STOPOVER ECOLOGY AND HABITAT USE OF MIGRATORY WILSON'S WARBLERS

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ABSTRACT.—The conservation of long-distance migratory songbirds is complicated by their life-history characteristics and the spatial scales that they traverse. Events during migratory stopovers may have significant consequences in determining the population status of migratory songbirds. Using Wilson's Warbler (*Wilsonia pusilla*) as a focal species, we investigated effects of age and sex on stopover parameters during spring and fall migration. Variation in stopover patterns was predominantly sex related in spring and age related in fall. In spring, males appeared at study sites earlier than females, and they carried higher fat stores and had lower recapture rates and higher rates of mass gain. In fall, migratory passage overlapped temporally among age and sex classes, but young birds had lower fat stores, higher recapture rates, and longer stopovers than adults. Habitat use differed between spring and fall migration and was affected by the combination of age and sex. Wilson's Warblers appeared to prefer native willow habitat during spring migration. Agriculture field/edge habitats may have represented "sink habitats" because birds in these habitats tended to be immatures and had a lower rate of fat deposition and longer stopovers. The data suggest that immatures were particularly vulnerable to habitat disturbances at stopover sites during fall migration, probably because of their lower social status and inexperience with long-distance migration. We conclude that knowledge of intraspecific variation in migration strategies is important for effective management of stopover habitats for migratory songbirds. *Received 5 November 1997, accepted 19 March 1998.*

THE CONSERVATION OF NEARCTIC-NEOTROP-ICAL SONGBIRDS has been the subject of considerable interest because populations of some species have declined in recent years (Askins et al. 1990, Finch 1991). Conservation of long-distance migratory birds is difficult because of their complicated life-history characteristics and the spatial scales over which these migrants are associated. Migratory species spend two-thirds of their lifetime away from breeding grounds in North America, which means that conservation efforts cannot be targeted at the breeding grounds alone. Although events during migration may play a critical role in determining the population status of migratory songbirds (Moore et al. 1995), stopover ecology and the importance of habitat during migration have been largely overlooked in developing conservation strategies for migratory songbirds

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(Berthold and Terrill 1991, Moore and Simons 1992).

Migratory behavior might be affected by constraints that vary between seasons and among age and sex classes (Francis and Cooke 1986, Nolan and Ketterson 1990, Carpenter et al. 1993, Spina et al. 1994). One such constraint is sex-related selective pressure for breeding success. In many passerines, males compete for territories and mates on the breeding grounds (Myers 1981) and are selected to arrive on the breeding grounds as early as food resources and/or weather conditions permit. In contrast, females arrive later, closer to the time they can nest successfully (Francis and Cooke 1986). A second constraint involves age-related differences in migration experience (Woodrey and Moore 1997). Migration is a high-risk event that can be energetically expensive. Transients must contend with fluctuations in food availability (Mehlum 1983), predation (Lindström 1989, Aborn 1994), the likelihood of inter- and intraspecific competition (Moore and Yong 1991), and limited stopover habitats (Moore et al.

1995). These challenges undoubtedly are magnified for young birds that are on their first migration to the wintering grounds in fall.

Moore et al. (1995) suggest that migrant songbirds select specific stopover habitats during migration because the probability that a migrant will meet its energetic requirements and achieve safe passage depends on the intrinsic suitability of the stopover habitat. Little is known about the potential effects of age- and sex-related constraints on parameters such as body condition, stopover length, rate of fat deposition, and habitat use during migration, not to mention implications for establishing conservation programs related to stopover habitats of migratory birds. Using the Wilson's Warbler (*Wilsonia pusilla*) as a focal species, we examined variation in those parameters during spring and fall stopover. We selected this species because it is one of the most common Nearctic-Neotropical migratory species in the western United States during both spring and fall migration. The sex of Wilson's Warblers can be reliably determined during spring and fall, and age determination is possible throughout the fall (Pyle 1997). Moreover, breeding populations of this species have declined continent-wide in the past two decades (Sauer et al. 1997, Yong and Finch 1997a).

