

Breeding habitat use by sympatric and allopatric populations of Wilson's Warblers and Yellow Warblers

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Received 25 September 2001; accepted 16 January 2002

ABSTRACT. We studied Wilson's Warbler (*Wilsonia pusilla*) and Yellow Warbler (*Dendroica petechia*) habitat use in allopatric and sympatric populations in the Rocky Mountains of northern Colorado and southeastern Wyoming in order to better understand the different habitat needs and interactions of these two species. Foraging Wilson's Warblers and Yellow Warblers used very similar habitat, both selecting larger, more open shrubs. In spite of similar foraging habitat, comparisons of habitat use by the two species at the sympatric sites yielded no evidence of foraging habitat partitioning or exclusion. There was evidence of nesting habitat partitioning. Wilson's Warblers nested on the ground, with some evidence that they used smaller, more densely stemmed shrubs under which to nest. Yellow Warblers are shrub nesters and selected larger, more open shrubs in which to nest. Results provide no evidence that Yellow Warblers can be blamed for population declines in Wilson's Warblers.

SINOPSIS. **Habitates reproductivos usados por las poblaciones de la *Wilsonia pusilla* y la *Dendroica petechia* en situaciones simpátricas y alopatricas**

Estudiamos el habitat de las *Wilsonia pusilla* y la *Dendroica petechia* en las Montañas Rocosas del norte de Colorado y sudeste de Wyoming con el fin de entender las diferentes necesidades en su habitat y interacciones de estos dos especies. La *Wilsonia pusilla* y la *Dendroica petechia* usaron habitats muy similares para alimentarse, seleccionando arbustos mas grandes y mas abiertos. A pesar de sus selecciones similares de habitats para alimentarse, las comparaciones sobre el uso de habitats por las dos especies en los sitios simpátricos no da evidencia de partición o exclusión de los habitats para su alimentación. Sí hubo evidencia de particion del habitat para anidar. La *Wilsonia pusilla* anidaba en el suelo, con evidencias de que usaban arbustos mas pequeños y densos debajo de los cuales hacian el nido. La *Dendroica petechia* anidaba en los arbustos y seleccionaba arbustos mas grandes y mas abiertos en los que anidar. Las resultas no proveen evidencia que la *Dendroica petechia* puede estar culpado para el decline de la población de la *Wilsonia pusilla*.

Key words: Colorado, *Dendroica petechia*, habitat use, montane willow habitat, resource partitioning, *Wilsonia pusilla*, Wyoming

In the Rocky Mountains, Wilson's Warblers (*Wilsonia pusilla*) and Yellow Warblers (*Dendroica petechia*) are among the most common species in the riparian bird community (Knopf 1985; Krueger 1985). In Colorado, Yellow Warblers breed in deciduous habitats across the state, while Wilson's Warblers breed primarily in montane riparian areas (Andrews and Righer 1992; Kingery 1998). Over relatively small areas and changes in elevation one can find riparian sites where breeding Yellow Warblers and Wilson's Warblers are sympatric (Knopf 1985).

As two of the most common species in montane riparian communities, evidence of their population declines raises concern about the

health of the ecosystem and an interest in causative factors. Based on the Breeding Bird Survey (Sauer et al. 2000), Wilson's Warbler populations show a significant survey-wide decline (2% per year) from 1980–1999, while Yellow Warblers show a significant increase (<1% per year). Due to declining populations, the Wilson's Warbler is identified as a priority high-elevation riparian species for the Southern Rocky Mountain physiographic area, while Yellow Warbler is listed as an "associated species," indicating that it may respond in similar ways to changes in these habitats (Colorado Partners in Flight 2000).

Declines in Wilson's Warbler populations, which contrast with population increases in Yellow Warblers, suggest the possibility that the two species may have different habitat needs or may use resources differently where populations are sympatric. A better understanding of differ-

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ences and similarities in habitat use may help explain differing population trends and assist resource agencies in managing riparian habitats. We have taken advantage of the occurrence of sites where the two species are either sympatric or allopatric to address these issues. Our study focuses on microhabitat characteristics within one type of relatively homogeneous habitat (montane willow riparian habitat). Because we have sampled only one allopatric site for each species and only two sympatric sites, the scope of inference for our study is limited to these sites.

