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AN EXPERIMENTAL STUDY OF NEST-SITE SELECTION BY YELLOW WARBLERS[1]

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Abstract. We studied nest-site selection of Yellow Warblers (*Dendroica petechia*) in a riparian community on the Arapaho National Wildlife Refuge, Colorado, from 1981–1984. Our methodology included (1) comparing nest sites selected by warblers to the structure and vigor of the woody community available as potential sites, (2) experimentally removing shrubs used for nest sites and describing new sites selected, and (3) evaluating the reliability of habitat descriptors measured at nest sites across three years of pooled nest-site information.

Warblers built nests proportionally among the seven species of willow (*Salix*) shrubs in the community. Of the original 34 descriptors of vegetation structure and vigor, 13 were considered insignificant to Yellow Warblers in used-vs.-available comparisons, an additional seven were eliminated comparing nest sites before and after the experimental manipulation of the shrub community, and another three were eliminated with a comparison of nest sites across all three years. In all, 11 descriptors remained after the multiple analyses.

Virtually all descriptors of structure and vigor of bushes where warblers built nests were eliminated with the multiple analyses. Birds selected nest sites based primarily upon descriptors of the vegetation patch, the most powerful being those that defined horizontal patterning of bushes within the patch. We conclude that (except for the immediate branch structure supporting the nest) Yellow Warblers select nest sites based upon patch characteristics surrounding the bush where the nest was built rather than on characteristics of the nest bush itself. This behavior probably reflects selective pressures to reduce rates of nest predation and brood parasitism by concealing nests in larger stands of shrubs. Finally, the results of the multiple tests led us to conclude that published information on passerine habitats and habitat selection likely contains a large component of statistically valid, but biologically meaningless, relationships.

Key words: *Yellow Warbler;* Dendroica petechia; *habitat selection; Colorado; predation; riparian.*

INTRODUCTION

Birds select habitats by responding to cues (proximate factors) that stimulate settling at a location. Natural selection operates on the appropriateness of those selections through ecological processes (ultimate factors) that influence survival and reproductive success of individuals (Hildén 1965). Although Hildén distinguished between the relative roles of proximate and ultimate factors in habitat selection, most field studies have been descriptive or correlative in nature (Cody 1985) and prone to severe ambiguities of interpretation (Terborgh 1985). Further understanding of how birds select habitats demands creative experiments rather than additional inferential studies (Partridge 1978, Wiens and Rotenberry 1981).

Experimental studies of habitat selection by birds have been primarily opportunistic, monitoring the responses of a population (Best 1972) or avian assemblage (Szaro and Balda 1979) to the manipulation of vegetative associations. Field tests of habitat selection of individual birds are difficult to design because of the mobility of birds and complexity of habitat features. In addition, site fidelity of individual birds from year to year (Wiens et al. 1986, Knopf and Sedgwick 1987) may compromise experimental tests by biasing the independence of samples recorded at a site.

Within a habitat, nest location is the most specific site selected by a bird, and it is the site that can be monitored most precisely for responses to an experiment. Morse (1985, 1989) encouraged experimental studies of nest-site selection among parulid warblers especially. These active, brightly colored birds are highly visible in vegetative communities and they occupy relatively small patches of vegetation. The Yellow Warbler

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(*Dendroica petechia*) breeds across North America in riparian and swamp-edge vegetation, being most abundant in shrub communities (Salt 1957, Ficken and Ficken 1966) on moist but unsaturated soils. From 1981 through 1984, we studied nest-site selection of Yellow Warblers in a shrub willow (*Salix* spp.) community on the Arapaho National Wildlife Refuge. Our study employed both traditional and experimental approaches to defining vegetative descriptors of nest sites selected by Yellow Warblers.

