The Condor 94:720–733

DESCRIBING WILLOW FLYCATCHER HABITATS: SCALE PERSPECTIVES AND GENDER DIFFERENCES[1]

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Abstract. We compared habitat characteristics of nest sites (female-selected sites) and song perch sites (male-selected sites) with those of sites unused by Willow Flycatchers (*Empidonax traillii*) at three different scales of vegetation measurement: (1) microplot (central willow [*Salix* spp.] bush and four adjacent bushes); (2) mesoplot (0.07 ha); and, (3) macroplot (flycatcher territory size). Willow Flycatchers exhibited vegetation preferences at all three scales. Nest sites were distinguished by high willow density and low variability in willow patch size and bush height. Song perch sites were characterized by large central shrubs, low central shrub vigor, and high variability in shrub size. Unused sites were characterized by greater distances between willows and willow patches, less willow coverage, and a smaller riparian zone width than either nest or song perch sites. At all scales, nest sites were situated farther from unused sites in multivariate habitat space than were song perch sites, suggesting (1) a correspondence among scales in their ability to describe Willow Flycatcher habitat, and (2) females are more discriminating in habitat selection than males. Microhabitat differences between male-selected (song perch) and female-selected (nest) sites were evident at the two smaller scales; at the finest scale, the segregation in habitat space between male-selected and female-selected sites was greater than that between male-selected and unused sites. Differences between song perch and nest sites were not apparent at the scale of flycatcher territory size, possibly due to inclusion of (1) both nest and song perch sites, (2) defended, but unused habitat, and/or (3) habitat outside of the territory, in larger scale analyses. The differences between nest and song perch sites at the finer scales reflect their different functions (e.g., nest concealment and microclimatic requirements vs. advertising and territorial defense, respectively), and suggest that the exclusive use of either nest or song perch sites in vegetation analyses can result in misleading, or at least incomplete, descriptions of a species' habitat. Habitat interpretations for Willow Flycatchers (and perhaps for many passerines) are a function of the gender-specific behavior of the birds observed and the scale of vegetation measurement.

Key words: Willow Flycatcher; Empidonax traillii; *habitat selection; scale; gender differences; riparian; Colorado.*

INTRODUCTION

Features of vegetation influence the manner in which habitats are occupied by birds (Hildén 1965). Structural characteristics, spatial dispersion, and floristics all play a role in avian habitat selection (e.g., Holmes and Robinson 1981, Rotenberry 1985, Wiens et. al. 1987, Knopf et al. 1990). The characteristic habitat dimensions of a species' niche constitute its niche-gestalt (sensu, James 1971) and this fundamental configuration of vegetational structure reflects environmental suitability in terms of song perches, roosting sites, foraging areas, and nesting sites.

Many recent studies of avian passerine habitat selection have examined habitat characteristics based on the vegetation surrounding song perch sites of singing males (James 1971; Whitmore 1975, 1977; Smith 1977; Morrison 1981; Kahl et al. 1985; Sedgwick 1987). It has generally been accepted that male song perch sites—especially those of forest-nesting species—may serve as unbiased and representative locations from which to obtain a view of a species habitat (James 1971, Collins 1981). In open habitats, however, vegetation characteristics at song perch sites may differ from those at foraging or nesting sites (James 1971). Males often sing from the most conspicuous, prominent sites and these locations may give a different view of a species habitat than those used for foraging or nesting. Even for some forest-nesting species, nest and song perch site vegetation structure may differ (Collins 1981). Recent studies of avian habitat selection have been based on the use of either nest sites exclusively (e.g., Holway 1991, Sakai and Noon 1991); or a combination of activity areas such as singing

[1] Received 12 December 1991. Accepted 11 March 1992.

and nesting (Morrison and Meslow 1983); or singing, nesting, and foraging sites (Knopf et al. 1990), suggesting that there is at least a tacit recognition of the potential differences between song perch sites and other activity centers. Despite the implied differences in habitat attributes at specific activity areas (e.g., song perch sites vs. nest sites), such differences have been explicitly tested only once (Collins 1981).

The predominant scale of vegetation measurement, at least in forested communities, is often quite small, incorporating only a small portion of an individual territory. The 0.04-ha circular plot technique is perhaps most frequently used, and a modification of this method has been recommended as a standard methodology for sampling avian habitats (Noon 1981). With this method, various attributes of vegetation structure are measured within a 0.04-ha circle around a central point (e.g., song perch site or nest site). This method is widely accepted, due in part to its ease of application and efficiency. Its ecological validity stems from the fact that plot size (0.04 ha) is smaller than the average territory size for virtually all passerines and thus should include vegetation typical of the species in question without including areas outside of the territory. Moreover, the 0.04-ha scale "should include an adequate sample of the vegetation" (James 1971:215). If the habitat structure within the territory is heterogeneous, however, this scale of measurement could give a biased view of habitat selection, whether song perch sites or nest sites are used as the central point for vegetation sampling. This shortcoming can be overcome by sampling at several points within an individual's territory, but this is seldom done (cf. Collins 1981).

We examined habitat selection in Willow Flycatchers (*Empidonax traillii*) with the foregoing in mind and asked: (1) What is the effect of the choice of site (i.e., nest or song perch) on the final description of the niche-gestalt? and (2) How do different scales of measurement affect the interpretation of a species' habitat characteristics? We described habitat selection of Willow Flycatchers based on analyses at both nest and song perch sites and compared this information to the vegetation structure at sites that were not used by Willow Flycatchers for two consecutive years. We also examined habitat selection based on three scales of measurement—microplot, mesoplot, and macroplot. Our objectives, then, were to describe and interpret habitat selection attributes of Willow Flycatchers based on nest, song perch, and unused site information collected at three different scales of measurement.

STUDY AREA

We studied habitat selection of Willow Flycatchers at Arapaho National Wildlife Refuge (NWR), located approximately 10 km south of Walden (Jackson County), north central Colorado. Arapaho NWR lies in an intermountain glacial basin where the dominant native vegetation type is sagebrush-steppe (Kuchler 1964). Willow Flycatchers occur there in the riparian floodplain along the Illinois River. Our study area encompassed an 8-km stretch of the floodplain where elevations range from 2,485 to 2,516 m. The woody community is dominated by coyote (*Salix exigua*), Geyer (*S. geyeriana*), Wolf (*S. wolfii*), planeleaf (*S. planifolia*), and Bebb (*S. bebbiana*) willows, and *S. monticola, S. caudata,* and *S. pseudocordata* (Cannon and Knopf 1984). Woods rose (*Rosa woodsii*) and golden current (*Ribes aureum*) are minor components of the woody community. Common timothy (*Phleum pratense*), bluejoint reedgrass (*Calamagrostis canadensis*), blue flag (*Iris versicolor*), and several species of sedges (*Carex* spp.) dominate the herbaceous layer.

