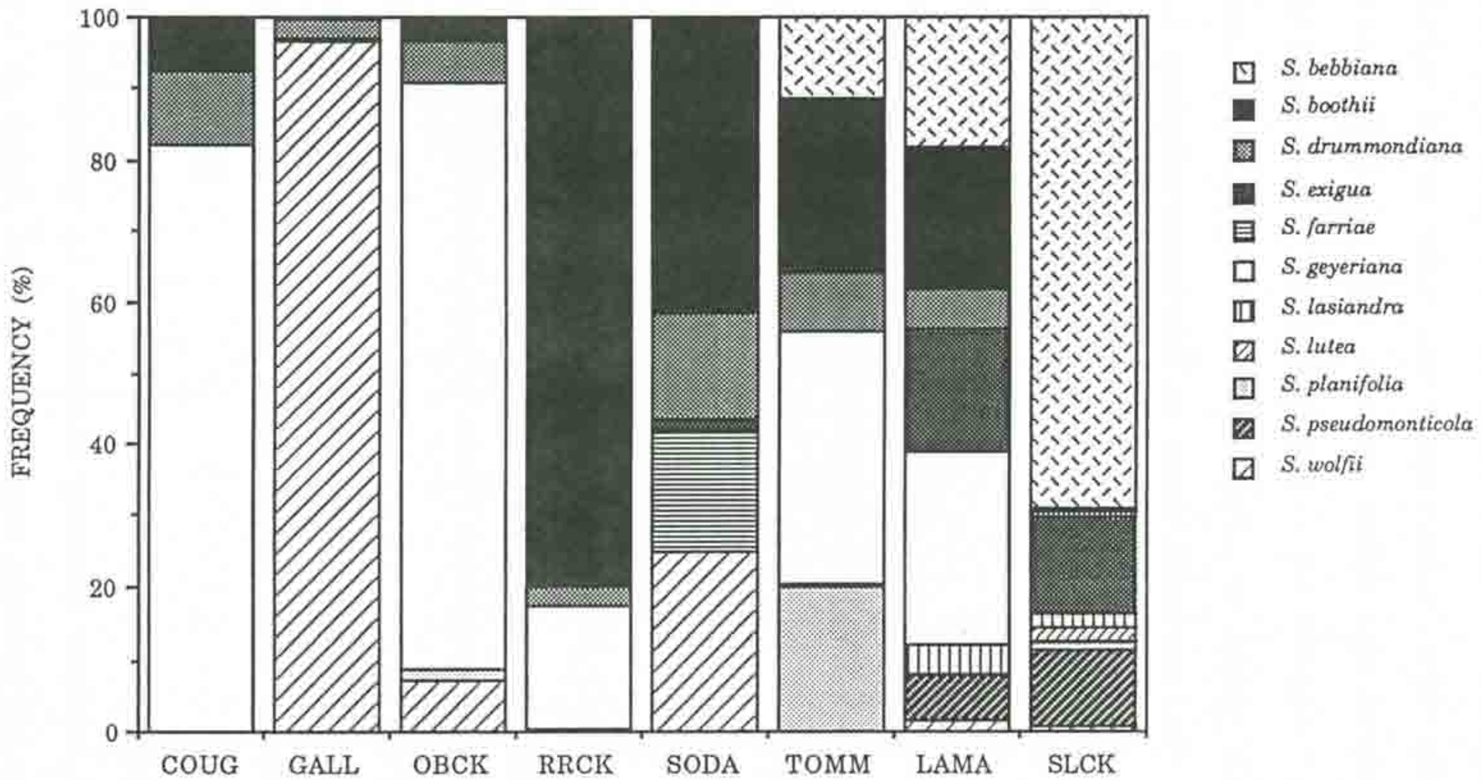

FIGURE 3. Distribution of 11 species of willow among the eight sites in 1990. (COUG=Cougar Creek, GALL=Gallatin River, OBCK=Obsidian Creek, RRCK=Red Rock Creek, SODA=Soda Butte Creek, TOMM=Tom Miner Creek, LAMA=Lamar Valley, SLCK=Slough Creek).

Creek site was dominated by Booth willow (S. boothii) and the Gallatin River site was comprised almost entirely of Wolf willow (S. wolfii). Slough Creek was dominated by Plane-leaf willow (S. planifolia). No single species dominated the Soda Butte, Tom Miner, or Lamar sites. The number of species recorded at each site varied: Cougar Creek (3), Gallatin River (4), Obsidian Creek (5), Red Rock Creek (4) Soda Butte Creek (5), Tom Miner Creek (6), Lamar Valley (8), and Slough Creek (9).

The frequency of willow shrubs which had experienced intense browsing varied considerably among sites, and frequencies were ranked in the same order as the number of species/site listed in the preceding paragraph: Cougar (6.35%), Gallatin (3.5%), Obsidian (31.7%), Red Rock (69.1%), Soda Butte (100%), Tom Miner (51.1%), Lamar (85.7%), and Slough (80%) (Fig. 4). Because these values varied little between years, they represent both years combined. There did not appear to be a consistent relationship between the mean height of each willow species (Fig. 5) and the frequency with which each species was severely browsed.

The relationship between total bird density at each site and frequency of intensely browsed shrubs is nonlinear (Fig. 6). A curve fit to the eight points using a third order polynomial equation has an $r^2=0.621$, and a significance level of $p=0.23$.

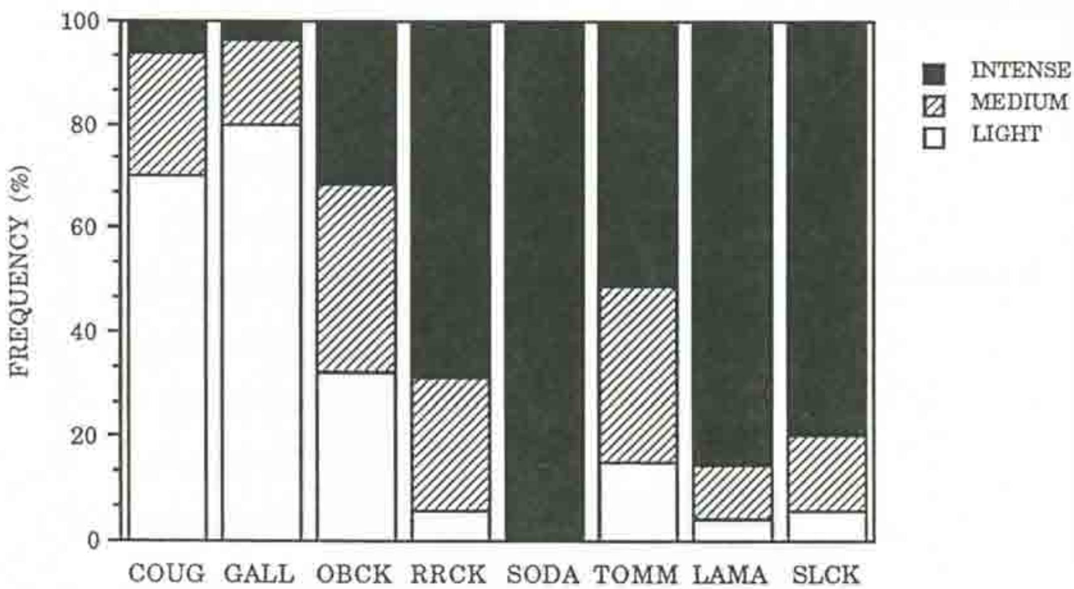

FIGURE 4. Frequency of shrubs in each site categorized according to the intensity of browsing experienced. Data were collected in 1989 and 1990 in COUG, GALL, RRCK, SODA, and TOMM, and in 1990 only in LAMA and SLCK. (COUG=Cougar Creek, GALL=Gallatin River, OBCK=Obsidian Creek, RRCK=Red Rock Creek, SODA=Soda Butte Creek, TOMM=Tom Miner Creek, LAMA=Lamar Valley, SLCK=Slough Creek).

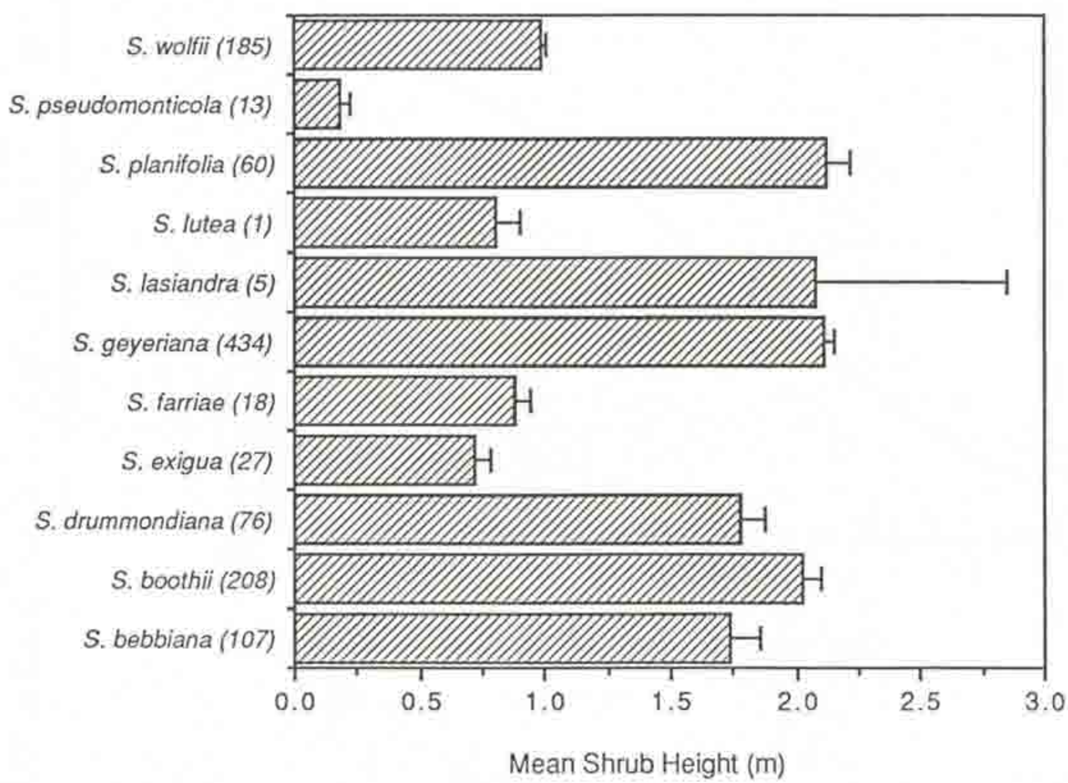

FIGURE 5. Mean heights of 11 willow species identified in the eight study sites. Data were collected in 1989 and 1990. Sample sizes are shown in parentheses.