We employed a progressive series of independent tests to identify which vegetative characteristics of a riparian, shrub community were used by warblers in selecting nest sites. Our field objectives were to (1) compare vegetation descriptors at sites where warblers built nests (= used sites) relative to potential nesting sites randomly available to warblers, (2) test predictions developed in the used-vs.-available analysis by describing nest-site locations after an experimental manipulation of the willow community, and (3) test the conclusions derived from the used-vs.-available and experimental studies with an analysis of correspondence among nest-site descriptors across three breeding seasons.

STUDY AREA

The sequential studies were conducted along the Illinois River on the Arapaho National Wildlife Refuge (NWR) between Walden and Rand (Jackson County), Colorado, at an elevation of 2,504 m. The riparian avifauna on the refuge has been monitored annually since 1980. Yellow Warblers are the most abundant species within the assemblage of breeding birds, which also includes American Robins (*Turdus migratorius*), Song Sparrows (*Melospiza melodia*), Savannah Sparrows (*Passerculus sandwichensis*), Red-winged Blackbirds (*Agelaius phoeniceus*), Brown-headed Cowbirds (*Molothrus ater*), Willow Flycatchers (*Empidonax traillii*), Lincoln's Sparrows (*Melospiza lincolnii*), and White-crowned Sparrows (*Zonotrichia leucophrys*). These species represent >90% of the breeding individuals within the local avifauna (Knopf et al. 1988).

The specific study site was approximately 1 km of floodplain along the Illinois River immediately south of the refuge headquarters. The site was historically grazed by cattle each winter through 1976, after which cattle were excluded. The landscape is a mosaic with 18.3% coverage of woody species interspersed with 12.8% water and 68.9% native grasses and forbs. Woody vegetation is almost exclusively willow shrubs (Cannon and Knopf 1984) that grow to heights >6 m.

METHODS

We quantified the horizontal and vertical patterning of vegetation from the perspective of a bird perched in a bush. The sampling methodology was developed in 1980 specifically for use on the refuge (Knopf et al. 1988), has been employed in other studies of shrub-nesting birds (Knopf et al. 1990), and is akin to the "bird-centered view" of habitat defined by Wiens (1985). For each bush containing a nest, we recorded the height, diameter, and lower height of the bush canopy. This latter measure was required to calculate shrub volumes accurately. Knopf et al. (1990) identified the importance of vegetative vigor as a reliable descriptor of passerine habitats in shrub communities, and we quantified vigor of the nest bush as the ratio of numbers of live and dead stems hitting each decimeter interval on a density pole inserted horizontally through the bush at one half of bush height.

To provide a perspective of vegetation structure from the nest bush, we measured the distance (edge-to-edge) to the nearest bush in each of the four quadrants delineated by the cardinal directions and repeated the "nest bush" structural measurements on those four bushes. Standing herbaceous biomass was indexed at a point midway between the nest bush and closest bush in each quadrant by the relative visual occlusion of a density pole (Robel et al. 1970). Finally, we summed structural and vigor measures for all five bushes to provide a description of the shrub patch. The raw measurements plus additional calculated values provided a total of 34 vegetation variables (Table 1) that characterized the nest bush, visual perspectives from that bush in horizontal and vertical planes, and the vegetative patch within the larger willow population.

The nest-site selection analysis included three efforts: a comparison of sites used for nesting relative to those available at random sites, a comparison of sites used before vs. after experimental manipulation of the woody vegetation, and an analysis of vegetation descriptors used by warblers across three nesting seasons. For the first effort, vegetative measurements were taken at 125 randomly selected bushes at the end of the 1981 growing season. From that sample, a

TABLE 1. Measured and calculated vegetation variables used to characterize nest sites of Yellow Warblers in a shrub willow community at Arapaho National Wildlife Refuge, Colorado.