Because a migrant's "goals" differ between seasons, we might expect variation in stopover length, capture rate, and fat deposition rate to be primarily age-related in fall and sex-related in spring. Thus, we make three predictions. First, intraspecific variation in stopover patterns should be sex-related in spring; specifically, we expect that males should occur at our study site earlier and have lower recapture rates, shorter stopovers, and faster rates of fat deposition than females. Second, assuming that males and females face similar time constraints in fall (Ellegren 1991, Morris et al. 1996), stopover variation should be small between adult males and females compared with the variation related to age. Specifically, we expect that young birds on their first migration should experience longer stopovers, higher recapture rates, and lower rates of fat deposition. Third, for the same reasons listed above, habitat distribution of Wilson's Warblers should differ between males and females in spring and between immatures and adults in fall. Because patterns of habitat use are affected by a bird's

energy requirements (Schoener 1968), selection for shorter stopover and faster fat deposition of males, intersexual competition, or both may result in intersexual differences in habitat use during spring stopover. In fall, young birds may use habitats where adults are less common. Although lower food resources may characterize these habitats, the advantages of reduced competition from adults may outweigh the feeding disadvantages.

METHODS

Study site.—The middle Rio Grande riparian forest in New Mexico, locally known as the "bosque," represents one of the largest cottonwood (*Populus* spp.) gallery forests in the southwestern United States. This wooded reach of the Rio Grande River extends from Cochiti Dam at Sandoval, downstream 260 km to San Marcial (Howe and Knopf 1991). We established netting sites at the Rio Grande Nature Center (35°07'N, 106°41'W), Bernalillo County, and at the Bosque del Apache National Wildlife Refuge (33°48'N, 106°52'W), Socorro County. The floodplain at these sites typically is level and broad, varying from 2 to 10 km. Riparian forest habitat lies within or immediately adjacent to the levees paralleling the river. The remainder of the floodplain has largely been converted to agriculture or residential areas. The netting locations were classified into cottonwood/native understory (including willows, mesquite, and New Mexico olive), cottonwood/Russian olive, cottonwood/saltcedar, saltcedar, willow, or agriculture field/edge based on a riparian/wetland vegetation community classification developed by Durkin et al. (1996). The first three habitat types are dominated by Rio Grande cottonwood (*Populus fremontii* var. *wislizeni*) in association with a variety of understory shrubs and small trees, chiefly willows (*Salix* spp.), screwbean mesquite (*Prosopis pubescens*), New Mexico olive (*Forestiera neomexicana*), false indigo (*Amorpha fruticosa*), seepwillow (*Baccharis glutinosa*), Russian olive (*Elaeagnus angustiflia*), and saltcedar (*Tamarix* spp.). Cottonwood trees generally reach 10 to 15 m in height, and the foliage volume varies depending on the age of the forest stands. The shrub layer is best developed in more open areas of these habitats. Cottonwood/Russian olive habitat is characterized by a nearly monotypic understory of dense to moderately dense Russian olive; herbaceous growth is sparse to absent. The saltcedar habitat essentially is dense monotypic saltcedar shrub stands with widely scattered wolfberry (*Lycium andersonii*) shrubs or patches of arrowweed (*Tessaria sericea*). The willow habitat is composed of dense shrubs 2 to 4 m tall and is located immediately along the banks of water channels. The agriculture habitat is composed primarily of alfalfa (*Medicago sativa*) and cornfields.

Capture and recapture.—We collected data in spring from 4 April to 15 June 1994, 3 April to 9 June 1995, and 8 April to 7 June 1996 and in fall from 1 August to 13 November 1994, 31 July to 12 November 1995, and 3 August to 10 November 1996. Forty standard mist nets (12 × 2.6 m) were used to capture birds (20 nets/site). The netting area was about 30 ha at each site (net density ca. 1.5 nets/ha). Nets were placed in proportion to availability of habitat types and opportunistically within each habitat, such as brushy portions of wooded areas, forest edges or breaks, or near water, where birds could be captured most efficiently (Ralph et al. 1993). Nets were kept at the same, or approximately the same locations throughout the study.