The objectives of this study were to characterize and compare the habitat use and territory selection of these two species in montane riparian habitats where they are allopatric and sympatric and determine whether they partition the habitat at sites where they are sympatric.

METHODS

Study areas. We studied warblers in montane riparian sites in the Rocky Mountains of northern Colorado and southeastern Wyoming. We used previous data where available, or preliminary visits where no information existed, to document the status of breeding sites (i.e., as allopatric or sympatric) for each species. Hereafter, for simplicity, these sites will be referred to as W (for allopatric Wilson's Warbler), S (for sympatric), and Y (for allopatric Yellow Warbler) sites. The W site was located in Pingree Park on Colorado State University land surrounded by the Roosevelt National Forest in Larimer County, Colorado. This site is along the South Fork of the Cache La Poudre River (elevation 2750 m). From 1981–1982, and again from 1987–1991, only breeding Wilson's Warblers were recorded at this site (Knopf 1985; R. Bereson, pers. comm.). Two S sites were sampled: the Colorado State Forest just north of Gould, Colorado, along the North Fork of the Michigan River (elevation 2616 m) in Jackson County; and the Medicine Bow National Forest near Mountain Home, Wyoming along Pelton Creek (elevation 2480–2550 m). During preliminary reconnaissance visits by one of us in 1996, both Wilson's and Yellow Warblers were observed during the breeding season at the Michigan River site. From 1982–1984, both Wilson's and Yellow Warblers were found breeding at the Pelton Creek site (Krueger

1985). For the Y site, we used the substantial data of Knopf and Sedgwick (1992). These data were collected from breeding seasons during 1981–1984 on the Illinois River (elevation 2504 m) at Arapaho National Wildlife Refuge (NWR) in Jackson County, Colorado. A MAPS (Monitoring Avian Productivity and Survivorship) station was located at the Arapaho NWR, and from 1995–2000 a total of 592 Yellow Warblers were banded (range of 73–125 per year). By comparison, a total of 18 Wilson's Warblers were banded (range of 1–6 per year). Of the Wilson's Warblers banded, 50% were immature, and all but two were captured after 15 July (P. Bilbeisi, pers. comm.), a date by which young have fledged and most have departed from breeding sites in the mountains (JMR, unpubl. data; R. Bereson, pers. comm.).

At all sites, willow shrubs were the primary woody vegetation. The Y site was a habitat mosaic with coverage of 18% woody species, 13% water, and 69% native grasses and forbs. Woody species included coyote willow (*Salix exigua*), Geyer willow (*S. geyeriana*), Wolf willow (*S. wolfii*), planeleaf willow (*S. planifolia*), Bebb willow (*S. bebbiana*), *S. monticola*, *S. caudata*, and *S. pseudocordata* (Knopf et al. 1988). The S site in Wyoming was dominated by Geyer willow, along with Wolf willow and *S. boothii* and was interspersed with meadows of sedges (*Carex* spp.), reedgrass (*Calamagrostis* spp.), and hairgrass (*Deschampsia caespitosa*; Raley and Anderson 1990). The W site was also dominated by willow species (*Salix* spp.), with other common woody species being bog birch (*Betula nana*) and shrubby cinquefoil (*Potentilla fruticosa*). Dominant herbs included beaked sedge (*Carex utriculata*), wire rush (*Juncus balticus*), Kentucky bluegrass (*Poa pratensis*), slender wheatgrass (*Agropyron cristatum*), and *Potentilla* spp. (W. Leininger, pers. comm.). The vegetation at the S site in Colorado was similar to that at the other sites and was at least superficially more similar to the S site in Wyoming than to the Y or W site.