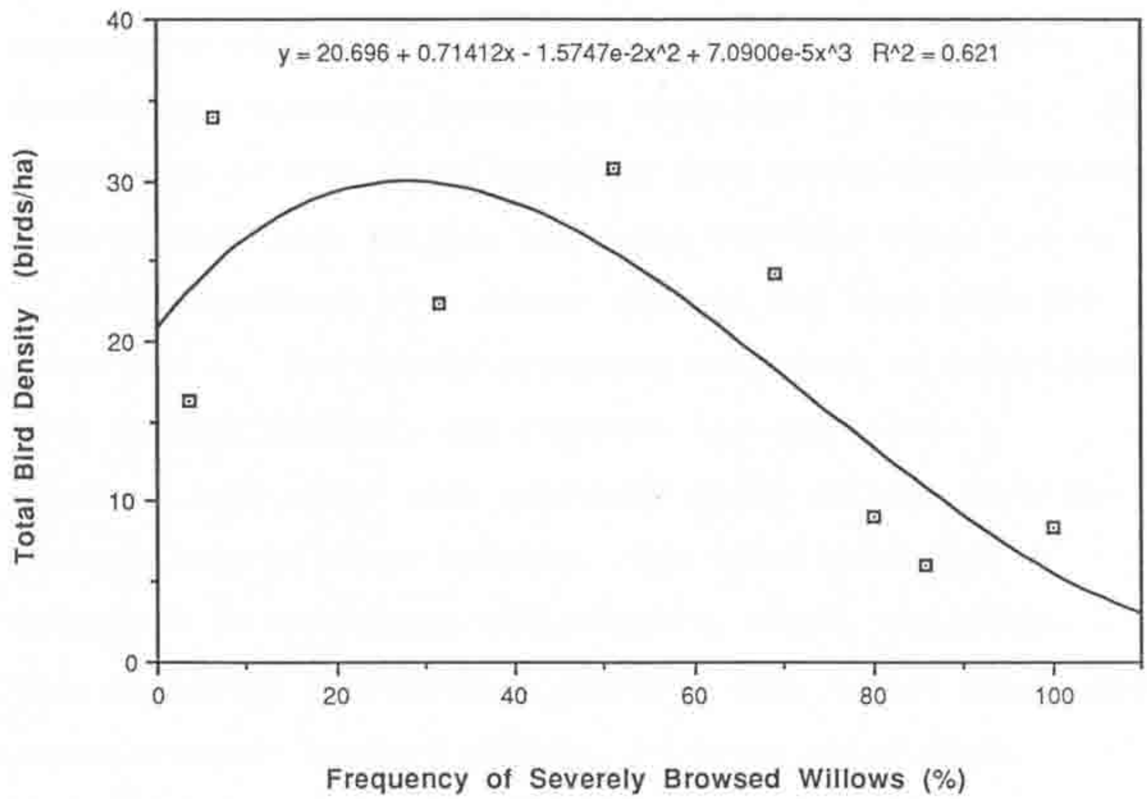

FIGURE 6. Plot of the relationship between total number of species of birds and mean frequency of intensely browsed shrubs. Curve was fit using a third order polynomial.

Principal Components Analysis reduced the 14 original variables to four principal components (PCs) with eigenvalues greater than 1.00. These four PCs explained 69.3% of the variation in the data. Results are summarized in Table 6.

The first principal component is most strongly correlated with SL80120, SL4080, -DCTR, SL0040, SD0040, SD4080, and SL120160 (Mnemonics explained in Table 3). It represents an ecological gradient from sparsely distributed willows with less foliage and fewer branches below 1.6 m, to crowded willows with denser foliage and more branches below 1.6 m. The second principal component is correlated with SDSHHT, SHRUBHT, and CVMAXHT. It represents a gradient from sites with uniformly short willows to sites with willows of mixed heights. The third principal component is correlated with -PCAREX, PFORB, and UTIL3. This component represents a gradient from wetter sites with fewer severely-browsed willows, to drier sites that experience more browsing. The fourth principal component is correlated with PFORB, and may represent a soil and hydrologic gradient.

The plots generated by plotting the scores of the first and second principal components show separation among the sites based on the random data from both years, and separation among species based on the bird-centered data from both years (Figs. 7a and 7b).

TABLE 5. Results of Principal Components Analysis of 14 habitat variables measured in 1989 and 1990. Variables which are highly correlated with each principal component are underlined.

Statistic	Principal Component 1	2	3	4
Eigenvalue	4.33	2.40	1.55	1.42
% of Variance	30.93	17.16	11.09	10.11
Cumulative %	30.93	48.09	59.18	69.29
$.5/(\text{eigenval})^{.5}$	0.24	0.32	0.40	0.42
		Loadings		
CVMAXHT	0.07	<u>0.34</u>	-0.01	-0.34
SHRUBHT	0.10	<u>0.50</u>	-0.18	0.27
SDSHHT	-0.02	<u>0.55</u>	-0.08	0.02
SL0040	<u>0.35</u>	-0.29	-0.15	0.03
SD0040	<u>0.34</u>	0.02	0.16	-0.32
SL4080	<u>0.39</u>	-0.24	-0.02	0.12
SD4080	<u>0.31</u>	0.15	0.14	-0.13
SL80120	<u>0.39</u>	0.04	-0.06	0.29
SL120160	<u>0.29</u>	0.27	-0.17	0.36
UTIL3	-0.15	0.07	<u>0.41</u>	-0.12
PFORB	-0.13	-0.03	<u>0.44</u>	<u>0.57</u>
PLITT	0.22	0.22	0.30	-0.31
PCAREX	-0.12	-0.05	<u>-0.66</u>	-0.09
DCTR	<u>-0.38</u>	0.17	0.08	0.05

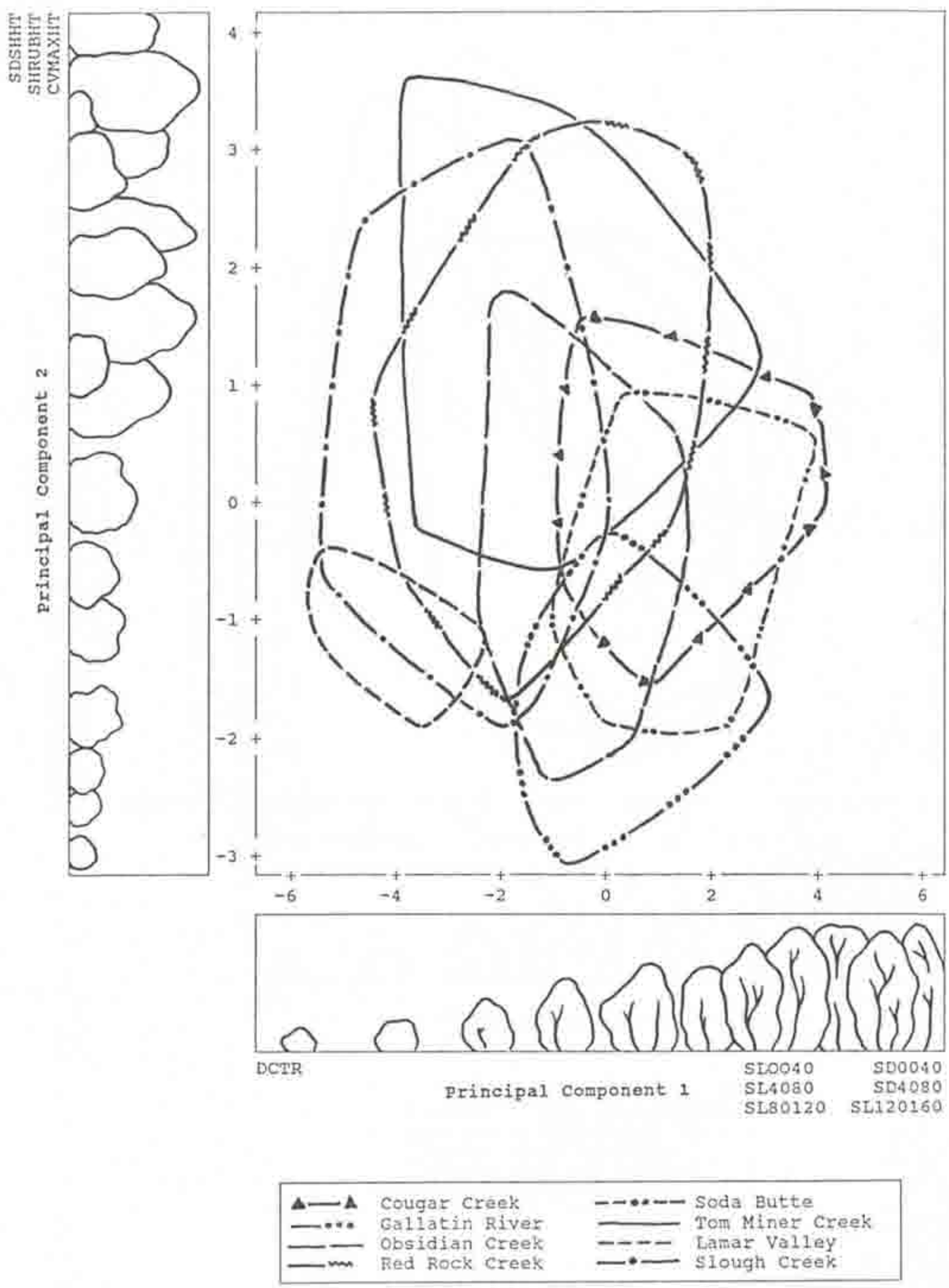

FIGURE 7a. Scores of data from random plots, plotted by site along the first two principal components.