METHODS

We located song perch, nest, and unused sites of Willow Flycatchers from early June through late July, in 1985 and 1986. We located nests by following females to suspected nest bushes and by searching individual bushes within territories. Based on the number of singing males on our study area, we found nests in >80% of the territories in both years. We marked nest sites and frequently used song perch sites (one per territorial male) with plastic flagging, and then identified areas unused by flycatchers. Areas along the Illinois River and >100 m from song perch sites and nest sites were defined as unused (but potentially suitable) habitat. These areas were unused in both 1985 and 1986. Unused sites were then selected by pacing random distances along, and then perpendicular to, the riverbank within these areas. We returned after fledging of nestlings to measure vegetation structure. Sample sizes for the three groups were 32 nest sites, 26 song perch sites, and 30 unused sites.

We believe that all song perch sites sampled were selected by males rather than females. We base this conclusion on the following: (1) males arrive on the breeding grounds and begin singing from elevated perches before females arrive, and thus, before females can influence the selection process; (2) whereas females do occasionally sing (Seutin 1987, Sedgwick and Knopf 1989) they do so infrequently, for short intervals, and only early in the breeding season; and, (3) females nearly always sing from low perches within a bush (unpubl. data) whereas males characteristically sing from the most elevated perches and do so for long periods of time over much of the breeding season. We controlled for these characteristics by selecting perch sites only for birds that sang for prolonged periods and from elevated perches. Likewise, we are confident that females, rather than males, selected nest sites. Although birds were not marked in this study, our studies of a marked population of Willow Flycatchers at Malheur NWR, Oregon (unpubl. data) suggest that although the male may accompany the female to and from a proposed nest site or to one with a nest already under construction, the female appears to actually select the site. Stein (1963) also reported that females select the nest site in the superspecies (Traill's Flycatcher). Thus, we use the terms song perch site and male-selected site interchangeably, as we do the terms nest site and female-selected site.

We collected information on habitat attributes at three different scales of measurement—microplot, mesoplot, and macroplot. Vegetation measurements at the microplot scale followed the methodology of Knopf et al. (1988) and included measurements at the central bush and the four nearest adjacent bushes (Table 1). Central bush variables (i.e., the song perch, nest, or unused site bush) included height, radius, and volume, and an index of shrub decadence and stem density (the number of 0.1-m intervals hit by live and dead branches on horizontal intercept lines along north-south and east-west directions at half bush height). Adjacent bush variables included height, radius, and volume of the bush nearest the central bush in each of four quadrants delineated by cardinal directions. Two other microplot variables were the range in heights of the five (1 central + 4 adjacent) site bushes and the difference in heights among the central and each adjacent bush. Separation variables (measuring horizontal dispersion) included mean, maximum, and minimum measured distances from the outer edge of the central bush to the outer edge of the nearest bush in the four quadrants. We obtained an index to herbaceous biomass by placing a visual obstruction pole (Robel et al. 1970) at a distance midway between the central bush and nearest bush in each quadrant and recording the number of decimeter intervals obscured by herbaceous vegetation. From these measurements we calculated estimates of central tendency, maximums, minimums, ranges, and heterogeneity (coefficient of variation).

At the mesoplot scale, we measured vegetation within a 0.07-ha circle around nest, song perch, and unused site bushes. We extended transect lines 15 m along the four cardinal directions from the central bush and recorded the distance along lines intercepted by willow and non-willow vegetation to the nearest decimeter. From these measures we derived estimates of willow coverage or "patch" size, "gap" coverage (i.e., distances along transect lines not intercepted by willows), and measures of heterogeneity: (maximum–minimum)/mean (after Rotenberry and Wiens 1980), and coefficients of variation of both willow and gap distances.

Macroplot variables were measured at the scale of flycatcher territory size. Territory size of Willow Flycatchers varies both geographically and within habitats, ranging from 0.32 to 2.47 ha (Stein 1958, Walkinshaw 1966, Eckhardt 1979). Based on a small sample of territories, average territory size of Willow Flycatchers at Arapaho NWR falls near the lower end of this range (Sedgwick and Knopf, unpubl. data). We used a uniform measure of territory size for macroplot analyses and selected the smallest reported size (0.32 ha) to minimize sampling outside of territories. We measured attributes of the vegetation at this scale from aerial photographs. To enable us to identify nest and song perch sites in photographs, we placed 1 × 5 m strips of butcher paper on the ground adjacent to sites just prior to photography. We randomly located unused sites on photos using the same criteria described earlier to locate unused sites on the ground. Color infrared aerial photographs of the study area were taken prior to leaf drop in September 1986 at a scale of 1:3300 (Fig. 1). We measured features of the habitat within 0.32-ha circular plots drawn on the photos and centered on nest, song perch, and unused sites. We used the dot grid technique to determine coverage of shrub, herbaceous, water, and upland cover types. A dot grid intensity

TABLE 1. Definitions of habitat features measured, or calculated from measured variables, at nest, song perch, and unused sites of Willow Flycatchers at Arapaho National Wildlife Refuge, Jackson County, Colorado, 1985–1986.