Field protocols. We used a "bird-centered" perspective to define habitat use (Wiens 1985). In order to define the range of habitats used, both foraging and nest sites were sampled. Searches for foraging birds were conducted from sunrise until approximately 10:00. We identified foraging-centered shrubs (hereafter simply foraging) by following warblers until the

initiation of the first new foraging bout, at which time that shrub was marked for later measurement. Nest-centered shrubs (hereafter simply nests) were identified as the shrubs in which, or under which, nests were found; marks were placed near shrubs to identify them for later measurement. Substantial effort was made to avoid collecting multiple observations from the same individual so as to ensure independence. For example, the observer flagged shrubs where foraging males had been observed, and subsequently sampled those territories only for foraging females or nests. The goal was to collect data from 30 foraging males, 30 foraging females, and 30 nests for each species. The foraging or nest shrub was considered the "focal shrub" for vegetation measurements and analysis. To define available habitat at each site, "random shrubs" were sampled throughout each study site ($N = 30$ for the W site and $N = 59$ for the two S sites). At the S and W sites, these random shrubs were located by pacing random distances and directions and selecting the closest shrub. At the Y site, random shrubs ($N = 292$) were located at 100-m intervals along and random distances perpendicular to the stream bank (Knopf and Sedgwick 1992).

The W site was sampled from 11 June–17 July 1996, the two S sites were sampled from 10 June–24 July 1997, and the Y site was sampled in the summers of 1981–1984 (Knopf and Sedgwick 1992). Horizontal and vertical vegetation structure was quantified using previously developed protocols (Knopf and Sedgwick 1992). For each focal and random shrub, we measured shrub height, maximum radius, and height of maximum radius measurement. We recorded the number of hits by live and dead stems along the north-south and east-west axes through this shrub at the height of maximum radius. The distance from the outer edge of the focal or random shrub to the nearest shrub was measured in each quadrant described by the cardinal directions, as well as the height, maximum radius, and height of radius of that nearest shrub.

Statistical analyses. Data for foraging individuals were pooled across sexes in order to focus on interspecific habitat use comparisons. There is evidence of sexual differences in foraging location for some warbler species (Morse 1968; Busby and Sealy 1979; Franzreb 1983; Petit et al. 1990). This could produce biased

estimates if males and females differ in their behavior (Hutto 1981; Hanowski and Niemi 1990). However, as Hutto (1981) points out in justifying pooling across sexes for foraging observations, when working in willow habitats with a canopy substantially lower than the habitats in which sexual differences were documented, the magnitude of intersexual differences is unlikely to be greater than that of interspecific differences in foraging heights.

In 1996, at the W site, observations were recorded for 30 foraging male Wilson's Warblers, 30 foraging females, and 32 nests. In 1997, two locations were necessary to obtain adequate sample sizes for S sites, and these data were pooled for analysis. Observations were recorded for 33 foraging male Wilson's Warblers, 27 foraging females, and 9 nests, and for 26 foraging male Yellow Warblers, 25 foraging females, and 19 nests. The existing data set at the Y site contained observations for 62 foraging male Yellow Warblers, 36 foraging females, and 58 nests.

A correlation analysis of the 23 variables measured at each random or focal shrub led to the retention of twelve vegetation structure variables for analysis (Table 1). Vegetation data for random, foraging, and nest shrubs were analyzed following the principal components analysis (PCA) procedure described by Rotenberry and Wiens (1981, 1998). First, to characterize available vegetation habitat and to create a framework for scoring all raw data, data for random shrubs from all sites were pooled to form a data set ($N = 381$) subjected to a PCA (Pielou 1977, 1984). Principal components with eigenvalues >1.0 were retained for further analysis (Guttman 1954), and were rescaled and transformed to yield a varimax rotated factor pattern matrix (Manly 1986). This matrix was used to interpret and label the factors retained for analysis. It was also used to score the raw vegetation data for random, foraging, and nest shrubs so as to create a new data set consisting of the factor scores for each shrub (Manly 1986). The scored data we present are a projection of the raw data into a smaller dimensional factor space and, for purposes of statistical analysis, were treated as if they were obtained by direct measurement on the sample units.

A one-way ANOVA, followed by the SNK multiple comparison procedure ($\alpha = 0.05$), was

Table 1. Vegetation variables measured at random shrubs, as used in the principal components factor analysis, and varimax-rotated factor loadings for principal components (with eigenvalues >1.0). Coefficients with an absolute value >0.5 (denoted by *) represent factor loadings used to interpret and apply labels to factors. Factor labels: Factor I = Random shrub size/density; Factor II = Size of surrounding shrubs; Factor III = Random shrub vigor.