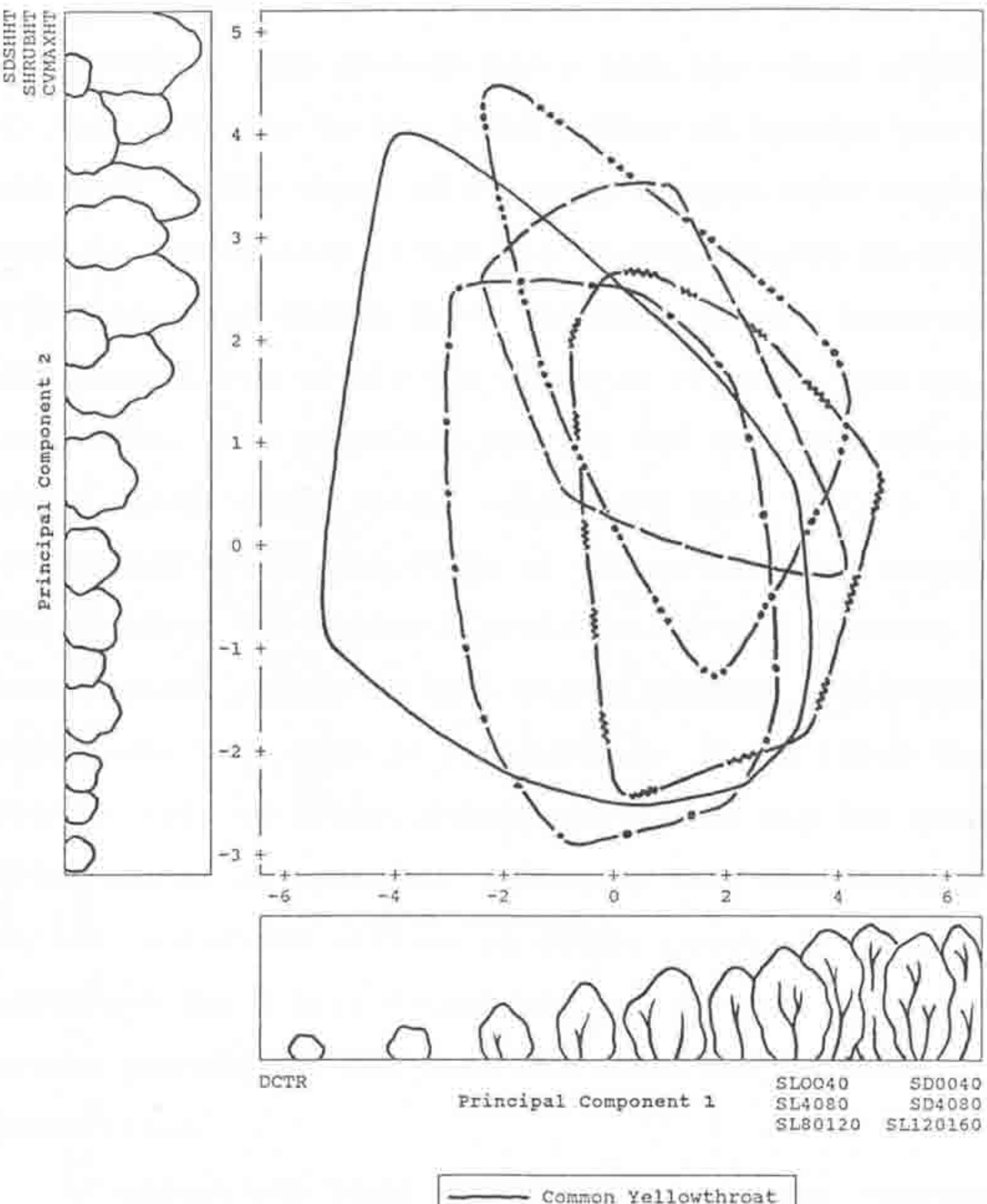

FIGURE 7b. Scores of data from bird-centered plots, plotted by species along the first two principal components.

DISCUSSION

1. Species Lists, Species Densities, and Relationship to Browsing. The species lists from the eight sites (Table 4) vary not only in the total number of species per site, but also in the types of riparian species they support. Most of the species listed are to some degree dependent on riparian zones during their breeding season; however, few are generalists within the range of riparian habitat available. The Lincoln's Sparrow was the only species found in all eight sites, suggesting that it is a generalist within the range of willow habitats sampled. Two species, the Willow Flycatcher and the Northern Waterthrush, appear to have strict habitat requirements which make them rare in Yellowstone. These birds were present only at Cougar Creek, which also had the greatest total number of species. I believe that dense stands of taller, unbrowsed willows at Cougar Creek may have attracted the Willow Flycatcher, while dense willows around oxbows and sloughs may have attracted the Northern Waterthrush.

Although all eight sites were within the "montane" elevation zone as described by McIneaney (1988), differences among sites in terms of species of birds may be related to elevation. Finch (1989) found that vegetation in "lowland" riparian zones (2050-2250m) in southeastern Wyoming was more complex structurally than in riparian zones at higher elevations (2290-2990m), and that both bird species richness and abundance were greatest in lowland riparian habitats. However, this pattern is not evident in my data; the sites with the lowest numbers of bird species were Slough Creek (lowest in elevation: 1900m), Lamar Valley (intermediate in elevation: 2050m), and Soda Butte Creek (highest in elevation: 2300m) (see Table 1). Limiting the study sites to large willow stands may have minimized the effects of elevation.

Brown-headed Cowbirds were present at most sites, and I observed parasitized nests of Yellow Warblers and Warbling Vireos at Cougar Creek both years. Birds nesting in riparian zones may be particularly vulnerable to brood parasitism by cowbirds because of the large amount of edge available and because of the relatively high density of nests. Further research is needed to measure the effect of brood parasitism on the reproductive success of these birds. Even those birds which recognize cowbird eggs, such as the Yellow Warbler, may experience a higher energetic cost of reproduction by starting a new nest or covering the parasitized clutch and re-laying (Bent 1963). However, if food is not limited, then the cost of re-nesting may be negligible (K. Sullivan, pers. comm.).

Although the high correlation between total bird densities and frequency of severely browsed willows is not statistically significant, the curvilinear relationship shown in Fig. 6 suggests that songbirds can tolerate and may actually benefit from a certain amount of browsing. In this case, peak densities of birds might occur when 20-40% of the willows are severely browsed. This browsing might create edge as well as mixtures of willow species and willow heights, and it might prevent the process by which a tall species such as S. geyeriana shades out other willow species (see Chadde and Kay 1988). Willow stands with an intermediate ratio of shrub cover and gaps maintained by browsing might have higher daily temperatures, thereby making them more favorable for the birds' insect prey.

However, a larger sample of points is needed to support these speculations. The relationship may involve a threshhold of tolerance at a frequency of about 70%, below which browsing does not affect bird assemblages. Above it, however, bird densities drop to the low numbers found at Soda Butte Creek, Slough Creek, and Lamar Valley.

In any case, Fig. 6 suggests that continued, intense browsing has a negative effect on the densities of birds in the study sites. If the eight sites are considered hypothetically as one site at different instants in time, with browsing increasing in time, bird numbers will decrease most drastically after the frequency of intensely-browsed shrubs exceeds about 70%.

2. Distribution of Willow Species and Willow Heights. I believe that the variation among sites in terms of willow species composition (Fig. 3) is primarily a product of varying soil-water dynamics; this is supported by the observations of Patten (1968) and Chadde et al. (1988). Soil-water relationships are influenced by the type and gradient of adjacent community, and by the activities of beaver.

During the research reported here, beaver were active at Cougar Creek, Gallatin River, Obsidian Creek, Red Rock Creek, and Tom Miner Creek. Compared to the sites without beavers, these five sites had greater total numbers of species of birds (Table 4), and greater total densities of birds (Fig. 6). Medin and Clary (1990) compared vegetation structure between a willow-dominated beaver pond habitat and an adjacent non-willow riparian habitat in east-central Idaho, and found that shrub height and shrub biomass values in the beaver pond habitat were about twice those of the non-ponded area. They also reported that the size of the beaver-ponded willow stand increased considerably after construction of dams.

Browsing history may also affect willow species composition in the sites (Chadde and Kay 1988). In my sites, the less heavily browsed sites had fewer species of willow, but because of my small sample size, it is unclear whether this represents an actual trend. In comparisons of vegetation inside and outside of a browsing exclosure along upper Slough Creek in Gallatin National Forest, Chadde and

Kay (1988) found three species of willow inside and four species outside. S. geyeriana dominated within the exclosure (percent cover=79%) but not outside the exclosure (percent cover=15%). The three species of willows inside the exclosure averaged 2.3-3.1 m in height and covered 115% of the area sampled, whereas the four species outside averaged 0.5-1.0 m and covered only 36% of the area. Given that the 11 willow species listed in Fig. 5 vary considerably in their average heights, a low or moderate amount of browsing might promote habitat complexity.

It is likely that willow species in the eight sites vary in their palatability, causing selective browsing by elk and moose. This selectivity may be influenced by forage nutritional quality as well the result of avoidance of plant secondary defensive compounds (Bryant and Kuropat 1980). Patten (1968) found that Salix lutea and S. exigua along the Gallatin River had more dwarfed, clubbed twigs than S. farrae (sic) and S. drummondiana. The data of Chadde and Kay (1988) suggest that S. geyeriana is a preferred species of moose and elk. Singer et al. (1990) suggested that S. boothii is a preferred species of elk on Yellowstone's northern range.

Browsing may change willow palatability by inducing the production of defensive compounds (Chapin et al. 1985). Cates et al. (1991) reported that twigs and leaves from suppressed, browsed plants of S. pseudomonticola showed significantly higher tannin levels than tall, unbrowsed plants. However, tannin content in S. bebbiana twigs and leaves was 42% lower in suppressed, browsed plants than in tall, unbrowsed plants on the northern range.