Variable	Definition
Microplot features	
Central bush	
CHT	Height (dm) of the central bush.
CRAD	Radius (dm) of the central bush.
CVOL	Volume (m^3) of the central bush (calculated as the volume of a spherical segment plus the frustum of a cone).
PSTEML	Percent live stems in central bush (% live hits along 2 intercept lines at ½ bush height).
STEMDEN	Stem density of central bush (no. hits/m along 2 intercept lines at ½ bush height).
Adjacent bushes	
ABHT	Height (dm) of adjacent bushes.
CVABHT	Coefficient of variation (%) of height of adjacent bushes.
ABRAD	Radius (dm) of adjacent bushes.
CVABRAD	Coefficient of variation (%) of radius of adjacent bushes.
ABVOL	Mean volume (m^3) of adjacent bushes.
CVABVOL	Coefficient of variation (%) of volume of adjacent bushes.
RANGHT	Range of heights (dm) of the central and 4 adjacent bushes.
HTDIF	Mean difference (dm) of heights of central and each adjacent bush.
Separation	
MEANSEP	Mean distance (dm) to the 4 adjacent bushes.
CVSEP	Coefficient of variation (%) of distance to adjacent bushes.
MAXSEP	Maximum distance (dm) to adjacent bushes.
MINSEP	Minimum distance (dm) to adjacent bushes.
PLNTDEN	Bush density (no./ha).
Herbaceous	
MNHERB	Mean index for herbaceous biomass (no. dm increments of 2-cm wide pole obscured by vegetation at a distance of 4 m).
CVHERB	Coefficient of variation (%) of herbaceous biomass.
Mesoplot features	
Willows	
SUMWILL	Total willow distance (dm) intercepted along 4, 15-m transects originating at the site bush in each of the 4 cardinal directions.
MEANWILL	Mean distance (dm) intercepted by willows along 4, 15-m transects.
RANGWILL	Range of distances (dm) intercepted by willows along 4, 15-m transects.
MAXWILL	Maximum distance (dm) intercepted by willows along 4, 15-m transects.
CVWILL	Coefficient of variation (%) of distances intercepted by willows along 4, 15-m transects.
WILHETIN	Willow heterogeneity index (calculated as [maximum − minimum distance]/mean).
Gaps	
SUMGAP	Total non-willow distance intercepted along 4, 15-m transects.
MEANGAP	Mean non-willow distance (dm) intercepted along 4, 15-m transects.
RANGGAP	Range of non-willow distances (dm) intercepted along 4, 15-m transects.
MAXGAP	Maximum non-willow distance (dm) intercepted along 4, 15-m transects.
CVGAP	Coefficient of variation (%) of non-willow distances intercepted along 4, 15-m transects.
GAPHETIN	Gap heterogeneity index (calculated as [maximum − minimum distance]/mean).
Macroplot features (from aerial photographs)	
PCTWILL	Percentage willow coverage/territory (0.32 ha).
PCTHERB	Percentage herbaceous coverage/territory (0.32 ha).
PCTHOH	Percentage water coverage/territory (0.32 ha).
PCTNOTWIL	Percentage non-willow coverage/territory (0.32 ha).
STREAMWID	Stream width (m); mean of 5 measures per territory.
DISTHOH	Distance (m) to open water.
WIDRIP	Riparian zone width (based on an index [1 = narrowest, 5 = widest]).

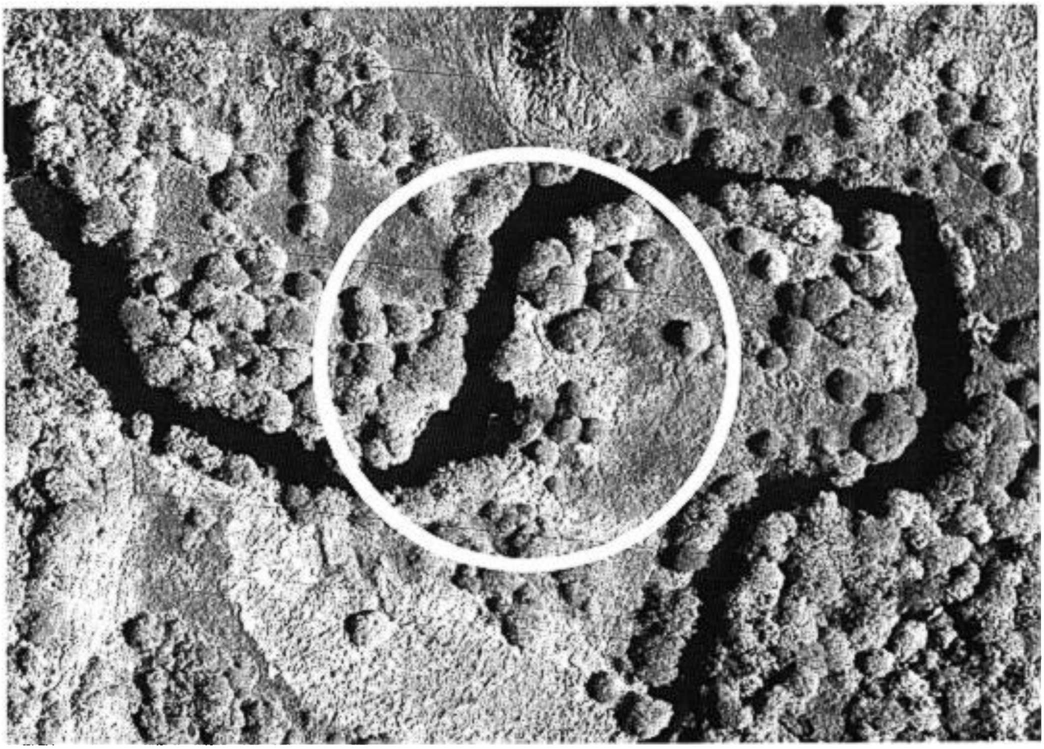

FIGURE 1. Aerial photograph of a portion of the study area on the Arapaho NWR, Colorado. The circled area, equivalent to 0.32 ha on the ground, is centered on a nest site (linear marker). A perch site ("T"-shaped marker) is situated in the lower left portion of the circle.

of 40 dots/cm^2 ensured a 95% probability of being within 8% of the true coverage for any given type (Avery 1978). We also recorded distance from sites to the stream, the width of the riparian zone, and average stream width ($\bar{x}$ of 5 measurements).

For the three scales, we measured or calculated 39 variables to describe habitats selected by Willow Flycatchers (Table 1). Variables not normally distributed were transformed using either log(x), log (x + 1), or arcsin transformations which either corrected or improved heteroscedasticity and deviations from normality (Sokal and Rohlf 1981). We compared means of continuous variables (one-way ANOVA) and used Bonferroni's multiple comparison test to determine specific differences among population means. We performed stepwise, canonical discriminant analyses (SAS Institute, Inc. 1987) for each scale of measurement to separate nest, song perch, and unused sites along axes of habitat structure. Variables considered in the stepwise procedures were those significant ($P < 0.05$) in univariate ANOVAs. Significance levels for entry and elimination of variables in the stepwise procedures were set at the default ($P = 0.15$), with variables contributing most or least to the discriminatory power of the model (as measured by Wilk's lambda) being entered or removed, respectively. Canonical discriminant analyses were then used to generate scores on canonical variables, plots and histograms of scores, and squared distances between class means (Mahalanobis distances) in discriminant habitat space. All statistical procedures were conducted on the Statistical Analysis System, Version 6 (SAS Institute, Inc. 1987).