Vegetation Variables	Description	Factor I	Factor II	Factor III
HT1	Height of random shrub (dm)	0.89*	0.29	0.12
DIAM1	Diameter of random shrub (dm)	0.85*	0.38	0.06
SHRBVOL1	Volume ¹ of random shrub (dm ³)	0.78*	0.39	0.00
PLIVE	Percent live stems in random shrub (%)	-0.00	-0.01	0.96*
DENSLIVE	Number of live stems in random shrub	-0.48	-0.21	0.77*
DENSDEAD	Number of dead stems in random shrub	-0.42	-0.16	-0.76*
DENSSTEM	Mean stem density in random shrub (hits/dm)	-0.72*	-0.30	0.21
MHT4	Mean height of 4 surrounding shrubs (dm)	0.30	0.88*	0.11
MDIAM4	Mean diameter of 4 surrounding shrubs (dm)	0.25	0.92*	0.05
MVOL4	Mean volume of 4 surrounding shrubs ¹ (dm ³)	0.24	0.90*	0.05
MDHT	Mean difference in height between random shrub and 4 surrounding shrubs (dm)	0.84*	-0.42	0.05
MSEP	Mean distance between random shrub and 4 surrounding shrubs (dm)	0.01	0.38	-0.12
% Total variance		44	18	16
Cumulative variance		44	62	78

¹ Volume is calculated as volume of a spherical segment plus the frustum of a cone.

used to identify site differences in available habitat (i.e., random shrubs). Two-tailed *t*-tests for independent samples ($\alpha = 0.05$) were used to test for differences in the means between two classes of observations (e.g., foraging vs. random shrubs). In cases where variances were not homogeneous, the Satterthwaite (1946) approximation of the degrees of freedom for the approximate *t* statistic was used. All analyses were carried out using SAS (SAS Institute, Inc. 1989).

RESULTS

Habitat characterization. Principal components analysis of the vegetation data from random shrubs, pooled across all sites, led to the retention of three components explaining a total of 78% of the variance (Table 1). High positive or negative loadings indicate important variables for that component. Factor I can be interpreted as a "size-stem density" variable for the random or focal shrub. Low values for Factor I indicate a small, densely stemmed shrub and high values a large, open shrub. Factor II is a "size" variable for the shrubs surrounding the random or focal shrub, where low and high values indicate small and large shrubs respec-

tively. Factor III is interpreted as a "vigor" variable for the random or focal shrub, where low and high values indicate low and high vigor respectively.

Site vegetation comparisons. ANOVAs testing for site differences in available habitat were significant for all factors (Factor I: $F_{2,378} = 7.0$, $P < 0.01$; Factor II: $F_{2,378} = 36.0$, $P < 0.001$; Factor III: $F_{2,378} = 3.3$, $P < 0.04$). The SNK test indicates that random shrub size (Factor I) at the Y site was greater than at the S and W sites (Fig. 1), with the same pattern seen for surrounding shrub size (Factor II). Although random shrub vigor (Factor III) varied by site, and it appears that it was greater at the S sites than at the Y and W sites (Fig. 1), the mean values could not be separated using the SNK procedure. Because of possible confounding effects of annual and between-site differences, we will focus our discussions on within-site habitat use comparisons. Table 2 provides means (\pm SD) for the raw data from selected variables used in the PCA to give a general idea of the actual vegetation measurements at random, foraging and nest shrubs.

Bird-habitat associations. At the Y site, tests for differences between random shrubs ($N = 292$) and Yellow Warbler foraging shrubs (N