Further information is needed on the ability of different willows to tolerate browsing during different seasons, and on the effect of intense browsing on willow leaf-out times in the spring. Soda Butte Creek, in which all shrubs were heavily browsed by moose, had the latest leaf-out time of the eight sites. This may be because moose browse these willows almost continually throughout the year (D. Tyers, pers. comm.). Few small twigs were present on willows at this site, and many of the willows were excessively "clubbed" from repeated browsing. Although I did not measure branch and twig characteristics, branch diameters at Soda Butte Creek seemed generally large, whereas the number of branches per unit volume appeared small.

3. Principal Components Analysis and Plots of Principal Component Scores. Principal Components Analysis is a technique to reduce the number of variables in a data set, and thus the results (Table 5) do not test hypotheses or make predictions. Interpretations of the components using the variables with high loadings suggest which variables might be used by the focal birds in habitat selection.

The high correlations of foliage variables, height variables, and the willow spacing variable with the first two principal components indicate that structural features of vegetation are particularly important in explaining the differences among bird assemblages in the sites. Browsing, which is correlated with the third principal component, does not by itself explain these differences, although its effect may be reflected in certain aspects of the structural variables associated with Principal Components 1 and 2.

The plots of principal component scores (Figures 7a and 7b) indicate ways in which the sites and the focal species vary in terms of the first two principal components. The amount of overlap among polygons reflects degree of similarity, and the size of each polygon reflects the range of choices available along the two gradients pictured. There was more overlap among the five focal species than I expected, given my observations of these birds during two breeding seasons. Ecological separation of the focal species may be related to other, unmeasured variables. Hutto (1981) concluded that absolute and relative foraging heights provided the greatest ecological separation of Common Yellowthroats, Yellow Warblers, Wilson's Warblers, and MacGillivray's Warblers in a willow stand just south of Yellowstone. His results suggest that competition may influence species assemblages in riparian communities.

I suspect that the "true" habitat polygons of at least two of these species--the Warbling Vireo and the Yellow Warbler--extend beyond the range of habitats measured in this study. These species are common in a wide variety of tall, deciduous shrubs and trees such as aspen, alder, and cottonwood.

These results are not consistent with those of a similar study by Finch (1989). Her plots of principal component scores indicated that the Wilson's Warblers used a very narrow range of riparian habitats, as did Common Yellowthroats and Lincoln's Sparrows. Yellow Warblers used an intermediate range of habitats, and Warbling Vireos showed quite high variability in habitat use. The most likely reason for this inconsistency is that Finch's study sites were scattered among three elevational zones, and included cottonwood-willow associations, mixed willows and shrubs, and subalpine willow stands.

While I expected the "available habitat" polygons for Lamar Valley and Gallatin River to be relatively small, I did not expect that the Slough Creek polygon to be so large. I can only speculate that at this site, the distribution pattern of the willows was not captured by my measurements. I measured distances between a "center" shrub and the four closest shrubs. The willows at Slough Creek were in clumps, with large spaces in between. Because these clumps provided the four distance measures needed, the longer distances were rarely recorded; however, I think that this high level of dispersion of tall willows is an important reason why the site had so few birds.

It is notable that Soda Butte Creek and Cougar Creek overlap as much as they do, given that these sites were so different in terms of bird densities and the intensity of browsing experienced. Incorporation of the third principal component as a third axis would separate these two sites in terms of their browsing histories. Also, variables which were not measured in this study (e.g., insect abundance) might have been useful in distinguishing these two sites.

In general, insect numbers and insect species composition are strongly influenced by abiotic factors such as temperature regime, moisture gradient, relative humidity, light, and wind. The temperature regime is a particularly good indicator of a site's potential insect population, since higher temperatures within a species' range of tolerance generally result in optimal conditions for reproduction and development. Biotic factors such as predation, competition, and host plant density also affect insect assemblages (Barbosa and Wagner 1989). As discussed previously, browsing could affect both the temperature regime and the density of host plants at a site.

SUMMARY AND CONCLUSIONS

The number of bird species and the densities of five focal birds varied considerably among the eight sites, and the proportion of severely browsed willows at the eight sites ranged from 3.5% to 100%. The two sites with all five focal species (Cougar Creek and Tom Miner Creek) also had the highest total densities of birds. However, at Cougar Creek only 6.5% of the willows were severely browsed, whereas at Tom Miner Creek, 51% of the willows were severely browsed. The relationship between browsing and bird densities is nonlinear; bird numbers may actually increase with a low or moderate amount of browsing, but when more than about 70% of the willows are severely browsed, bird numbers drop.

Principal Components Analysis of 14 habitat variables indicates that the study sites varied primarily in terms of distances between shrubs, foliage at certain height intervals, shrub heights, and height heterogeneity. Browsing history may be reflected in the values of these variables, since they might be influenced by the removal of foliage and twigs.

Common Yellowthroats and Lincoln's Sparrows occupied the widest array of avialable habitat, whereas Warbling Vireos, Yellow Warblers, and Wilson's Warblers were associated with willows of specific heights, foliage at certain levels, and certain willow spacing. These structural variables are thus useful in explaining the differences among sites in terms of bird assemblages. Shrub characteristics which may be important but were not measured include twig diameters and twig densities. Site level characteristics that are believed important include dispersion of willow clumps, timing of leaf-out, soil-water dynamics, and food abundance. Landscape level features that should be considered include type and gradient of adjacent community and width of the riparian zone. Because of these larger scale influences, not all willow stands have the same potential in terms of vegetation and birds, no matter how little browsing they experience.

CHAPTER 3

PREDICTING PRESENCE/ABSENCE OF BREEDING BIRDS IN WILLOW STANDS USING PLOTS OF PRINCIPAL COMPONENT SCORES

INTRODUCTION

Hutchinson (1958) defined the fundamental niche as an "n-dimensional hypervolume," composed of all the ranges of tolerance of a species. Thus, describing a species's niche involves measuring numerous aspects of the habitat where it is found, as well as its interactions with other species. The multidimensionality of the niche as defined by Hutchinson (1958) provided the conceptual foundation for the use of multivariate statistical techniques in measuring and describing wildlife habitat.

MacArthur and MacArthur (1961) emphasized the influence of foliage height diversity on habitat selection by birds, and MacArthur et al. (1962) used foliage profiles from different habitats to make qualitative predictions of which birds would be common, uncommon, or absent in those habitats. James (1971) used multivariate techniques to ordinate birds along gradients of vegetational structure. The relative positions of the species were located within multidimensional space, and analyses of the habitat data suggested a distinct multivariate habitat profile for each species.

Numerous investigators since James (1971) (e.g., Anderson and Shugart (1974), Whitmore (1975), Dueser and Shugart (1978), Dueser and Shugart (1979)) have used multivariate techniques to identify ecological factors separating species' niches and to discover which habitat variables are most useful as predictors of species presence, density, or abundance. The ability to make such predictions is highly desirable for wildlife managers, who save time and money if they have simple, reliable models with which to predict wildlife population responses to habitat changes. These responses may be in the form of occurrence, physiological condition, abundance, distribution, or other responses of interest (Schamberger and O'Neil 1986).

The use of habitat models has increased considerably in recent years (Verner et al. 1986, Haas 1991), and with this proliferation has come the task of model testing. The testing or "validation" of a predictive model not only shows how well the model simulates reality, but also indicates what additional data might improve the model. Although many wildlife habitat models have been developed and used, few have been adequately tested (Lancia et al. 1982).

Three main criteria can be addressed in evaluations of predictive models: (1) reliability, or the proportion of model predictions that are empirically correct, (2) accuracy, or the degree to which a simulation reflects reality, and (3) generality, or the capability of the model to represent a broad range of similar systems (Haas 1991). Model testing with independent data--that is, data not used in model construction--is essential to determine whether the model is applicable in situations beyond that used to construct the model (Capen et al. 1986).

Evaluation of predictive models by investigators such as Bart et al. (1984), Maurer (1986), and Morrison et al. (1987) indicate that models are subject to numerous pitfalls. Models are not often general; that is, they do not often perform well outside of the spatial and temporal boundaries in which they were developed. Thus, models built from short-term data sets are not particularly suitable to address long-term questions. Also, some variables which could be strong predictors are inevitably difficult or impossible to measure accurately. Thus, choosing variables to include in a model is not always based entirely on biological factors. Habitat Suitability Index (HSI) models, for example, incorporate only those variables (1) to which the species responds, (2) that can be measured or estimated readily, (3) whose value can be predicted for future conditions, (4) that are vulnerable to change during the course of the project, and (5) that can be influenced by planning and management decisions. These criteria might exclude from a model such variables as weather, predation, and competition, which could then result in overemphasis of more easily measured variables such as vegetation physiognomy, floristics, overall habitat structure, and distance to water or important landforms (Schamberger and O'Neil 1986).

Even if a model does perform well in predicting presence or abundance, it does not indicate the condition of the population. Van Horne (1983) believes that factors such as reproductive success or mean body weight might be better indicators of habitat quality than density, presence, or abundance.

Morrison et al. (1987) evaluated multivariate models which predicted abundances of 21 species of birds using "same place-different time" tests as well as "different place-different time" tests. The former underestimated bird abundances by 25-50%, whereas the latter underestimated by 50-75%. However, the models were successful in predicting presence-absence of most species.

The objective of this segment of the research was to use Principal Components Analysis, a multivariate technique, to develop and evaluate predictive models that relate presence or absence of five focal species (Common Yellowthroat, Lincoln's Sparrow, Warbling Vireo, Wilson's Warbler, and Yellow Warbler) to aspects of vegetation structure in eight study sites. Evaluation included both "same place-different time" tests and "different place-different time" tests. The eight study sites were chosen to represent responses of willow stands to different intensities of browsing by elk and moose.

METHODS

1. Model Foundation. All statistical analyses were conducted using PC/SAS Version 6.0 (SAS Institute, Inc. 1988). Principal Components Analysis of 12 habitat variables measured in random plots in six sites in 1989 was used to generate a smaller number of new, uncorrelated variables which explained a high proportion of the variation in the data. The eigenvectors of these principal components were used as coefficients to score all random and bird-centered data collected in 1989 and 1990. Two-dimensional plots of these scores were then used to test the ability of the first two principal components to predict presence or absence of each focal species at each site. I used the first two principal components for these tests because they explain more of the variation in the data than any other pair of components.