RESULTS

MICROPLOT SCALE

Univariate analysis. Of 20 measured or calculated descriptors of habitat at the microplot scale, 16 differed among the three site types ($P < 0.05$). All central bush variables differed among sites (Table 2). Central bushes at song perch sites were taller (CHT), of greater radius (CRAD), and of

TABLE 2. Microplot habitat features ($\bar{x} \pm$ SE) at nest (N), song perch (P), and unused (U) sites of Willow Flycatchers at Arapaho NWR, Colorado, 1985–1986.

Variable	Nest (n = 32)		Song Perch (n = 26)		Unused (n = 30)			
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	P	Bonferroni
Central bush								
CHT (dm)	33.88	2.01	46.88	2.01	33.40	2.15	0.0001	P > N = U
CRAD (dm)	29.00	1.77	37.29	2.15	26.28	1.97	0.0014	P > N = U
CVOL (m^3)	67.75	11.84	152.79	22.66	61.56	12.57	0.0001	P > N = U
PSTEML (%)	61.25	4.05	46.08	3.63	66.24	3.77	0.0009	P < N = U
STEMDEN (no. hits)	1.17	0.08	1.10	0.09	1.47	0.11	0.0317	U > P; N = P; N = U
Adjacent bush								
RANGHT (dm)	18.84	1.93	27.62	2.32	24.83	1.64	0.0028	N < U = P
HTDIF (dm)	8.84	0.85	14.82	1.43	10.25	0.64	0.0006	P > N = U
ABHT (dm)	33.09	1.16	34.93	1.66	33.84	1.24	0.9074	P = N = U
CVABHT (%)	22.51	2.55	30.15	2.95	32.90	2.45	0.0030	N < P = U
ABRAD (dm)	27.02	1.61	24.48	1.55	24.76	1.21	0.9144	P = N = U
CVABRAD (%)	32.11	2.68	45.58	3.67	41.16	2.81	0.0091	N < P; U = P; U = N
ABVOL (m^3)	63.38	8.83	68.33	10.73	60.14	6.95	0.6955	P = N = U
CVABVOL (%)	70.02	5.41	89.42	6.98	92.38	6.31	0.0245	N < U; P = U; P = N
Separation								
MEANSEP (dm)	7.76	1.53	25.75	4.50	140.09	38.96	0.0001	N < P < U
CVSEP (%)	128.26	7.86	157.70	8.24	134.64	7.89	0.0012	N < P; U= P; U = N
MAXSEP (dm)	20.09	4.25	72.54	11.91	437.90	138.40	0.0001	N < P < U
MINISEP (dm)	0.13	0.13	0.04	0.04	7.00	3.04	0.0001	U > P = N
PLNTDEN (no./ha)	367.20	57.00	182.38	28.00	128.19	29.00	0.0002	N > U = P
Herbaceous								
MNHERB (index)	2.16	0.28	2.48	0.32	3.25	0.25	0.0074	U > N; P = N; P = U
CVHERB (%)	80.79	8.16	101.51	11.66	75.77	9.03	0.0824	P = N = U

TABLE 3. Summary of three discriminant analyses of micro-, meso-, and macro-variable habitat features at nest, song perch, and unused sites of Willow Flycatchers at Arapaho NWR, Colorado, 1985–1986.

	MICRO		MESO		MACRO
	DF1	DF2	DF1	DF2	DF1
Canonical correlation	0.7313	0.5951	0.5687	0.2485	0.7601
Wilks' lambda	0.3005	0.6459	0.6348	0.9382	0.4193
Eigenvalue	1.1495	0.5483	0.4780	0.0658	1.3681
Significance (*P*)	0.0001	0.0001	0.0001	0.0203	0.0001
Micro variables entered		Correlation with function			
MNHERB	0.3143	−0.1662			
MINSEP	0.3240	−0.3381			
MAXSEP	0.7611	−0.0723			
CVSEP	0.0265	0.3676			
STEMDEN	0.1956	−0.2901			
HTDIF	0.1044	0.5934			
CHT	0.0308	0.7084			
Meso variables entered					
SUMGAP			0.9927	0.1209	
MAXGAP			0.6533	0.7571	
Macro variables entered					
PCTWILL					0.5392
WIDRIP					0.7269

greater volume (CVOL) than those at either nest or unused sites. Central bushes at song perch sites also were less vigorous, having a lower percentage of live stems (PSTEML) than those at nest or unused sites, and stem density (STEMDEN) was less at song perch than at unused sites.

There were no differences among song perch, nest, and unused sites in three measures of bush size (ABHT, ABRAD, an ABVOL) for the four adjacent bushes around the central bush (Table 2). Habitat heterogeneity as measured by these variables did differ, however. Vegetation structure was most homogeneous at nest sites for all three variables: the coefficient of variation (CV) of bush height (CVABHT) was less at nest than at either song perch or unused sites; the CV of bush radius (CVABRAD) was less at nest than at song perch sites; and the CV of bush volume (CVABVOL) was less at nest than at unused sites. The mean difference in heights between the central bush and four surrounding bushes (HTDIF) was greatest at song perch sites and the range in bush heights of all five bushes (RANGHT) was less at nest than at either song perch or unused sites.

All five measures of separation between bushes differed among the three site types. Mean distance (MEANSEP) and maximum distance (MAXSEP) between the central bush and four adjacent bushes were least at nest and greatest at unused sites. The minimum distance between bushes (MINSEP) was greater at unused than at song perch or nest sites, and the CV of distances between bushes (CVSEP) was less at nest than at song perch sites. Similarly, shrub density (PLNTDEN) was greater at nest than at either unused or song perch sites. Herbaceous biomass (MNHERB) differed among site types ($P = 0.007$), and was greatest at unused sites (Table 2). Heterogeneity of herbaceous cover (CVHERB) was similar among types ($P = 0.082$).

Thus, song perch sites were characterized by larger, less vigorous central bushes, and nest sites by higher bush densities and more uniform-sized, evenly spaced bushes. Unused sites had the most widely spaced bushes and greater herbaceous cover than nest sites.