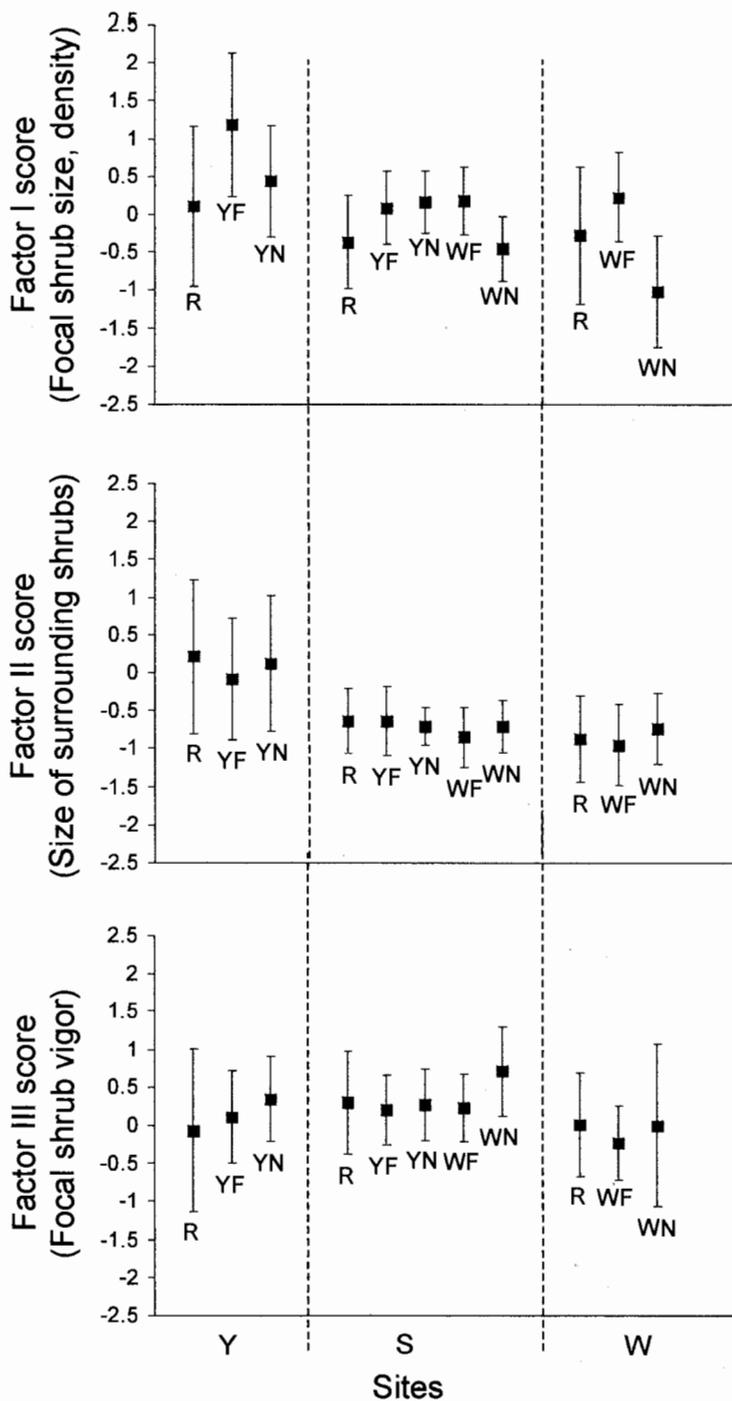


Fig 1. Factor scores (mean \pm SD) for random, foraging, and nest shrubs by site. Factor score labels: R = random; YF = Yellow Warbler foraging; YN = Yellow Warbler nest; WF = Wilson's Warbler foraging; WN = Wilson's Warbler nest. Site labels: Y = Allopatric Yellow Warbler site; S = Sympatric sites; W = Allopatric Wilson's Warbler site.

Table 2. Means (\pm SD) of raw data for selected variables used in PCA analyses to characterize available habitat (random measurements) and habitat used by foraging and nesting warblers.