2. "Same place-different time" Model Development and Validation. This modelling effort involved data from six sites which were sampled during two different years: Cougar Creek, Gallatin River, Obsidian Creek, Red Rock Creek, Soda Butte Creek, and Tom Miner Creek.

First, scores of the bird-centered data collected in

1989 were pooled from the six sites and plotted by species along principal components 1 and 2. Each cluster of points from the same species was enclosed in a hand-drawn polygon to show the habitat selected in 1989.

Scores of the random data collected in 1990 were then plotted along the first two principal components, and polygons were drawn to enclose points from each of the six sites. The 1990 "site" polygons were then overlain on the 1989 "species" polygons to evaluate overlap. Overlap of a site polygon and a species polygon was interpreted as "predicted presence" of that species in that site. Non-overlap was interpreted as "predicted absence." These predicted species presences and absences were then compared to observed presences and absences in 1990.

3. "Different place-different time" Model Development and Validation. Scores of the bird-centered data collected in 1989 were pooled for Cougar Creek, Gallatin River, Obsidian Creek, Red Rock Creek, Soda Butte Creek, and Tom Miner Creek, and were plotted by species along principal components 1 and 2. Each cluster of points from the same species was enclosed in a hand-drawn polygon to show the habitat selected in 1989.

Scores of the random data collected in 1990 at two new sites, Lamar Valley and Slough Creek, were then plotted along the first two principal components, and polygons were drawn to enclose points from these two sites. The 1990 "new site" polygons were then overlain on the 1989 "species" polygons to evaluate overlap. Overlap of a site polygon and a species polygon was interpreted as "predicted presence" of that species in that site. Non-overlap was interpreted as "predicted absence." These predicted species presences and absences were then compared to observed presences and absences of focal species at Lamar Valley and Slough Creek in 1990.

RESULTS

1. Model Foundation. Four principal components with eigenvalues greater than 1.00 explained 73.1% of the variance in the 1989 random data (Table 6). The ecological interpretations of these variables, based on those original variables which are most highly correlated with the individual principal components, are similar to those described in Chapter 2.

2. "Same place-different time" Model Development and Validation. The polygons generated by plotting scores from bird-centered data collected in six sites in 1989 are shown in Fig. 8a, and the polygons generated by plotting scores from random data collected at the same sites in 1990 are shown in Fig. 8b. The usefulness of overlaying 1990 random habitat polygons and 1989 bird-centered habitat polygons to predict presence-absence of focal birds in 1990 varied among the five focal species (Table 7). The presence or

TABLE 6. Results of Principal Components Analysis of 12 habitat variables measured in 1989 at random points in Cougar Creek, Gallatin River, Obsidian Creek, Red Rock Creek, Soda Butte Creek, and Tom Miner Creek. Variables which are highly correlated with individual principal components are underlined.

	Principal Component			
Statistic	1	2	3	4
Eigenvalue	3.39	3.06	1.32	1.00
% of variance	28.22	25.53	11.04	8.34
Cumulative %	28.22	53.75	64.79	73.13
$.5/(\text{eigenval})^{.5}$	0.27	0.28	0.43	0.50
MAXHT	-0.01	0.50	-0.17	-0.15
PLITT	0.18	0.23	0.35	0.53
PCAREX	-0.15	-0.03	-0.46	0.69
SHRUBHT	-0.17	0.46	-0.07	-0.14
DCTR	-0.42	0.04	0.10	0.36
SDSHHT	-0.28	0.33	0.06	-0.06
SL0040	0.46	-0.07	-0.03	-0.00
SD0040	0.33	-0.02	-0.17	0.15
SL4080	0.46	0.05	0.10	0.09
SL80120	0.32	0.34	0.02	0.12
SL120160	0.11	0.49	-0.05	0.00
UTIL3	-0.08	0.01	0.76	0.10

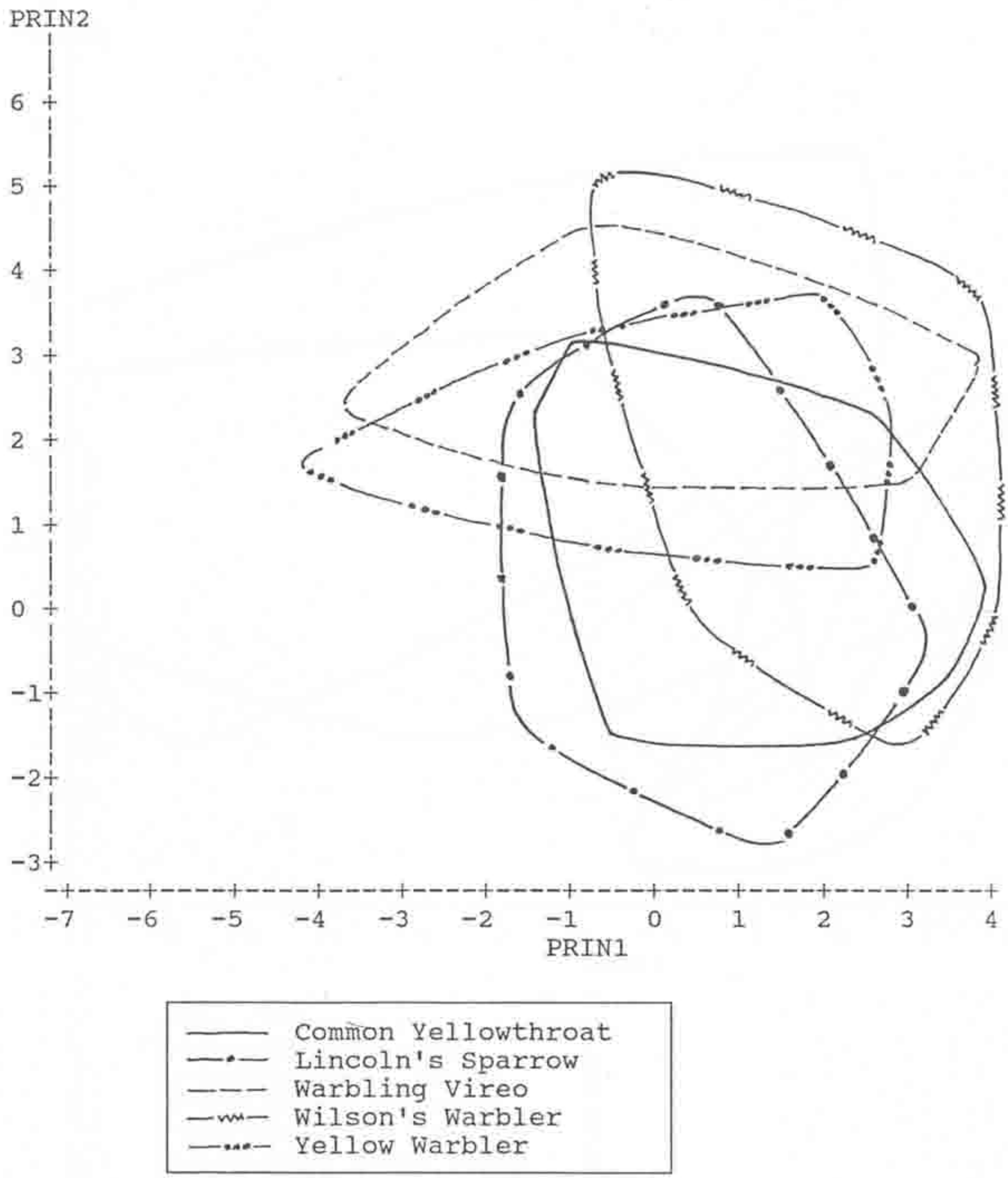

FIGURE 8a. Principal component scores from bird-centered data collected at six sites in 1989, plotted along the first two principal components for use in the "same place-different time" and "different place-different time" validations.