Variable	Description
Vertical measures	
NBHT	Height of nest bush
HTDIF	Sum of height differences between nest bush and nearest bush in each quadrant
HTNRBUSH	$\bar{x}$ height of nearest bush in each quadrant
CVNRBUSH	CV height of nearest bush in each quadrant
RANGHT	Range in heights among the five bushes
MHT	$\bar{x}$ height of the five bushes
CVHT	CV height of the five bushes
HTRAD	Height of maximum radius of nest bush
MHTRAD	$\bar{x}$ height of maximum radius for the five bushes
CVHTRAD	CV height of maximum radius for the five bushes
Horizontal measures	
NBRAD	Radius of nest bush
MRAD	$\bar{x}$ radius for the five bushes
CVRAD	CV radius for the five bushes
MINSEP	Distance to closest bush in any quadrant
MAXSEP	Distance to furthest bush in any quadrant
RANGSEP	Range in distance to nearest bush for four quadrants
MSEP	$\bar{x}$ distance to nearest bush in each quadrant
CVSEP	CV distance to bushes in 4 quadrants
OPEN	No. of quadrants with no bush $\leq$100 m from nest bush
PDENS	No. willows/hectare
DH2O	Distance from nest bush to water
WRIP	Width of riparian community
Volume measures	
NBCVOL	Canopy volume for the nest bush calculated as the volume of a spherical segment
MCVOL	$\bar{x}$ canopy volume for all five bushes
NSVOL	Shrub volume for the nest bush calculated as volume of a spherical segment plus the frustum of a cone
MSVOL	$\bar{x}$ shrub volume for all five bushes
MCVOLAR	MCVOL times plant density (calculated from MSEP)
MSVOLAR	MSVOL times plant density (calculated from MSEP)
Vigor measures	
TSTEM	Total number of stems in nest bush
STEML	No. of live stems in nest bush
STEMD	No. of dead stems in nest bush
PSTEML	Percentage of stems alive in nest bush (arcsin transformed)
CMPT	Stem density within nest bush
HBB	Standing biomass of herbaceous layer in four quadrants

random subset of 20 bushes (equalling the number of nest bushes subsequently found in 1982) was selected to represent the population of bushes "available" to Yellow Warblers for nest construction when they arrived early in 1982.

During June 1982, we searched the study area for Yellow Warbler nests. The searches coincided with the nestling phase of the breeding cycle when adult birds were actively feeding young. Birds with nestlings became agitated when approached, which assisted in locating both territories and bushes containing nests within territories. Each bush with a warbler nest was marked with fluorescent flagging and revisited following fledging of nestlings to conduct vegetative measurements. Vegetative descriptors at 20 Yellow Warbler nest sites were then compared in a traditional approach to those at the subset of 20 available sites. Variables with *differed* were deemed valid predictors of nest sites selected by warblers. *Only* those descriptors were retained for subsequent analyses. Although some shrub growth occurred between the available and used measurement periods, differences created by this potential bias would have resulted in a descriptor being retained for subsequent tests/comparisons

rather than eliminated. Elimination of a valid descriptor would have constituted a Type I Error, but retention only subjected a descriptor to additional tests.

In the second (1983) effort we experimentally manipulated the willow community. After Yellow Warblers left the area in September 1982, we returned to each bush that had contained a nest and severed all woody structure at ground level, leaving cut branches piled on the site. The removal of bushes where birds nested ensured that warblers returning to the study area in 1983 would be forced to select new nest sites. During the 1983 breeding season, we again searched the area for warbler nests and repeated vegetative measurements at nest sites to test 1982 predictions about nest-site selection. We compared 1982 and 1983 nest-site information for only those variables that differed in the used-vs.-available comparisons. In this analysis, variables that did *not* differ between 1982 and 1983 nest sites were retained as predictors of warbler nest sites. Those differing between years (indicating a lack of correspondence between nest-site selections) were considered less meaningful vegetation features (Knopf et al. 1990) and were not considered in the final analysis.