Multivariate analysis. Seven of 16 microplot variables were selected for inclusion in the canonical discriminant analysis (Table 3). Two discriminant functions (DF) were significant ($P < 0.0001$): DF1 was largely a measure of MAXSEP ($r = 0.7611$) and DF2 was most highly correlated with CHT and HTDIF. Nest sites were situated to the left along DF1, having low values of MAXSEP; unused sites were situated to the right along DF1; and, song perch sites were located near the top of DF2, being associated with central bush height and differences in height between the central and adjacent bushes (Fig. 2). Multivariate

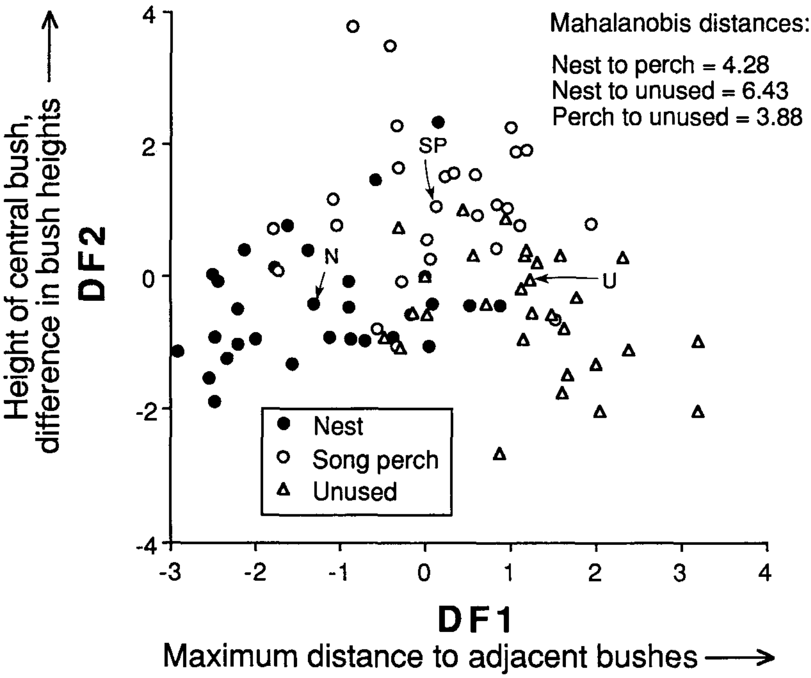

FIGURE 2. Ordination of discriminant scores of nest, song perch, and unused sites of Willow Flycatchers on two axes (DF1 and DF2) derived from an analysis of the microplot habitat data, Arapaho NWR, Colorado, 1985–1986. Site means are designated by arrows.

habitat (= Mahalanobis) distances between site means were greatest for nest vs. unused sites ($M = 6.43$) and were greater for nest vs. song perch ($M = 4.28$) than for song perch vs. unused sites ($M = 3.88$). Thus, (1) habitat segregation between the genders was greater than that between song perch sites and unused sites, and (2) females were more selective than males in their choice of habitats since their multivariate habitat mean was further from the unused site mean than was that of males. All three site types (nest, song perch, and unused) were significantly segregated from each other in multivariate habitat space (multivariate F tests, 7, 74 df, $P < 0.0001$).

MESOPLOT SCALE

Univariate analysis. All 12 measured or calculated habitat descriptors at the mesoplot scale of measurement differed among site types (Table 4). The sum of willow intercept distances (SUMWILL), mean willow intercept distance (MEANWILL), the range of willow intercept distances (RANGWILL), and maximum willow intercept distance (MAXWILL) were all significantly less ($P < 0.05$) at unused than at either song perch or nest sites. Variability in willow coverage (CVWILL) was less at nest than at either song perch or unused sites.

Measures of openings between willows, or "gaps" mirrored measures of willow intercept distances. The sum of gap distances (SUMGAP), mean gap intercept distance (MEANGAP), the range of gap distances (RANGGAP), and maximum gap distance (MAXGAP) were all less at nest than at either song perch or unused sites. The variability in gap distances (CVGAP) was less at unused than at either song perch or nest sites.

In summary, song perch and nest sites were characterized by greater total willow intercept distance, greater average and maximum willow patch size, and a greater range of patch sizes than unused sites. Nest sites were the most homogenous for total willow coverage (CVWILL). As defined by gap distances, nest sites had less total distance, smaller average and maximum distances, and less range in gap distances than at either song perch or unused sites. Both song perch and nest sites were more heterogenous for total gap coverage than unused sites.

Multivariate analysis. Of the 12 mesoplot habitat features, two were selected by the stepwise

TABLE 4. Mesoplot habitat features ($\bar{x}$ ± SE) at nest (N), song perch (P), and unused (U) sites of Willow Flycatchers at Arapaho NWR, Colorado, 1985–1986.

Variable	Nest (n = 32) $\bar{x}$	Nest SE	Song Perch (n = 26) $\bar{x}$	Song Perch SE	Unused (n = 30) $\bar{x}$	Unused SE	P	Bonferroni
Willows								
SUMWILL (dm)	361.69	20.90	299.23	18.46	208.20	16.24	0.0001	U < P = N
MEANWILL (dm)	41.48	3.52	38.90	2.95	26.93	1.51	0.0008	U < P = N
RANGWILL (dm)	101.53	5.26	86.04	6.59	62.20	5.02	0.0001	U < P = N
MAXWILL (dm)	107.75	5.36	94.04	6.55	67.97	5.16	0.0001	U < P = N
CVWILL (%)	43.26	4.31	60.85	5.09	76.32	6.87	0.0008	N < P = U
WILHETIN (index)	0.95	0.09	1.30	0.11	1.63	0.14	0.0002	N < U; P = U; P = N
Gaps								
SUMGAP (dm)	234.38	19.54	301.12	18.34	393.33	16.45	0.0001	N< P < U
MEANGAP (dm)	37.70	5.18	50.77	4.67	66.33	5.63	0.0001	N < P < U
RANGGAP (dm)	79.28	6.35	107.50	6.11	109.33	5.84	0.0007	N < P < U
MAXGAP (dm)	88.66	6.98	115.96	5.71	124.60	4.88	0.0001	N < P < U
CVGAP (%)	65.52	6.01	59.06	4.86	36.50	3.16	0.0001	U < P = N
GAPHETIN (index)	1.44	0.13	1.30	0.11	0.79	0.07	0.0001	U < P = N

discriminant analysis—SUMGAP and MAXGAP (Table 3). DF1 explained 87.9% of the variability and was highly correlated with both variables. Unused sites, lying to the right along DF1, were associated with large gaps (Fig. 3). Nest sites had smaller gaps and were situated to the left along DF1, and song perch sites were intermediate. Mahalanobis distances between nest and unused site means were greater (M = 2.59; F = 19.85, df = 2, 84, P < 0.0001) than between song perch and unused site means (M = 1.27; F = 8.71, df = 2, 84, P = 0.0004), and were smallest between nest and song perch site means (M = 0.71; F = 5.03, df = 2, 84, P = 0.009). As at the