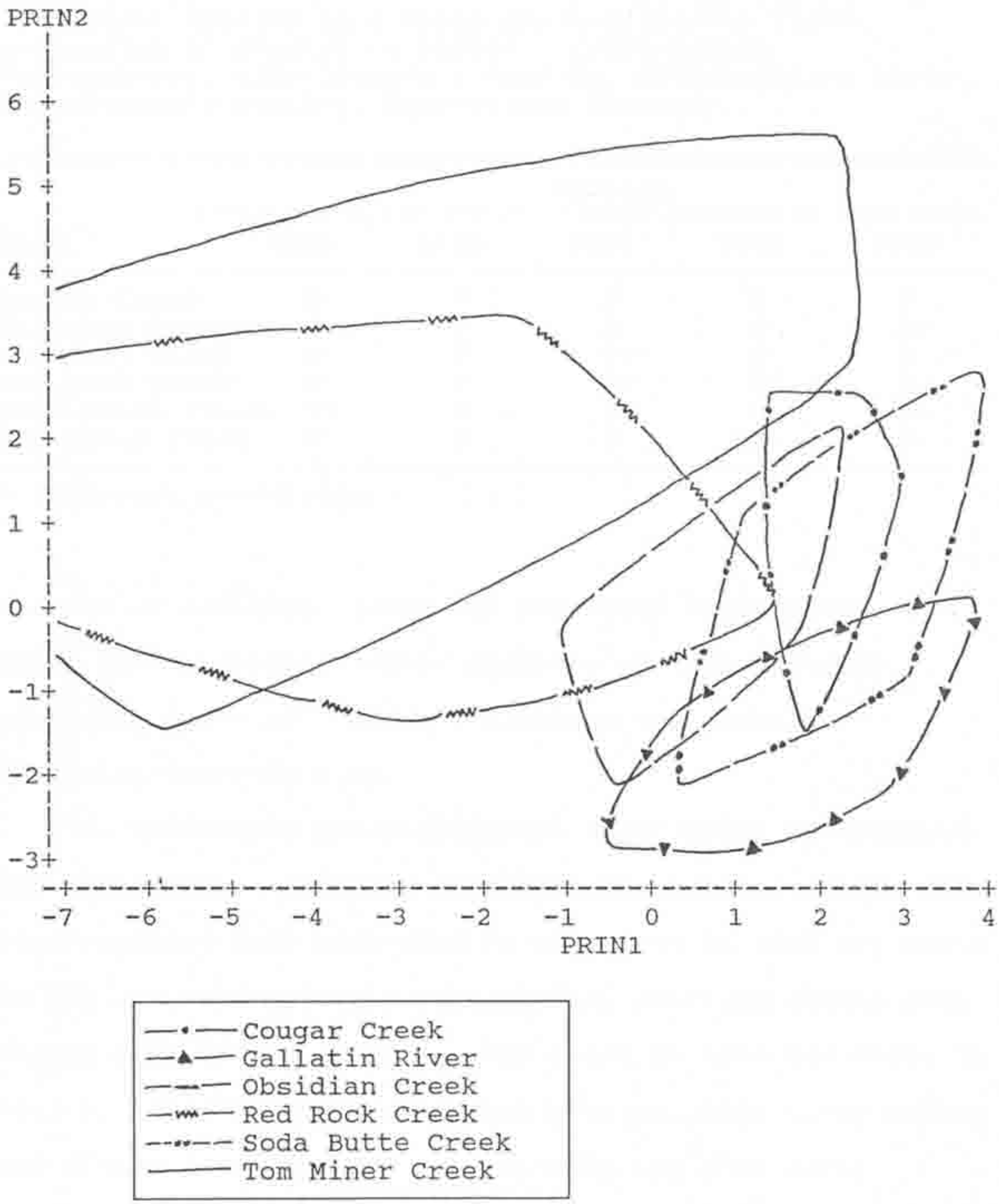

FIGURE 8b. Principal component scores from random data collected at six sites in 1990, plotted along the first two principal components for use in the "same place-different time" validation. Two observations were out of range.

TABLE 7. Predicted presence (P) and absence (A) of the five focal species in a "same place-different time" evaluation of predictive models. (CoYe=Common Yellowthroat, LiSp=Lincoln's Sparrow, WaVi=Warbling Vireo, WiWa=Wilson's Warbler, YeWa=Yellow Warbler).

	Species				
Site	CoYe	LiSp	WaVi	WiWa	YeWa
Cougar Creek	P	P	P	P	P
Gallatin River	P	P	A	P	A*
Obsidian Creek	P	P	P*	P	P
Red Rock Creek	P	P	P*	P*	P
Soda Butte Creek	P*	P	P*	P	P*
Tom Miner Creek	P	P	P	P	P

* Incorrect prediction

absence of Warbling Vireos was predicted incorrectly in three sites, whereas Yellow Warblers were incorrectly predicted twice and Wilson's Warblers and Common Yellowthroats once each.

3. "Different place-different time" Model Development and Validation. Polygons generated by plotting scores from bird-centered data collected in six sites in 1989 are shown in Fig. 8a, and polygons generated by plotting scores from random data collected at two new sites in 1990 are shown in Fig. 9. The 1990 random habitat polygons from Lamar Valley and Slough Creek did not overlap with any 1989 focal species polygons; therefore, all species were predicted to be absent (Table 8). However, Yellow Warblers were present at Slough Creek, and Common Yellowthroats and Lincoln's Sparrows were present at both sites (Figures 2a and 2b).

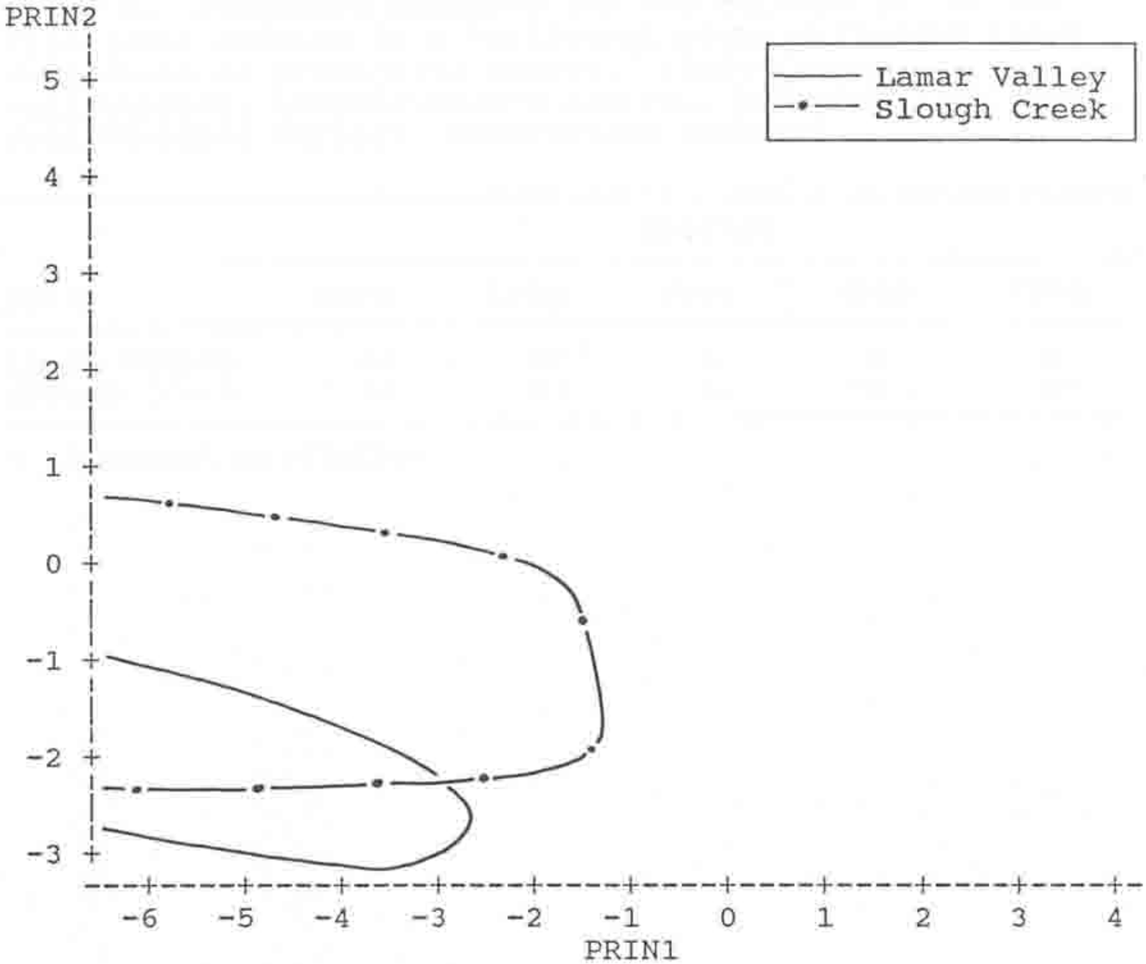

FIGURE 9. Principal component scores from random data collected at two new sites in 1990, plotted along the first two principal components for use in the "different place-different time" validation. Eleven observations were out of range.

TABLE 8. Predicted presence (P) and absence (A) of the five focal species in a "different place-different time" evaluation of predictive models. (CoYe=Common Yellowthroat, LiSp=Lincoln's Sparrow, WaVi=Warbling Vireo, WiWa=Wilson's Warbler, YeWa=Yellow Warbler).

	Species				
Site	CoYe	LiSp	WaVi	WiWa	YeWa
Lamar Valley	A*	A*	A	A	A
Slough Creek	A*	A*	A	A	A*

* Incorrect prediction

DISCUSSION

1. "Same place-different time" Validation. The "same place-different time" test (Table 7) generated seven incorrect predictions for four of the five focal species.

The model worked well for Lincoln's Sparrows. This species is essentially a generalist within the sites measured, and is thus well-suited to the polygon overlay technique. However, another apparent generalist, the Common Yellowthroat, was incorrectly predicted as present at Soda Butte Creek. There is no obvious explanation for this error.

The Wilson's Warbler was incorrectly predicted as present at Red Rock Creek. This species is present in the Red Rock Lakes area, but was never seen in the transect established for this study. Based on observations made during fieldwork, I speculate that this species prefers riparian areas that are adjacent to conifers. Wilson's Warblers were often observed foraging in and singing from adjacent conifers at Soda Butte Creek, Cougar Creek, Obsidian Creek, and Tom Miner Creek.

Yellow Warblers were incorrectly predicted as absent at Gallatin River. In fact, this species was represented by only one pair which nested in the only clump of tall willows present within the transect. Apparently this clump was not included in the randomly-located 0.04-ha plots. There is no obvious explanation for the incorrect prediction of presence of Yellow Warblers at Soda Butte Creek. I speculate that this site is unsuitable because intense browsing seems to have created a very high ratio of branches to twigs and leaders within the shrubs. These shrubs may be unsuitable as nest sites for Yellow Warblers, which, according to my observations, nest 1-2 m up in willows with dense foliage and twig growth.

The presence of Warbling Vireos was incorrectly predicted at three sites. It is possible that most of the sites chosen for this study represented marginal habitat for Warbling Vireos, and that their "true" habitat polygons include riparian zones with much taller vegetation (e.g., aspen and cottonwood). Tom Miner Creek was the only site with a high density of Warbling Vireos (Fig. 2a); this site not only had tall willows but also had adjacent stands of aspen, alder, and conifers. I do not believe that the model for Warbling Vireos is reliable enough to use without incorporating measurements from a wider range of riparian vegetation.

These models might be improved by the addition of a number of other habitat variables measured at scales other than the 0.04-ha plot, such as branch:twig ratios within shrubs, dispersion of willow clumps, insect abundance (e.g., Blenden et al. 1986, Brush and Stiles 1986), thermal regimes within sites and within shrubs, and aspects of adjacent habitat. However, it should be noted that complex, all-inclusive models can become cumbersome and less general (Haas 1991). The models presented here could perhaps be improved by adding a small number of new variables, while eliminating or combining some of the variables that were used. For example, the four 0.4-m height intervals used for foliage measurements could be combined into 2 0.8-m intervals, or into some index of foliage height diversity.