For the third effort, we collected data on nest bushes used by warblers on the area in 1984. These data were compared to the 1982 and 1983 nest-site data as a final test of variables used by warblers when selecting nest sites. Only variables retained from the first two analyses were considered and, again, those that *did not* differ across the three years were regarded as valid predictors of Yellow Warbler nest sites. Thus, across the entire study we attempted to identify vegetative descriptors relevant to nest-site selection by warblers by eliminating descriptors that either did not differ from available site data or that lacked correspondence between nest sites actually selected in successive years.

In addition to vegetation structure, we also compared the frequency of nest placement in willow bushes of different species to a random characterization of floristic composition conducted by Cannon and Knopf (1984: Table 1, Pasture 2). Willows were identified to species after Dorn (1977) plus reference to regional specimens within herbaria collections at the U. S. Forest Service's Rocky Mountain Forest and Range Experiment Station, Colorado State University, and the University of Wyoming.

Data on most structural measures of the vegetation were not normally distributed (Knopf and Cannon 1982), so we tested for differences in vegetation descriptors with Kruskal-Wallis Nonparametric Analyses of Variance. Variables were retained for successive tests if they differed ($P < 0.05$) between the used and available data sets. The second and third tests were designed to identify similarities between vegetative descriptors across years. Variables from these tests were retained if they were similar ($P > 0.05$) between data sets, which increased the probability of the Type II Errors. Power ($1-\beta$) for these latter tests was determined from the Power Tables for the χ^2 (Cohen 1988). We used G-tests to examine frequency of warbler use of the willow species.

RESULTS

Twenty nests were found on the study site in 1982, 18 in 1983, and 20 in 1984. Nests were generally at heights of 0.5–2.0 m in bushes (1982: 1.6 ± 0.65 m, 1983: 1.2 ± 0.40 m, 1984: 1.6 ± 0.76 m; $F = 1.16$, $P = 0.322$).

Yellow Warblers placed nests nonrandomly among the willow species in 1982 ($G = 19.7$, $P = 0.004$). Confidence in this association was low (Phi = 0.08), however, because of a large sample ($n = 125$) of random bushes. Subsequent comparisons of 1983 and 1984 bushes used as nest sites indicated no selection of willow species relative to that expected on the basis of random occurrence of the various species within years ($G = 5.2$, $P = 0.519$ and $G = 0.5$, $P = 0.997$, respectively). Individual cell comparisons (Table 2) indicated that warblers may tend to avoid *S. exigua, S. wolfii,* and *S. pseudocordata.*

USED VS. AVAILABLE COMPARISONS

Comparisons of vegetation structure and vigor at 1982 nest sites with structure and vigor measures at available sites resulted in 21 of the 34 original vegetation parameters appearing significant to warblers when selecting nest sites (Table 3). Birds appeared to select nest sites based on many features in the vertical plane. Nests were in bushes that were taller (NBHT) than those at randomly selected willows. Those bushes had neighboring bushes (and occurred in shrub patches) that were also taller (HTNRBUSH) and of more uniform size (CVNRBUSH) than occurred in the overall shrub community. In addition, the heights of maximum radius of the nest bush and bushes within the patch were greater

TABLE 2. Frequency of occurrence of willow (*Salix*) species at 125 randomly selected sites on the Arapaho National Wildlife Refuge study area compared with species used by Yellow Warblers for nest placement, 1982–1984. Random data are from Cannon and Knopf (1984). Percentages appear in parentheses.

Species	Random	No. of nests		
		1982	1983	1984
S. exigua	3 (2)	0	0	0
S. monitcola	46 (37)	9 (45)	10 (56)*	8 (40)
S. geyeriana	39 (31)	2 (10)*	5 (27)	6 (30)
S. wolfii	4 (3)	0	0	0
S. lasiandra	12 (10)	8 (40)**	3 (17)*	1 (5)
S. planifolia	19 (15)	1 (5)	0	3 (15)
S. pseudocordata	2 (2)	0	0	0
Unknown/other	0	0	0	2 (10)
Totals	125	20	18	20

* $P < 0.05$.
** $P < 0.01$.

than at randomly selected willows (HTRAD, MHTRAD). The remaining 13 variables did not differ ($P > 0.05$) and were eliminated from further consideration.