To avoid sampling bias, nets were operated simultaneously throughout the season and across habitat types and were checked regularly at intervals of 20 to 30 min. Weather permitting, nets were opened 15 min before sunrise and remained open for about 6 h every morning during the sampling period. For each bird captured, we measured body mass (± 0.1 g using an electronic balance), unflattened wing chord (± 0.5 mm), tail length (± 0.5 mm), and tarsus length (± 0.1 mm). Each bird was banded with an aluminum leg band. Recaptured birds were re-weighed without reference to previous records. Age and sex determination were based on Stewart (1972) and Pyle at el. (1987). Birds were excluded from this study if they could not be aged or sexed.

We estimated the amount of fat stores by two methods. First, the visible subcutaneous fat in the interclavicular fossa and on the abdomen was scored following a 6-point scale (Helms and Drury 1960). Fat scores provide a fairly precise index of fat stores as long as the variability between observers is controlled (Krementz and Pendleton 1990). Field assistants were trained so that observational variation among individuals was minimized. Second, fat-free body mass of each bird was estimated using the linear model from Winker (1995):

$$Y = 0.1878 + 0.8357X, \qquad (1)$$

where Y is fat-free body mass (g) and X is body mass of captured individuals. The amount of stored fat was estimated by subtracting estimated fat-free mass from mass at capture. For convenience, we refer to the first method as "fat class" and the second method as "fat deposit." Wilson's Warblers are transient at our study area; the nearest breeding population is along the border of New Mexico and Colorado. In fall, most Wilson's Warblers have finished molting when they arrive at our study area, so we assumed that the effect of molt on mass change was minimal.

We estimated stopover length by subtracting the date of first capture from the date of last capture. This method yielded a conservative estimate because we assumed that birds arrived on the day of initial banding and departed on the day of last recapture

(Cherry 1982). Individuals that were not recaptured were assumed to have departed from the study site the same day that they were banded, and were assigned a stopover length of zero. We refer to birds captured after the day of initial capture as "recaptures" and all other birds as "non-recaptures." Body-mass change during stopover was estimated as the difference between mass at initial capture and mass at last capture. We performed a regression on capture time and body mass of all birds captured, which yielded an overall rate of body-mass change of 0.14g/h. Body masses of captured and recaptured individuals were then corrected to 1200 by using this index (Cherry 1982, Moore and Kerlinger 1987). We also estimated body-mass change by performing a regression on initial capture time and amount of fat stores (modified from Winker 1995). The rate of mass change was estimated by dividing mass change by stopover length (g/day) and by the slope of the regressions between initial capture time and amount of deposited fat. We assumed that water gain or loss was negligible (Nisbet et al. 1963, Rogers and Odum 1966, Winker 1995).

Data analysis.—Netting efforts were recorded as net-hours (net-h). To compare the relative abundance of Wilson's Warblers among habitats, we adjusted net-h variation by calculating a capture-rate index for each age/sex class in relation to each habitat. We divided the total number of captures by the total number of net-h in a given habitat and then multiplied the result by 1,000. This calculation produced an abundance index of birds/1,000 net-h of banding effort. Because population size differed among age and sex classes, we divided the abundance index of each age/sex class in each habitat type by the overall abundance index across habitats for the respective age/sex class so that we could compare the relative distribution among habitats.

Normality and homogeneity among groups were examined for all variables. We applied Model I (fixed effect) two-way general linear models when assumptions for parametric statistics were met, and used Kruskal-Wallis or Mann-Whitney U-tests otherwise. A Tukey multiple comparisons test was performed when an ANOVA was significant. For categorical data, we used log-linear models to uncover the potentially complex relationships among variables (Everitt 1977). After examination of among-year variation, we combined three years of data to investigate the effects of age and sex. Such combinations should not affect our analyses because mist nets were operated simultaneously in most net locations during the field season, and variation among years was small. We did not include "site" as a variable in our models because net locations at the two study sites represented different habitat types in most cases. Means and standard deviations are reported throughout the manuscript, and a statistical significance level of $\alpha = 0.05$ is used unless indicated oth-

erwise. Sequential Bonferroni tests for multiple com-
parisons were performed when necessary. All anal-
yses were conducted with SPSS/PC (SPSS 1996).