It is possible that not all suitable habitat is occupied by each species; that is, willow stands in northern Yellowstone may not be "saturated." This seems quite possible, given that densities of certain species in certain sites varied considerably during the two years of the study (Figures 2a and 2b).

2. "Different place-different time" Validation. The models failed to predict any species's presence correctly in the "different place-different time" validation. I believe that the main factor contributing to this failure is the fact that the two new sites, Lamar Valley and Slough Creek, were characterized by habitat outside the gradient of vegetation structure used to develop the models. Both sites were severely browsed, the willows tended to be in widely-dispersed clumps, and many were kept short and clubbed by repeated browsing. Like many predictive models, the ones developed here did not extrapolate beyond the range of data used to build them. A future model should therefore be constructed to include the random data from Lamar Valley and Slough Creek, so that extrapolation to at least one part of the habitat gradient will be more accurate.

3. General Comments. A potentially more accurate method of prediction from principal component scores is to incorporate habitat features from several scales, such as nest-site scale, shrub scale, site scale, and landscape scale. The 0.04-ha circular plot used for this study provides information at only one scale, and it is not one that is necessarily meaningful to birds. Territories are much larger than this plot size, but nest-trees or nest-sites are much smaller.

A notable shortcoming in the polygon overlay method as used here is that "presence" is predicted even if the random polygon overlaps the species polygon only slightly. There is no mechanism by which to distinguish the degree of overlap between polygons, even though common sense suggests that predictions based on a large degree of overlap (or non-overlap) are more likely to match observations than predictions based on slight overlap or slight separation. It also seems likely that a large degree of overlap between a site polygon and a species polygon could indicate that the species is not only present in that particular site but is also relatively abundant.

I performed a subjective test to examine the relationship between correct predictions and degree of overlap. Table 9 shows that in six of seven incorrect predictions, the amount of overlap between polygons was low or none. While this does not mean that low overlap is equivalent to no overlap, it at least suggests that low overlap should be interpreted with caution. The incorrect prediction of presence of Common Yellowthroats at Soda Butte Creek is not so easily explained. Possibly habitat variables which were not measured in this study are important to this species. Soda Butte Creek was the highest site, the narrowest site, and it leafed out weeks later than the other sites. Perhaps one or more of these factors precluded use of this site by Common Yellowthroats.

Larger sample sizes might increase the probability of correct predictions. In plotting scores of bird-centered data from three study sites, Wiens et al. (1987) found that within the habitat polygons generated for each species in each study region, points generated from sites with similar bird densities tended to clump. Thus the polygons themselves represented gradients of habitat use, and suggested which habitats were most and least desirable. My data do not behave so conveniently; however, if my sample sizes were larger or had I incorporated a wider gradient of riparian zones into this research, such "clusters within clusters" might emerge. If this occurred, then I could base predictions not only on the degree of overlap but also

TABLE 9. Subjective test to examine the relationship between degree of polygon overlap and species density in the "same place-different time" validation. Incorrect predictions are underlined. Site polygons are scores of 1990 random data; species polygons are scores of 1989 bird-centered data.

Site	Species: CoYe	LiSp	WaVi	WiWa	YeWa
	(degree of overlap/species density)				
Cougar	high/low	high/med	low/low	high/med	high/high
Gallatin	med/med	high/med	none/none	low/low	none/low
Obsidian	high/high	high/high	low/none	med/med	low/low
Red Rock	low/low	med/low	low/none	low/none	med/high
Soda Butte	med/none	med/med	low/none	high/low	low/none
Tom Miner	low/med	low/med	high/med	low/low	med/med

on the general quality (as indicated by species density, assuming that density can be an indicator of quality) of the site for a particular species.

LITERATURE CITED

Afifi, A.A., and V. Clark. 1984. Computer-aided multivariate statistics. Lifetime Learning Pub., Belmont, CA.

Anderson, B.W., and R.D. Ohmart. 1986. Vegetation, p. 639-660. In A.Y. Cooperrider, R.J. Boyd, and H.R. Stuart [eds.], Inventory and monitoring of wildlife habitat. U.S.D.I., B.L.M. Services Center, Denver, CO.

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

Balda, R.P. 1975. Vegetation structure and breeding bird diversity, p. 59-80. In D.R. Smith [tech. coord.], Proc. symp. on management of forest and range habitats for nongame birds. U.S.D.A., For. Serv. Gen. Tech. Rep. WO-1.

Barbosa, P., and M.R. Wagner. 1989. Introduction to forest and shade tree insects. Academic Press, San Diego, CA.

Bart, J., D.R. Petit, and G. Linscombe. 1984. Field evaluation of two models developed following the habitat evaluation procedures. Trans. No. Amer. Wildl. and Natur. Resour. Conf. 49:489-499.

Beetle, A.A. 1974. The zootic disclimax concept. J. Range Manage. 27(1):30-32.

Bent, A.C. 1963. Life histories of North American wood warblers: part one. Dover Publications, New York.

Blakesley, J.A. 1986. Avian habitat relationships in riparian zones of northern Utah. M.S. thesis, University of Idaho, Moscow.

Blenden, M.D., M.J. Armbruster, T.S. Baskett, and A.H. Farmer. 1986. Evaluation of model assumptions: the relationship between plant biomass and arthropod abundance, p. 11-14. In J. Verner, M.L. Morrison, and C.J. Ralph [eds.], Wildlife 2000: modelling habitat relationships of terrestrial vertebrates. Univ. Wisc. Press, Madison.

Brush, T., and E.W. Stiles. 1986. Using food abundance to predict habitat use by birds, p. 57-63. In J. Verner, M.L. Morrison, and C.J. Ralph [eds.], Wildlife 2000: modelling habitat relationships of terrestrial vertebrates. Univ. Wisc. Press, Madison.

Bryant, J.P., and P.J. Kuropat. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. Ann. Rev. Ecol. Syst. 11:261-285.

Capen, D.E. [ed.]. 1981. The use of multivariate statistics in studies of wildlife habitat. Rocky Mtn. For. and Range Expt. Sta., U.S. For. Serv. Gen Tech. Rep. RM-87.

Capen, D.E., J.W. Fenwick, D.B. Inkley, and A.C. Boynton. 1986. Multivariate models of songbird habitat in New England forests, pp. 171-175. In J. Verner, M.L. Morrison, and C.J. Ralph [eds.], Wildlife 2000: modelling habitat relationships of terrestrial vertebrates. Univ. Wisc. Press, Madison.

Carothers, S.W., R.R. Johnson, and S.W. Atchinson. 1974. Population structure and social organization of Southwestern riparian birds. Amer. Zool. 14:97-108.

Casey, D., and D. Hein. 1983. Effects of heavy browsing on a bird community in deciduous forest. J. Wildl. Manage. 47(3):829-836.

Cates, R.G., F.J. Singer, and L.J. Mack. 1991. Water stress and secondary metabolite production in suppressed, grazed and intermediate, ungrazed willows, p. 9-10. In Agenda and Abstracts, First Biennial Scient. Conf. the Greater Yellowstone Ecosystem, 16-17 Sept. 1991, Yellowstone National Park, WY.

Caughley, G. 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. Ecology 51(1):53-72.

Caughley, G. 1981. Comments on 'Natural regulation of ungulates (what constitutes a real wilderness?)'. Wildl. Soc. Bull. 9(3):232-233.

Chadde, S., and C.E. Kay. 1988. Willows and moose: a study of grazing pressure, Slough Creek exclosure, Montana, 1961-1986. Research Note No. 24, Montana Forest and Conservation Expt. Sta., School of Forestry, Univ. Montana, Missoula.

Chadde, S.W., P.L. Hansen, and R.D. Pfister. 1988. Wetland plant communities on the northern range of Yellowstone National Park. School of Forestry, Univ. Montana, Missoula. Final contract report to National Park Service, Mammoth, WY.

Chapin, F.S. III, J.P. Bryant, and J.F. Fox. 1985. Lack of induced chemical defense in juvenile Alaskan woody plants in response to simulated browsing. Oecologia 67:457-459.

Chase, A. 1986. Playing God in Yellowstone: the destruction of America's first national park. Atlantic Monthly Press, Boston.

Cody, M.L. 1981. Habitat selection in birds: the roles of vegetation structure, competitors, and productivity. BioScience 31(2):107-113.

Cole, G.F. 1971. An ecological rationale for the natural or artificial regulation of native ungulates in parks. Trans. No. Amer. Wildl. Conf. 36:417-425.

Cope, O.B. [ed.]. 1979. Forum: grazing and stream/riparian ecosystems. Trout Unlimited, Denver.

Despain, D., D. Houston, M. Meagher, and P. Schullery. 1986. Wildlife in transition: man and nature on Yellowstone's northern range. Roberts Rinehart, Boulder, CO.

Dueser, R.D., and H.H. Shugart, Jr. 1978. Microhabitats in a forest-floor: small-mammal fauna. Ecology 59:89-98.

Dueser, R.D., and H.H. Shugart, Jr. 1979. Niche pattern in a forest-floor small-mammal fauna. Ecology 60:108-118.

Finch, D.M. 1989. Habitat use and habitat overlap of riparian birds in three elevational zones. Ecology 70(4):866-880.

Grimm, R.L. 1939. Northern Yellowstone winter range studies. J. Wildl. Manage. 3:295-306.

Haas, C.S. 1991. Empirical evaluation of desert bighorn sheep habitat models. M.S. thesis, Utah State Univ., Logan.

Hanley, T.A., and R.D. Taber. 1980. Selective plant species inhibition by elk and deer in three conifer communities in western Washington. Forest Sci. 26(1):97-107.

Harner, E.J., and R.C. Whitmore. 1981. Robust principal component and discriminant analysis of two grassland bird species habitats, p. 209-221. In D.E. Capen [ed.], The use of multivariate statistics in studies of wildlife habitat. Rocky Mtn. For. and Range Expt. Sta., U.S. For. Serv. Gen Tech. Rep. RM-87.

Hilden, O. 1965. Habitat selection in birds: a review. Ann. Zool. Fenn. 2:53-75.

Hill, E.P. 1982. Beaver, p. 256-281. In J.A. Chapman and G.A. Feldhamer [eds.], Wild mammals of North America: biology, management, economics. Johns Hopkins Univ. Press, Baltimore and London.