Many vegetation features from the horizontal plane also were associated with the presence of nests. Nests occurred in bushes of larger radius (NBRAD) and in patches of greater willow density (PDENS) and more uniform bush radius (CVRAD) than occurred around randomly selected willows. Most measures of separation between nest bushes and adjacent bushes (MINSEP, MAXSEP, RANGSEP, and MSEP) were significant; nest bushes definitely occurred in "clumps" of more closely spaced bushes. Nest bushes were also nearer to surface water (DH20) than were random bushes.

Because nests were in bushes of greater height and radius than was available to birds, we expected bushes with nests to have larger canopies (NBCVOL) and total shrub (NSVOL) volumes, and they did. Both canopy (MCVOL) and shrub (MSVOL) volume of bushes within the patch, however, were not important until standardized per unit area (MCVOLAR and MSVOLAR), further emphasizing the close spacing and higher density of willows at nest sites as compared to available sites.

Of the vegetation vigor measures, warblers selected bushes with more total stems (TSTEM) and greater stem density (CMPT) than were randomly available on the area. The ratio of live-to-dead stems (PSTEML) was similar for bushes with nests and randomly located bushes.

WARBLER SELECTIONS OF NEW SITES

Comparisons of the 1982 and 1983 nest-site data resulted in the elimination of seven additional variables (Table 4) as predictors of warbler nest sites. Those seven included three of four remaining variables that quantified bush volume and all remaining indices of bush vigor. Six other variables were marginally significant ($0.10 < P < 0.05$), suggesting a possible lack of correspondence between years, considering the power of the tests. These latter variables were retained. Most notable in this analysis, the four separation variables were strongly supported as predictors of warbler nest sites. In all, the original set of 34 vegetation variables had been reduced to 14 following the experimental test. Those 14 included 5 variables in the vertical plane, 8 in the horizontal plane, and 1 measure of bush volume.

NEST-SITE CORRESPONDENCE ACROSS YEARS

Tests of vegetation descriptors among the three years, 1982–1984, eliminated three additional variables: MHTRAD, NBRAD, and DH20 (Table 4). The 11 variables surviving all three analyses included descriptors of perspective and patch based on the height and variation in height of bushes, horizontal patterning of the community, variation in radius, and number and volume of bushes per unit area. The most powerful remaining descriptors were those variables that described the tendency for bushes with nests to occur in clumps of uniform-sized bushes (CVRAD, MINSEP, MAXSEP, MSEP).

DISCUSSION

Our objective was to define vegetation factors influencing nest-site selection by Yellow Warblers. Habitat selection among shrub-associated passerines appears to be a hierarchal procedure of selecting landscape features at a regional scale,

TABLE 3. Kruskal-Wallis comparisons of vegetation variables at randomly located sites vs. those at Yellow Warbler nest sites at Arapaho National Wildlife Refuge, Colorado.