Site	Variable	Random shrubs	Yellow Warbler		Wilson's Warbler	
			Foraging	Nest	Foraging	Nest
Y Site	HT1 (m)	2.7 (\pm 1.3)	4.0 (\pm 1.2)	3.4 (\pm 1.1)	—	—
	DIAM1 (m)	3.6 (\pm 2.3)	5.1 (\pm 1.6)	4.3 (\pm 1.4)	—	—
	PLIVE (%)	61 (\pm 29)	65 (\pm 21)	70 (\pm 15)	—	—
	MDHT (m)	0.2 (\pm 1.1)	1.3 (\pm 1.2)	0.6 (\pm 0.9)	—	—
S Sites	HT1 (m)	2.0 (\pm 0.7)	2.6 (\pm 0.6)	2.6 (\pm 0.5)	2.5 (\pm 0.5)	1.8 (\pm 0.7)
	DIAM1 (m)	2.1 (\pm 1.0)	2.9 (\pm 0.9)	3.1 (\pm 0.8)	3.0 (\pm 1.0)	1.5 (\pm 0.6)
	PLIVE (%)	69 (\pm 15)	68 (\pm 12)	70 (\pm 12)	69 (\pm 12)	82 (\pm 16)
	MDHT (m)	0.1 (\pm 0.6)	0.5 (\pm 0.7)	0.6 (\pm 0.5)	0.7 (\pm 0.6)	0.1 (\pm 0.6)
W Site	HT1 (m)	2.3 (\pm 1.0)	—	—	2.8 (\pm 0.6)	1.2 (\pm 1.0)
	DIAM1 (m)	2.1 (\pm 1.2)	—	—	2.7 (\pm 1.0)	1.0 (\pm 0.9)
	PLIVE (%)	60 (\pm 14)	—	—	56 (\pm 14)	61 (\pm 23)
	MDHT (m)	0.5 (\pm 1.0)	—	—	1.0 (\pm 0.7)	-0.3 (\pm 0.7)

= 98) were significant for all three factors (Factor I: $t_{388} = 9.0$, $P < 0.001$; Factor II: $t_{210} = -3.0$, $P < 0.01$; Factor III: $t_{298} = 2.0$, $P < 0.05$). This indicates that foraging Yellow Warblers used larger, more open and vigorous shrubs surrounded by smaller shrubs (Fig. 1). Tests for differences between nest ($N = 58$) and random shrubs were significant for two factors (Factor I: $t_{109} = 2.9$, $P < 0.01$; Factor III: $t_{154} = 4.2$, $P < 0.001$), indicating that nesting Yellow Warblers also used larger, more open and vigorous shrubs (Fig. 1).

At the S sites, tests for differences between random shrubs ($N = 59$) and both Yellow Warbler foraging ($N = 51$) and nest shrubs ($N = 19$) were significant for Factor I (foraging: $t_{107} = 4.4$, $P < 0.001$; nests: $t_{46} = 4.3$, $P < 0.001$), indicating that both foraging and nesting Yellow Warblers used larger, more open shrubs (Fig. 1).

At the W site, the test for differences between random shrubs ($N = 30$) and Wilson's Warbler foraging shrubs ($N = 60$) was significant for Factor I ($t_{42} = 2.8$, $P < 0.01$), indicating that foraging Wilson's Warblers used larger, more open shrubs (Fig. 1). The test for differences between random shrubs and nest shrubs ($N = 32$) was significant for Factor I ($t_{60} = -3.5$, $P < 0.001$), indicating that nesting Wilson's Warblers used smaller, more densely stemmed shrubs (Fig. 1).

At the S sites, tests for differences between random shrubs ($N = 59$) and Wilson's Warbler foraging shrubs ($N = 60$) were significant for two factors (Factor I: $t_{106} = 5.6$, $P < 0.001$;

Factor II: $t_{117} = -2.8$, $P < 0.01$), indicating that foraging Wilson's Warblers used larger, more open shrubs surrounded by smaller shrubs. Tests found no significant differences between random and Wilson's Warbler nest shrubs ($N = 9$).

Interspecific bird-habitat comparisons.

At the S sites, results of tests for differences in both foraging and nest shrubs between the two species indicate that foraging Yellow Warblers used sites with larger surrounding shrubs (Factor II) than foraging Wilson's Warblers ($t_{109} = 2.6$, $P < 0.01$). There was no evidence of differences in the size and density (Factor I) or vigor (Factor III) of foraging shrubs used by the two species. Comparisons indicate that nesting Wilson's Warblers used smaller, more densely stemmed (Factor I: $t_{26} = 3.7$, $P < 0.01$) and more vigorous (Factor III: $t_{26} = 2.1$, $P = 0.04$) shrubs than nesting Yellow Warblers.

DISCUSSION

The results presented here allow us to reject the hypothesis that Yellow Warblers situate territories randomly within willow habitats. Yellow Warblers clearly use larger, more open shrubs in which to forage and nest, a pattern demonstrated at both the Y and S sites.