Hobbs, N.T., D.L. Baker, J.E. Ellis, and D.M. Swift. 1979. Composition and quality of elk diets during winter and summer: a preliminary analysis, p. 47-53. In M.S. Boyce and L.D. Hayden-Wing [eds.], North American elk: ecology, behavior, and management. Univ. Wyoming Press, Laramie.

Houston, D.B. 1982. The northern Yellowstone elk: ecology and management. MacMillan, New York.

Hutchinson, G.E. 1958. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22:415-427.

Hutto, R.L. 1981. Seasonal variation in the foraging behavior of some migratory western wood warblers. Auk 98:765-777.

Hutto, R.L. 1985. Habitat selection by nonbreeding, migratory land birds, p. 455-476. In M.L. Cody [ed.], Habitat selection in birds. Academic Press, Orlando, FL.

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

James, F.C., and H.H. Shugart. 1970. A quantitative method of habitat description. Aud. Field Notes 24(6):727-736.

Johnson, R.R., and D.A. Jones [tech. coords.]. 1977. Importance, preservation, and management of riparian habitat: a symposium. U.S.D.A., For. Serv. Gen. Tech. Rep. RM-43, Rocky Mtn. For. and Range Exp. Sta., Fort Collins, CO.

Johnson, R.R., C.D. Ziebell, D.R. Patton, P.F. Ffolliott, and R.H. Hamre [tech. coords.]. 1985. Riparian ecosystems and their management: reconciling conflicting uses. U.S.D.A. For. Serv. Gen. Tech. Rep. RM-120.

Kauffman, J.B., and W.C. Kreuger. 1984. Livestock impacts on riparian ecosystems and streamside management implications. . . a review. J. Range Manage. 37(5):430-438.

Kay, C.E. 1990. Yellowstone's northern elk herd: a critical evaluation of the "natural regulation" paradigm. Ph.D. diss., Utah State University, Logan.

Knopf, F.L., J.A. Sedgwick, and R.W. Cannon. 1988. Guild structure of a riparian avifauna relative to seasonal cattle grazing. J. Wildl. Manage. 52(2):280-290.

Lack, D. 1933. Habitat selection in birds, with special reference to the effects of afforestation on the Breckland avifauna. J. Anim. Ecol. 2(2):239-262.

Lancia, R.A., S.D. Miller, D.A. Adams, and D.W. Hazel. 1982. Validating habitat quality assessment: an example. Trans. No. Amer. Wildl. and Nat. Resour. Conf. 47:96-110.

Leopold, A.S. 1963. Study of wildlife problems in national parks. Trans. No. Amer. Wildl. Conf. 28:28-45.

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

MacArthur, R.H., J.W. MacArthur, and J. Preer. 1962. On bird species diversity, II. Predictions of bird census from habitat measurements. Amer. Nat. 96:167-174.

Marcot, B.G., M.G. Raphael, and K.H. Berry. 1983. Monitoring wildlife habitat and validation of wildlife-habitat relationships models. Trans. No. Amer. Wildl. and Nat. Resour. Conf. 48:315-329.

Marcum, C.L. 1979. Summer-fall food habits and forage preferences of a Western Montana elk herd, p. 54-62. In M.S. Boyce and L.D. Hayden-Wing [eds.], North American elk: ecology, behavior, and management. Univ. Wyoming Press, Laramie.

Maurer, B.A. 1986. Predicting habitat quality for grassland birds using density-habitat correlations. J. Wildl. Manage. 50:556-566.

McEneaney, T. 1988. Birds of Yellowstone. Roberts Rinehart, Boulder, CO.

Medin, D.E., and W.P. Clary. 1990. Bird populations in and adjacent to a beaver pond ecosystem in Idaho. Resear. Pap. INT-432. U.S.D.A., U. S. For. Serv., Intermountain Research Station, Ogden, UT.

Morrison, M.L., I.C. Timossi, and K.A. With. 1987. Development and testing of linear regression models predicting bird-habitat relationships. J. Wildl. Manage. 51:247-253.

Mosconi, S.L., and R.L. Hutto. 1982. The effect of grazing on the land birds of a western Montana riparian habitat, p. 221-233. In Proc. of the Wildlife-Livestock Relationships Symposium, April 20-22, 1981, Couer d'Alene, ID. Forest, Wildlife and Range Exp. Sta., Univ. Idaho, Moscow.

Olmsted, C.E. 1979. Aspen utilization by large herbivores in Rocky Mountain National Park and implications for management, p. 1125-1133. In R. Linn [ed.], Proc. of the 1st Conf. on Scient. Research in the National Parks, Nov 9-12, 1976, New Orleans, LA. U.S.D.I., N.P.S. Trans. and Proc. Series No. 5.

Partridge, L. 1978. Habitat selection, p. 351-376. In J.R. Krebs and N.B. Davies [eds.], Behavioural ecology: an evolutionary approach. Sinauer, Sunderland, MA.

Patten, D.T. 1968. Dynamics of the shrub continuum along the Gallatin River in Yellowstone National Park. Ecology 49(6):1107-1112.

Peek, J.M. 1974. On the nature of winter habitats of Shiras moose. Naturaliste Can. 101:131-141.

Peek, J.M. 1980. Natural regulation of ungulates (what constitutes a real wilderness?). Wildl. Soc. Bull. 8(3): 217-227.

Peek, J.M. 1981. Comments on Caughley's comments. Wildl. Soc. Bull. 9(3):234-237.

Petit, K.E., D.R. Petit, and L.J. Petit. 1988. On measuring vegetation characteristics in bird territories: nest sites vs. perch sites and the effect of plot size. Amer. Midl. Nat. 119(1):209-215.

Reynolds, R.T., J.M. Scott, and R.A. Nussbaum. 1980. A variable circular-plot method for estimating bird numbers. Condor 82:309-313.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution 43(1):223-225.

Rotenberry, J.T. 1985. The role of habitat in avian community composition: physiognomy or floristics? Oecologia 67:213-217.

Rotenberry, J.T., and J.A. Wiens. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61:1228-1250.

SAS Institute, Inc. 1988. SAS/STAT User's Guide, Release 6.03 Edition. Cary, NC.

Schamberger, M.L., and L.J. O'Neil. 1986. Concepts and constraints of habitat-model testing, p. 5-10. In J. Verner, M.L. Morrison, and C.J. Ralph [eds.], Wildlife 2000: modelling habitat relationships of terrestrial vertebrates. Univ. Wisc. Press, Madison.

Singer, F.J., J. Whipple, and L. Chorpening. 1988. Draft study plan: a survey of willows and mammal browsing in northeast sector of Yellowstone's northern range. Yellowstone National Park, WY.

Singer, F.J., L. Mack, and R. Cates. 1990. Willow species abundance, herbivory, and the role of secondary compounds on the northern elk winter range, p. 47-51. In F.J. Singer [comp.], Grazing influences on Yellowstone's northern range II: research summaries. Yellowstone National Park, Mammoth, WY.

Taylor, D.M. 1986. Effects of cattle grazing on passerine birds nesting in riparian habitat. J. Range Manage. 39(3):254-258.

Thomas, J.W., C. Maser, and J.E. Rodiek. 1979. Riparian zones in managed rangelands--their importance to wildlife, p. 21-31. In O.B. Cope [ed.], Forum: grazing and stream/riparian ecosystems. Trout Unlimited, Denver.

Tucker, T.L. 1987. Cattle grazing affects nongame wildlife populations and fish habitat in a montane riparian area. M.S. thesis, Colorado State Univ., Fort Collins.

Tyers, D.B. 1981. The condition of the northern winter range in Yellowstone National Park--a discussion of the controversy. M.S. thesis, Montana State Univ., Bozeman.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47:893-901.

Verner, J., M.L. Morrison, and C.J. Ralph [eds.]. 1986. Wildlife 2000: modelling habitat relationships of terrestrial vertebrates. Univ. Wisc. Press, Madison.

Warner, R.E., and K.M. Hendrix [eds.]. 1984. California riparian systems: ecology, conservation, and productive management. Univ. Calif. Press, Berkeley.

Whitmore, R.C. 1975. Habitat ordination of passerine birds of the Virgin River Valley, southwestern Utah. Wilson Bull. 87:65-74.

Wiens, J.A., J.T. Rotenberry, and B. Van Horne. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. Oikos 48:132-147.

Willard, E.E., and C.M. McKell. 1978. Response of shrubs to simulated browsing. J. Wildl. Manage. 42(3):514-519.

Willson, M.F. 1974. Avian community organization and habitat structure. Ecology 55:1017-1029.

Wolff, J.O. 1978. Burning and browsing effects on willow growth in interior Alaska. J. Wildl. Manage. 42(1):135-140.

APPENDIX

Appendix A. Scientific names of avian species mentioned in the thesis.

Common name	Scientific Name
American Robin	Turdus migratorius
Belted Kingfisher	Ceryle alcyon
Black-billed Magpie	Pica pica
Brewer's Blackbird	Euphagus cyanocephalus
Brown-headed cowbird	Molothrus ater
Common snipe	Gallinago gallinago
Common Yellowthroat	Geothlypis trichas
Fox Sparrow	Passerella iliaca
Lazuli Bunting	Passerina amoena
Lincoln's Sparrow	Melospiza lincolnii
MacGillivray's Warbler	Oporornis tolmei
Northern Waterthrush	Seiurus noveboracensis
Red-winged Blackbird	Agelaius phoeniceus
Rufous Hummingbird	Selasphorus rufus
Sandhill Crane	Grus canadensis
Savannah Sparrow	Passerculus sandwichensis
Song Sparrow	Melospiza melodia
Sora	Porzana carolina
Spotted Sandpiper	Actitis macularia
Warbling Vireo	Vireo gilvus
White-crowned Sparrow	Zonotrichia leucocephalus
Willow Flycatcher	Empidonax trailii
Wilson's warbler	Wilsonia pusilla
Yellow Warbler	Dendroica petechia
Yellow-bellied Sapsucker	Sphyrapicus varius
Yellow-headed Blackbird	Xanthocephalus xanthocephalus