Variable	$\bar{x}$ Random	$\bar{x}$ Warbler	χ^2	P	Retained[a]
Vertical measures					
NBHT (dm)	24.7	38.0	9.1	0.003	Yes
HTDIF (dm)	9.8	10.3	0.0	0.927	No
HTNRBUSH (dm)	24.1	29.8	4.9	0.028	Yes
CVNRBUSH (%)	36.0	24.1	5.5	0.019	Yes
RANGHT (dm)	20.3	18.9	0.4	0.533	No
MHT (dm)	24.3	31.5	6.6	0.010	Yes
CVHT (%)	35.7	24.8	5.3	0.022	Yes
HTRAD (dm)	7.9	12.1	7.2	0.007	Yes
MHTRAD (dm)	8.2	10.5	7.3	0.007	Yes
CVHTRAD (%)	38.0	34.8	0.1	0.766	No
Horizontal measures					
NBRAD (dm)	15.4	24.0	8.0	0.005	Yes
MRAD (dm)	15.7	18.8	3.0	0.086	No
CVRAD (%)	52.5	34.4	6.3	0.012	Yes
MINSEP (dm)	15.2	1.6	4.3	0.038	Yes
MAX SEP (dm)	194.1	42.7	6.4	0.011	Yes
RANGSEP (dm)	178.9	41.1	8.2	0.007	Yes
MSEP (dm)	81.8	15.8	7.0	0.008	Yes
CVSEP (%)	116.0	136.2	1.5	0.226	No
OPEN (no.)	0.01	0.005	0.4	0.553	No
PDENS (no./ha)	298.0	428.0	5.3	0.023	Yes
DH2O (m)	39.9	35.6	6.5	0.011	Yes
WRIP (m × 25)	4.9	4.7	1.5	0.229	No
Volume measures					
NBCVOL (m^3)	20.9	43.2	7.5	0.006	Yes
MCVOL (m^3)	20.1	26.3	1.4	0.234	No
NSVOL (m^3)	27.0	59.0	7.9	0.005	Yes
MSVOL (m^3)	26.7	36.0	2.1	0.152	No
MCVOLAR (m^3/ha)	2,296.0	7,338.4	13.5	0.000	Yes
MSVOLAR (m^3/ha)	3,596.7	10,568.2	13.1	0.000	Yes
Vigor measures					
TSTEM (no.)	19.4	24.6	4.4	0.037	Yes
STEML (no.)	13.4	16.3	1.0	0.303	No
STEMD (no.)	6.0	8.3	2.9	0.085	No
PSTEML (%)	68.5	65.0	0.8	0.365	No
CMPT (no. Stems/dm)	0.38	0.26	5.2	0.023	Yes
HBB (dm)	19.7	25.0	0.7	0.399	No

[a] Variables deemed significant ($P < 0.05$) predictors of Yellow Warbler nest sites and retained for subsequent analyses (Table 4).

floristic associations at a local scale, and vegetation quality at a site (Wiens and Rotenberry 1981, Knopf et al. 1990). Our study is an investigation of site selection only, and likely has limited application to the description of Yellow Warbler habitats at the regional scale. In addition, passerine microhabitats can vary dramatically between nest sites and song posts, and such variation has been reported for Yellow Warblers specifically (Collins 1981). To this end, our study on nest-site selection is, by design, a study of the selection of a specific site, with the actual site possibly reflecting the choice of the female only.

Field studies of habitat selection by birds have historically relied heavily on used-vs.-available descriptions of vegetation. The application of multivariate statistical analyses to describe passerine habitats in the last 15 years attests to the difficulty of both defining the appropriate habitat variables and designing experiments in the field. This study (as all field studies of habitat selection) assumed that those vegetative parameters measured were valid predictors of visual cues actually used by the birds when selecting a site. We tried to minimize bias associated with this assumption by using the "bird-centered view" of

TABLE 4. Kruskal-Wallis Test comparisons of mean values of vegetation variables at nest sites of Yellow Warblers (1) at control (1982) and experimental (1983) sites, and (2) among all three years (1982–1984) of the study. Variables differing significantly in the experimental test were discarded and not considered in the among-year analyses. Among-year comparisons (1982 vs. 1983 vs. 1984) sought to identify variables that were similar all three years. Power $(1 - \beta)$ of these latter tests for $\alpha = 0.05$ and a posited w (effect size) of 0.5 is 0.93 (Cohen 1988).