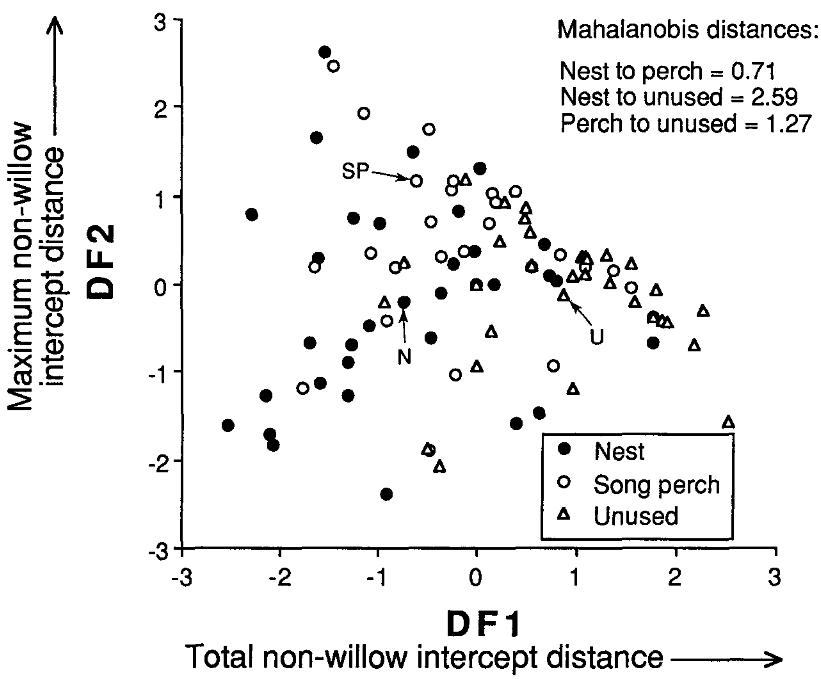

FIGURE 3. Ordination of discriminant scores of nest, song perch, and unused sites of Willow Flycatchers on two axes (DF1 and DF2) derived from an analysis of the mesoplot habitat data, Arapaho NWR, Colorado, 1985–1986. Site means are designated by arrows.

TABLE 5. Macroplot habitat features ($\bar{x}$ ± SE) at nest (N), song perch (P), and unused (U) sites of Willow Flycatchers at Arapaho NWR, Colorado, 1985–1986.

	Nest (n = 32)		Song Perch (n = 26)		Unused (n = 30)			
Variable	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	P	Bonferroni
PCTWILL (%)	49.29	2.34	43.75	2.06	30.84	2.64	0.0001	U < P = N
PCTHERB (%)	37.47	2.36	41.62	1.94	53.57	2.32	0.0001	U > P = N
PCTHOH (%)	9.97	1.34	11.13	0.72	13.37	1.07	0.0780	U = P = N
PCTNOTWIL (%)	50.71	12.39	56.25	2.06	69.16	2.64	0.0001	U > P = N
STREAMWID (index)	5.31	0.21	5.17	0.24	4.79	0.23	0.2456	U = P = N
DISTHOH (index	10.71	2.04	5.96	0.99	4.13	0.80	0.0033	N > U; P =N; P = U
WIDRIP (index)	4.16	0.21	3.88	0.27	1.97	0.18	0.0001	U < N = P

microplot scale, this suggests that females (nest sites) were more selective of habitats than males (song perch sites).

MACROPLOT SCALE

Univariate analysis. Of seven habitat descriptors at the macroplot scale of analysis, five differed ($P < 0.05$) among site types (Table 5). Both nest and song perch sites had a greater percentage cover of willow (PCTWILL) and a smaller percentage cover of non-willow (PCTNOTWIL) than did unused sites. Similarly, nest and song perch sites had less herbaceous coverage (PCTHERB) than unused sites. Width of the riparian zone (WIDRIP) was less at unused than at either song perch or nest sites and, surprisingly, nest sites were located farther from the stream (DISTHOH) than unused sites. This results from unused site locations in narrow riparian zones and nest site locations in wider riparian zones. Hence, unused sites were generally located closer to the stream than were nest sites. Song perch, nest, and unused sites were similar for percentage water cover (PCTHOH) and width of the stream (STREAMWID). At this scale, song perch and nest sites were similar to one another for willow, non-willow, herbaceous, and water coverage and width of the riparian zone; both differed from unused sites.

Multivariate analysis. Two of the five variables significant in univariate ANOVAS were selected by the stepwise discriminant procedure—PCTWILL and WIDRIP (Table 3). One DF was significant ($P < 0.0001$). Nest sites, associated with wide riparian zones and high percentage willow cover, were situated to the right along DF1, unused sites were to the left, and song perch sites were intermediate (Fig. 4). As was the case for the two smaller scales of analysis, the Mahalanobis distance between nest and unused site means ($M = 6.76$; $F = 48.33$, df = 2, 80, $P < 0.0001$) was greater than that between song perch and unused site means ($M = 4.45$; $F = 30.62$, df = 2, 80, $P < 0.0001$). This suggests that at this scale as well, females (nest sites) were more selective than males in their choice of habitats. The Mahalanobis distance was smallest between nest and song perch sites and the difference between nest and song perch sites and the difference between these two groups in multivariate habitat space was not significant ($M = 0.28$; $F = 1.89$, df = 2, 80, $P = 0.16$).

DISCUSSION

FLYCATCHER HABITAT IN COLORADO

Throughout their range, Willow Flycatchers use a variety of open, brushy habitats (Kahl et al. 1985). They require the presence of small tree and/or shrub thickets (Bent 1942, Berger and Parmalee 1952, King 1955, Stein 1958, Graber et al. 1974). Willow Flycatchers occur under both xeric and mesic conditions, although they seem to reach their highest densities in mesic sites. They are commonly associated with willow thickets (Grinnell and Miller 1944, Graber et al. 1974) and the presence of surface water (Bent 1942, Walkinshaw 1966). They use areas of moderate (Whitmore 1977) to abundant (Salt 1957) ground vegetative cover. In Utah, they occurred in areas having high shrub densities (Whitmore 1975), and flycatcher occurrence and abundance were correlated with shrub volume and height classes in Oregon (Taylor 1984). Kahl et al. (1985) identified intermediate to tall ground vegetation and a low, open canopy as the most consistent descriptors of flycatcher habitat.