RESULTS

Stopover patterns.—We captured 3,354 Wil-
son's Warblers during 95,777 net-h over the
three years (35 birds/1,000 net-h). We excluded
562 individuals that we were unable to identify
with respect to age or sex. Of the remaining
2,792 birds, 591 (21.2%) were captured in
spring and 2,201 (78.8%) in fall. Females ac-
counted for 32% of the spring captures and
males accounted for 68%. Among the fall cap-
tures, 42% were adults (after hatching-year, or
AHY) and 58% were immatures (hatching-
year, or HY). Among the 928 fall adults, 36%
were females and 64% were males. Of the 1,273
immatures captured in fall, 47% were females
and 53% were males.

As predicted, males occurred and migrated
through the study sites earlier than females in
spring (median Julian date: males = 137, fe-
males = 142; Mann-Whitney U = 25,537, P <
0.001; Fig. 1A, C), although overlap in passage
was obvious. Passage time did not differ
among age and sex classes during fall migra-
tion (Fig. 1B, D).

Upon initial capture, about 48% of the birds
had no observable fat stores (i.e. fat class 0), and
44% possessed only a small amount of stored
fat (fat class 1 and 2; Fig. 2). Fat stores differed
among age and sex classes (G = 230.20, df =
20, P < 0.001; Fig. 2). In fall, 62% of the im-
mature females and 57% of the immature males
had no observable fat stores. In spring, males
carried larger fat stores than did females, and
females captured in spring had smaller fat
stores than females captured in fall (F = 97.17,
df = 3 and 2,746, P < 0.001; Table 1). In fall,
adults carried more fat than immatures in both
sexes (F = 85.91, df = 3 and 2,160, P < 0.001;
Table 1).

As predicted, the recapture rate of males
(5.2%) was significantly lower than that of fe-
males in spring (13.2%; G = 9.16, df = 1, P <
0.01). In fall, the recapture rate for adults (7.6%)
tended to be lower than that for immatures
(9.7%; G = 2.30, df = 1, P = 0.13). The proba-
bility of recapture was related to the amount of
fat upon initial capture. In spring, the amount
of fat at the time of initial capture for recap-
tures (1.06 ± SD of 0.12 g) was lower than that

of non-recaptures (1.12 ± 0.12 g; t = 3.17, df =
584, P < 0.01). The pattern was evident in both
sexes (F = 25.98, df = 3 and 582, P < 0.001) in
spring. In fall, the difference in the amount of
fat between the two groups was smaller (1.08 ±
0.09 g for recaptures and 1.07 ± 0.08 g for non-
recaptures; t = 2.3, df = 2,162, P < 0.05), and
the same was evident among age and sex class-
es (F = 38.16, df = 7 and 2,156, P < 0.001). The
stopover length of recaptures was 2.52 ± 3.14
days in spring and 2.34 ± 2.06 days in fall, and
no difference was detected between the sexes in
either season. Recaptured adults had shorter
stopover lengths than recaptured immature
birds in fall (2.20 vs. 2.42 days; U = 1,642, n =
132, P = 0.05). A positive relationship existed
between estimated fat and initial capture time
(Fig. 3). The recapture data suggest that in
spring, males tended to have a higher rate of
mass gain (0.17 ± 0.33 g/day) than females
(−0.01 ± 0.46 g/day; U = 184.5, n = 46, P =
0.09), whereas no differences in rate of mass
gain were detected among age and sex classes
in fall.

Habitat use.—Capture rate differed among
habitats in spring (G = 142.60, df = 5, P <
0.001; Fig. 4), when 72% of all Wilson's War-
blers were captured in willow habitat. After ad-
justing the samples of each sex class, the cap-
ture rate of females was proportionately higher
in willow and saltcedar habitats, whereas
males were relatively more common in the oth-
er four habitat types (G = 13.43, df = 1, P <
0.001).