Variable	Control/experimental (1982/1983) P	Retained[a]	Among years (1982–1984) P	Retained[b]
Vertical measures				
NBHT	0.029	No	—	—
HTNRBUSH	0.087	Yes	0.267	Yes
CVNRBUSH	0.144	Yes	0.216	Yes
MHT	0.047	No	—	—
CVHT	0.057	Yes	0.170	Yes
HTRAD	0.069	Yes	0.107	Yes
MHTRAD	0.061	Yes	0.008	No
Horizontal measures				
NBRAD	0.075	Yes	0.045	No
CVRAD	0.152	Yes	0.382	Yes
MINSEP	0.394	Yes	0.496	Yes
MAXSEP	0.372	Yes	0.348	Yes
RANGSEP	0.299	Yes	0.218	Yes
MSEP	0.327	Yes	0.498	Yes
PDENS	0.401	Yes	0.270	Yes
DH2O	0.120	Yes	0.032	
Volume measures				
NBCVOL	0.035	No	—	—
NSVOL	0.047	No	—	—
MCVOLAR	0.018	No	—	—
MSVOLAR	0.068	Yes	0.134	Yes
Vigor measures				
TSTEM	0.005	No	—	—
CMPT	0.000	No	—	—

[a] Variables *not* significantly different ($P > 0.05$) between years (1982–1983) were deemed possible predictors of Yellow Warbler nest sites and retained for the among-years comparisons.
[b] Variables *not* significantly different ($P > 0.05$) among all three years (1982–1984) were deemed valid predictors of Yellow Warbler nest sites on the refuge, having survived all three tests.

the vegetative community. This approach reduced the potential of using inappropriate, irrelevant variables, especially when compared to the traditional techniques for describing vegetation and site characteristics (e.g., basal area) employed in the forestry and wildlife management professions.

Birds of many warbler species return to breed at the same site in successive years (Walkinshaw 1953, Berger and Radabaugh 1968, Nolan 1978). A subsequent study of banded warblers on our study area (Howe and Knopf, unpubl. data) revealed that Yellow Warblers returned to our study site at the rates of 60–62% for males and 32–44% for females. In the present study, we could have selectively removed individual birds from territories and described territories subsequently established by new birds. In such an approach, however, colonizing birds would likely have been younger individuals from different habitats, and of unknown previous breeding experiences.

Shrub species. Warblers used the willow species in proportion to their respective abundances on the study area, with species occurring in very low numbers not being used at all. The avoidance of one of these latter species, *S. exigua,* by warblers did not appear biologically important. This willow species was highly preferred as forage by moose (*Alces alces*), which readily browsed bushes to heights <0.25 m, precluding warbler use. *Salix exigua* is used readily by Yellow Warblers for nest sites in southeastern Oregon (Taylor and Littlefield 1986).

Floristics may be important in other locales where structural characteristics are more variable among plants. All willow species at Arapaho NWR, however, are of a similar range of sizes, branching patterns, and leaf dimensions, and apparently met minimum nest-site requirements.

Shrub structure. Knopf et al. (1988) concluded that Yellow Warblers are habitat generalists compared to other bird species in the Illinois River floodplain, using both vegetatively vigorous and decadent sites as affected by different histories of cattle grazing. Annual densities of warblers are similar between historically damaged and undamaged woody communities. In the present study, all structural descriptors of shrubs containing nests were eliminated (with the exception of HTRAD) during the course of the analyses. The two studies together led us to conclude that all bushes on the area provided the minimal structural cues for nest-site selection by this species. We speculate that the selection of a given bush for a nest site may be no more elaborate than the gestalt created by the size and separation of those twigs actually supporting the nest structure. We did not attempt to define branching structure at the nest in this study.

Shrub vigor. We were initially surprised that all measures of shrub vigor were eliminated as predictors of nest sites selected by Yellow Warblers. Recent studies of Green-tailed Towhees (*Pipilo chlorurus*) and Brewer's Sparrows (*Spi-*

zella breweri) identified shrub vigor as a primary descriptor for habitats of those shrub-nesting species across their geographic range (Knopf et al. 1990). We attribute this discrepancy to three factors. (1) Yellow Warblers nest in a riparian landscape in which annual variation in soil moisture (and thus shrub vigor) is modulated. (2) Yellow Warblers often arrive on the breeding grounds prior to leafing of the shrubs and thus may not be able to distinguish between live and dead stems. Green-tailed Towhees and Brewer Sparrows, on the other hand, nest in a semi-evergreen shrub association where decisions based on vigor are more easily made. (3) The current study of Yellow Warblers only included vegetation descriptors at nest sites whereas the earlier effort was more robust, sampling across behaviors (i.e., foraging, nesting, and song-post sites) of the two species being studied. This explanation would hold if vegetative vigor was important to shrub-steppe species primarily as it was a descriptor of patches with greater food resources.