In our study, regardless of the scale of measurement, Willow Flycatchers were consistently associated with the abundance, density, and cov-

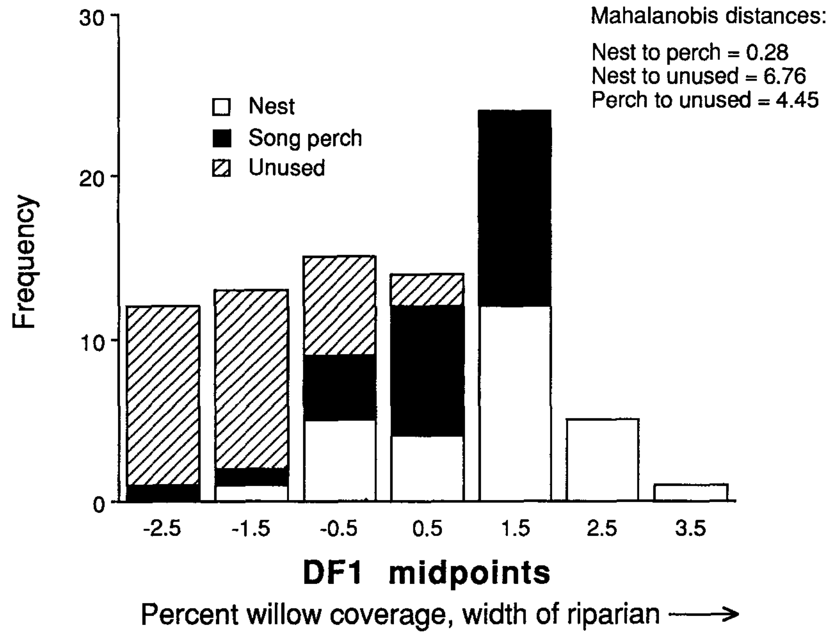

FIGURE 4. Frequency distribution of discriminant scores of nest, song perch, and unused sites of Willow Flycatchers for the first discriminant function (DF1) derived from an analysis of the macroplot habitat data, Arapaho NWR, Colorado, 1985–1986.

erage of willows. Smaller distances between willows and greater willow densities (microplot variables); larger willow patches and smaller gaps (mesoplot variables); and, greater percentage willow coverage and less non-willow coverage (macroplot variables) all distinguished nest sites and/or nest and song perch sites from unused sites. We found no specific association between flycatchers and stream width, and contrary to our expectations, we found that nest sites were farther from open water than unused sites. We attribute the lack of correspondence between flycatchers and water to the "mesic" nature of all sites in our study area and to an analysis at the "individual" spatial scale (sensu Wiens et al. 1987). Arapaho NWR contains mesic habitats in a xeric region, and at a regional scale of analysis, we would expect a positive correlation between flycatchers and mesic habitats.

GENDER DIFFERENCES IN HABITAT SELECTION

The vegetation structure at song perch sites of Willow Flycatchers is substantially different from that at nest sites. We conclude that this dissimilarity reflects independent selections by males for song perch sites and by females for nest sites. Collins (1981) found differences between song perch and nest site vegetation structure for several (mostly open-area nesting) warbler species, but only 29% of the nest sites in his sample differed from corresponding perch sites. Apparently such differences do not occur in all habitats for all species. Whereas Collins cautioned that use of song perch sites may overestimate the tree component of the habitat, nest sites and song perch sites of Willow Flycatchers at Arapaho NWR—where there are few trees—differed in other ways. Song perch and nest sites differed in measures of gap distances and variability in willow patch size (mesoplot variables), and for 12 of 20 microplot variables, including those assessing central bush size and vigor, variability in bush dimensions, and separation and density of willows.

Such differences may occur in many other passerines, as well, since males of most species arrive on the breeding grounds before females, select habitats and set up territories, and subsequently attempt to attract arriving females. Males may, in fact, choose territories based in large part on song perch site availability and quality and only partially and secondarily on the basis of suitable nest sites. Females arrive later and are presumably responsible for selection of the nest site. Natural selection theory suggests that territories selected by males should include suitable nest site habitat, but there is no *a priori* reason to believe that song perch site microhabitat should be similar to nest site microhabitat. The very different functions of nest site habitat (nest concealment, appropriate microenvironment for eggs and nestlings) vs. song perch site habitat (exposure and visibility, and perhaps high foraging resource quality as well) suggest different niche-gestalts at nest and song perch sites. However, in very homogenous, non-patchy environments, such differences may not occur.

The relevance of differences in vegetation structure at nest and song perch sites is underscored if one examines how the interpretations of a species' niche-gestalt would differ had only either nest or song perch site microhabitats been measured. For example, had we measured only song perch and not nest site habitat, the univariate analyses would *not* have detected differences between bird and unused sites for plant density, variability in distances between bushes, variability of bush size, and willow patch size variability. Had we measured vegetation only at nest and not at song perch sites, the univariate analyses would *not* have detected bird/unused site differences for central bush size and vigor, and HTDIF, CVABRAD, and CVSEP. Thus, conclusions from habitat studies based upon nest or song perch sites alone are limited within population or species contexts and should be interpreted as sex specific analyses.

Similarly, the multivariate analyses indicate differences between song perch and nest sites, although the differences become less pronounced as the measurement scale increases. At the finest scale, differences between sites selected by males and females were, in fact, greater than those between song perch and unused sites. At all three scales of measurement, habitat selection of females was more discriminating than that of males. This suggests that nest site selection, associated with offspring production, may be more closely tied to fitness (Martin and Roper 1988) than song perch site selection. The greater distances between nest and unused sites than between song perch and unused sites, further suggests that nest site habitat is more distinctive, and in fact may be at a premium relative to song perch site habitat (cf. Anderson and Shugart 1974).

SCALE PERSPECTIVES ON HABITAT DESCRIPTION

Significant differences between nest and song perch sites occurred only at the two smaller scales of measurement. Differences did not occur at the larger scale either because the scale was large enough to include both nest and song perch habitat within the area sampled, or because the types of variables measured (areal coverage and long-range distances) did not, in fact, differ. Because similar measures of vegetation at the two finer scales did differ between nest and song perch sites (e.g., MEANSEP, MEANGAP), the lack of differences at the largest scale are likely due to scale size.

Given that microhabitat differences between sexes occur, and that sites based on behavioral attributes (e.g., foraging or roosting sites) may have equally distinctive habitat features, authors need to acknowledge the limitations of habitat descriptions based on only one type of site. Vegetation measurements based on only one sex or behavior at a very fine scale may result in a different interpretation of the niche-gestalt than those based on another sex or behavior. Accordingly, studies describing the general habitat requirements for a species should use a territory-based (large scale) measure of vegetation analysis or should sample randomly at several locations within each territory. This would assure that each of the sexually and behaviorally different microhabitats is included in the analysis. However, habitat differences at a larger scale may be partially obscured if sizable areas of defended, but unused, habitat are included in the analysis (cf. Odum and Kuenzler 1955). The presence of song perch sites at the periphery of territories might also bias a macro-scale analysis since large areas of habitat outside of territories could be included in the sample. Studies examining differences in behavioral or sexual microhabitat attributes should analyze vegetation at finer scales of measurement.