For Wilson's Warblers we also rejected the hypothesis that territory site selection is random. In a pattern quite similar to Yellow Warblers, Wilson's Warblers use larger, more open shrubs in which to forage at both the W and S sites. Because insectivorous birds are often re-

sponsive to insect abundance and density, our observations on foraging shrub selection in both species are consistent with a strategy of selecting foraging substrates that support larger prey populations (Cody 1981; Hutto 1985; Rotenberry and Wiens 1998), or a strategy of selecting sites that provide higher perches and more open structure for viewing approaching predators (Pulliam and Mills 1977; Martin 1992; Rotenberry and Wiens 1998).

Differences in food habits, foraging strategies, or microhabitat selection are potential means of partitioning limiting resources (MacArthur 1958; Cody 1978). However, for this resource (larger, more open shrubs for foraging) there was neither evidence of resource partitioning (i.e., no evidence of significantly different foraging shrub sizes for the two species where they are sympatric), nor exclusion (i.e., no clear evidence that either species changed its habitat use at the sympatric sites). We conclude that foraging Wilson's and Yellow Warblers use habitat in a very similar way, but do not appear to partition these resources as defined in our study. This is consistent with other studies comparing foraging behavior in these two species (Whitmore 1977; Eckhardt 1979; Hutto 1981), although foraging heights within shrubs seem to differ (Hutto 1981).

When resources are limiting, competition, habitat partitioning, or displacement may occur. However, when resources are plentiful, these factors may be reduced or absent, and differences between coexisting species may not be obvious (Wiens 1977; Frakes and Johnson 1982). Insect resources and foraging substrates may be available in such great quantities in these willow habitats that Wilson's and Yellow Warblers do not partition the habitat for access to resources. It is also possible that these two species are partitioning food resources in a different way, perhaps through use of different prey types or sizes (Eckhardt 1979; Raley and Anderson 1990) or through different locations within shrubs (Hutto 1981).

Wilson's Warbler nesting strategy is distinct from that of Yellow Warblers, most obviously in the Wilson's Warbler's placement of nests on the ground rather than in shrubs. Wilson's Warblers clearly nested under smaller, more densely stemmed shrubs (Factor I) at the W site. This finding is consistent with previous research conducted at this site (R. Bereson, pers. comm.).

Although there is no similar statistical evidence for the same nesting preference at the S site when comparing nests with available habitat, we did observe that Wilson's Warblers used smaller, more densely stemmed shrubs for nesting when compared with Yellow Warbler nests.

In light of our results, montane riparian resource managers should carefully consider any management practices, such as grazing, that might have negative impacts on shrub size, density, and vigor (Knopf and Cannon 1982). Although we found no evidence of interspecific habitat partitioning or exclusion, additional studies and analyses would be helpful in determining whether habitat is partitioned in other ways (e.g., interspecific territoriality, diet, or foraging height) and exploring whether the pooling of foraging observations across sexes is indeed warranted. At a larger scale (a broader continuum of habitat types) than the focus of our study, there is evidence of differences in habitat preferences between these two species related to gradients in elevation, moisture, vegetation height, and composition (Hutto 1981; Finch 1989). This may help explain the existence of sympatric populations, particularly if our sympatric sites represent "intermediate" sites along these gradients. Our results provide no evidence that Yellow Warblers can be blamed for the negative trends in Wilson's Warbler populations. This supports the strategy of managing high elevation riparian habitats for priority species like Wilson's Warblers, with the assumption that this will also benefit associated species like Yellow Warblers (Colorado Partners in Flight 2000).

ACKNOWLEDGMENTS

We thank Fritz L. Knopf and James A. Sedgwick for sharing their data from the Arapaho NWR and Rachel Bereson for sharing her insights on Wilson's Warblers at Pingree Park. Access to study areas was granted by Colorado State University, Colorado State Forest, and Medicine Bow National Forest. Financial and logistical support was provided by the U.S. Geological Survey, and housing during the field season was provided by the Roosevelt National Forest and the Colorado Division of Wildlife. We thank Fritz L. Knopf, James A. Sedgwick, Natasha B. Kotliar, Sandi Godbey, Richard L. Hutto, Jacqueline Weicker, and anonymous reviewers for valuable comments that improved earlier versions of this manuscript.

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