Significant age, sex, and habitat effects were
detected (G = 143.10, df = 7, P < 0.0001) in fall,
although birds were more evenly distributed
among habitats in that season than they were
in spring (Fig. 4). Capture rate was highest in
agricultural field/edges (47 birds/1,000 net-h),
followed by cottonwood/Russian olive (40
birds/1,000 net-h) and willow (39 birds/1,000
net-h) (Fig. 4). Capture rates were lowest in
saltcedar habitat (15 birds/1,000 net-h).

After adjusting the samples of each sex and
age class, capture rates of adults were propor-
tionally higher in willow, cottonwood/salt-
cedar, and cottonwood/native understory hab-
itats than were capture rates of immatures,
whereas immatures were relatively more abun-
dant in agriculture field/edge, cottonwood/
Russian olive, and saltcedar habitats (G =
121.49, df = 1, P < 0.0001). Although relative

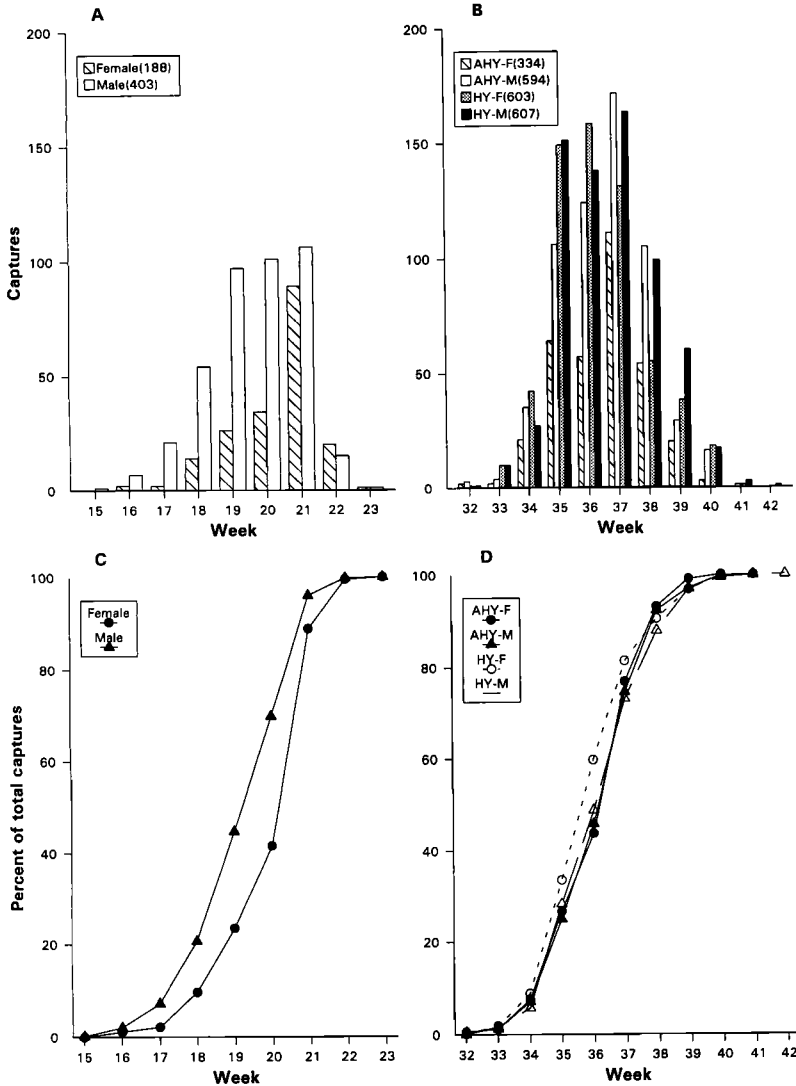FIG 1.   Timing of migration in Wilson's Warblers along the middle Rio Grande, New Mexico. Shown are captures per week in (A) spring and (B) fall and the cumulative percentage of captures in each category having migrated at a certain time in (C) spring and (D) fall. Sample sizes are in the parentheses. Week 15 is the second week of April, and week 32 is the second week of August.

capture rates among habitats differed between the sexes ($G = 7.30$, df $= 1$, $P < 0.01$), the difference was small compared with the variation between age classes within a given habitat (Fig. 4).