ACKNOWLEDGMENTS

We thank E. C. Patten, Manager, Arapaho National Wildlife Refuge, for his interest and support. R. J. Myhre (U.S. Forest Service) took aerial photographs of the study area and kindly provided the space and equipment to analyze them. We thank J. G. Corn, J. F. Ellis, and N. C. Sedgwick for assistance in the field and W. H. Howe, L. Allen-Johnson, and B. Allen-Johnson for technical assistance. D. M. Finch, R. L. Hutto, R. A. McCabe, A. L. A. Middleton, M. L. Morrison, and R. C. Whitmore provided thoughtful reviews of the manuscript.

LITERATURE CITED

ANDERSON, S. H., AND H. H. SHUGART. 1974. Habitat selection of breeding birds in an east Tennessee deciduous forest. Ecology 55:828–837.

AVERY, T. E. 1978. Forester's guide to aerial photo interpretation. USDA For. Serv., Agric. Handb. 308.

BENT, A. C. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. U.S. Natl. Mus. Bull. 179:1–555.

BERGER, A. J., AND D. F. PARMALEE. 1952. The Alder Flycatcher in Washtenaw County, Michigan: breeding distribution and cowbird parasitism. Wilson Bull. 64:33–38.

CANNON, R. W., AND F. L. KNOPF. 1984. Species composition of a willow community relative to seasonal grazing histories in Colorado. Southwest Nat. 29:234–237.

COLLINS, S. L. 1981. A comparison of nest-site and perch-site vegetation structure for seven species of warblers. Wilson Bull. 93:542–547.

ECKHARDT, R. C. 1979. The adaptive syndromes of two guilds of insectivorous birds in the Colorado Rocky Mountains. Ecol. Monogr. 49:129–149.

GRABER, R. R., J. W. GRABER, AND E. L. KIRK. 1974. Illinois birds: Tyrannidae. Ill. Natl. Hist. Survey Biol. Note 86:1–56.

GRINNELL, J., AND A. H. MILLER. 1944. The distribution of the birds of California. Pacific Coast Avifauna No. 27.

HILDÉN, O. 1965. Habitat selection in birds. Ann. Zool. Fenn. 2:53–75.

HOLMES, R. T., AND S. K. ROBINSON. 1981. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. Oecologia 48:31–35.

HOLWAY, D. A. 1991. Nest-site selection and the importance of nest concealment in the Black-throated Blue Warbler. Condor 93:575–581.

JAMES, F. C. 1971. Ordinations of habitat relations among breeding birds. Wilson Bull. 83:215–236.

KAHL, R. B., T. S. BASKETT, J. A. ELLIS, AND J. N. BURROUGHS. 1985. Characteristics of summer habitats of selected nongame birds in Missouri. Res. Bull. 1056. Univ. Missouri-Columbia Agric. Exp. Stn., Columbia:1–155.

KING, J. R. 1955. Notes on the life history of Traill's Flycatcher (*Empidonax traillii*) in southeastern Washington. Auk 72:148–173.

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. 52:280–290.

KNOPF, F. L., J. A. SEDGWICK, AND D. B. INKLEY. 1990. Regional correspondence among shrub-steppe bird habitats. Condor 92:45–53.

KUCHLER, A. W. 1964. Potential natural vegetation of the conterminous United States. Am. Geogr. Soc. Spec. Publ. 36:1–39.

MARTIN, T. E., AND J. J. ROPER. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. Condor 90:51–57.

MORRISON, M. L. 1981. The structure of western warbler assemblages: analysis of foraging behavior and habitat selection in Oregon. Auk 98:578–588.

MORRISON, M. L., AND E. C. MESLOW. 1983. Bird community structure on early-growth clearcuts in western Oregon. Am. Midl. Nat. 110:129–137.

NOON, B. R. 1981. Techniques for sampling avian habitats, p. 42–52. *In* D. E. Capen [ed.]. The use of multivariate statistics in studies of wildlife habitat. USDA For. Serv. Gen. Tech. Rep. RM-87.

ODUM, E. P., AND E. J. KUENZLER. 1955. Measurement of territory and home range size in birds. Auk 72:128–137.

ROBEL, R. J., J. N. BRIGGS, A. D. DAYTON, AND L. C. HULBERT. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. J. Range Manage. 23:295–297.

ROTENBERRY, J. T. 1985. The role of vegetation in avian habitat selection: physiognomy or floristics? Oecologia 46:7–12.

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.

SAKAI, H. F., AND B. R. NOON. 1991. Nest-site characteristics of Hammond's and Pacific-slope Flycatchers in northwestern California. Condor 93: 563–574.

SALT, G. W. 1957. An analysis of avifaunas in the Teton Mountains and Jackson Hole, Wyoming. Condor 59:373–393.

SAS INSTITUTE, INC. 1987. SAS/STAT guide for personal computers, 6th ed. SAS Institute Inc., Cary, NC.

SEDGWICK, J. A. 1987. Avian habitat relationships in pinyon-juniper woodland. Wilson Bull. 99:413–431.

SEDGWICK, J. A., AND F. L. KNOPF. 1989. Regionwide polygyny in Willow Flycatchers. Condor 91:473–475.

SEUTIN, G. 1987. Female song in Willow Flycatchers (*Empidonax traillii*). Auk 104:329–330.

SMITH, K. G. 1977. Distribution of summer birds along a forest moisture gradient in an Ozark watershed. Ecology 58:810–819.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry, second ed. W. H. Freeman, New York.

STEIN, R. C. 1958. the behavioral, ecological and morphological characteristics of two populations of the Alder Flycatcher, *Empidonax traillii* (Audubon). New York State Mus. Sci. Serv. Bull. No. 371.

STEIN, R. C. 1963. Isolating mechanisms between populations of Traill's Flycatchers. Proc. Am. Philos. Soc. 107:21–50.

TAYLOR, D. M. 1984. The effects of cattle grazing and other factors on passerine birds nesting in willow riparian habitat. M.S.thesis, Idaho State Univ., Pocatello.

WALKINSHAW, L. H. 1966. Summer biology of Traill's Flycatcher. Wilson Bull. 78:31–46.

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

WHITMORE, R. C. 1977. Habitat partitioning in a community of passerine birds. Wilson Bull. 89: 253–265.

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.