Support for the conclusion that vegetative vigor was not important to warblers was subsequently obtained in 1988, when a portion of the study area burned just prior to the breeding season. Most warblers returned to the area and nested in skeletonized, dead bushes (W. H. Howe and F. L. Knopf, unpublished data)—some in the same bushes in which they built nests in 1987. Some nests were visible at distances >20 m. From these collective observations, we speculate that the current health of bushes seemed less relevant to Yellow Warblers than the bush health at some time in the past when the bush produced the branching structure necessary for nest placement.

Shrub patch. Yellow Warblers selected nest sites based on many descriptors of the vegetative patch surrounding the bush holding the nest. Warbler nest sites occurred in patches of uniformly sized (height and radius descriptors) bushes. Nest bushes occurred in areas of higher densities within the willow shrub landscape. Raw measures of foliage volume within the patch became significant when standardized per unit area.

The most powerful descriptors of the shrub patch were those that defined the distance between individual, neighboring bushes. The universal strength of these descriptors relative to measures of individual bush structure, vigor, and floristics led us to postulate that the separation measures were either the visual cues being used by warblers when selecting a vegetative patch, or that they were strongly correlated with those cues.

CONCLUSIONS

We conclude that Yellow Warblers select nest sites based primarily on patterns of bush distribution within a vegetation patch and not on factors associated with the nest bush itself. A study designed solely to investigate the descriptors of individual bushes in which nests were located would have defined vegetation parameters at a scale more precise than that apparently used by warblers. Because branches of adjacent willow bushes often intermingle within the canopy, individual shrubs may be functionally indistinguishable to a warbler.

Warblers probably select nest sites that favor nest concealment from predators and brood parasites. Studies of Willow Flycatchers at Arapaho NWR (Sedgwick and Knopf 1992) also identified CVNRBUSH, CVHT, the four separation variables, and PDENS as significant descriptors of habitats of that species. Considering the very different foraging techniques of warblers (foliage gleaners) and flycatchers (salliers), the need for nest concealment may have strongly influenced habitat selection of species in mesic-shrub communities. Martin (1988a, 1988b) identified nest predation as a major selective force influencing dispersion patterns of passerine birds in woody communities, and Martin and Roper (1988) provided earlier evidence that predation pressures may force birds to select nest sites based on patch-scale descriptors. Subsequent studies (Sedgwick and Howe, unpublished data) at Arapaho National Wildlife Refuge have identified predation as the primary source of nesting mortality for both the warbler and flycatcher.

This paper is one of three (Knopf et al. 1990, Sedgwick and Knopf 1992) developing alternative approaches to defining biologically meaningful relationships in avian habitats. Relative to this study, we recognize that experiments may be dangerous if they create a false sense of confidence simply because an experiment was done (Wiens 1989:16). The multiple approaches implemented here, however, enabled us to elaborate on the biological significance of many vegetative variables beyond that possible using only the used-vs.-available, experimental, or among-year-comparison approach. The collective efforts resulted in the dismissal of 23 of 34 vegetation variables as being poor predictors of warbler nest-

site selection, compared with a maximum of 13 of 34 variables dismissed by employing a used-vs.-available comparison only. Assuming that the patterns detected here apply to field studies employing only a single approach, we conclude that published information on passerine habitats and habitat selection contains a large component of statistically valid, but biologically meaningless, relationships.

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