Body mass of females in spring and within all age and sex class in fall did not differ among habitats (Table 2). In spring, males captured in the cottonwood/Russian olive habitat were heavier than those captured in willow and agriculture field/edge habitats ($F = 6.12$, df $= 5$ and 394, $P < 0.001$; Table 2). Slopes of the regression models between initial capture time and the amount of deposited fat were positive in all habitats except agriculture field/edge in spring, and they were significantly positive in cottonwood/Russian olive and saltcedar habitats (Table 3). However, rates of fat deposition were not significantly different among habitats (ANCOVA for equality of slopes, $F = 1.14$, df $= 3$ and 575, $P = 0.33$; Table 3). In fall, all age and sex groups in all habitats showed positive
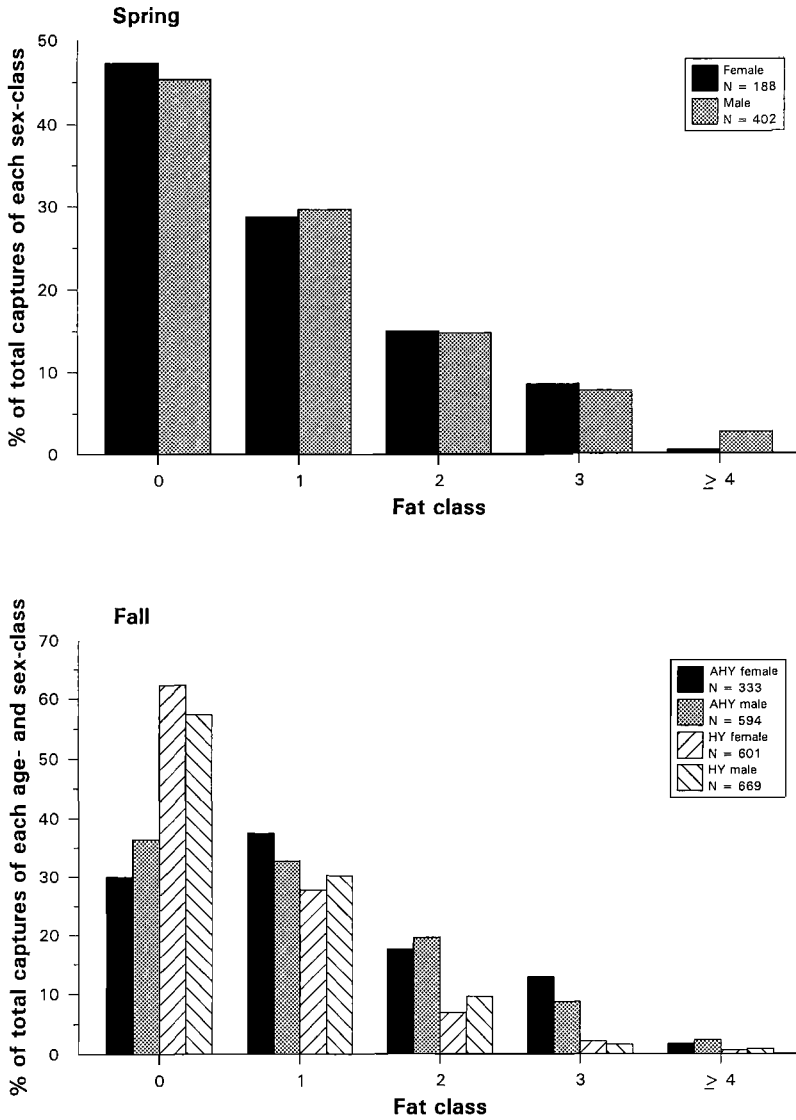
FIG 2.　Distribution of fat classes of Wilson's Warblers captured during spring (upper) and fall (lower) migration along the middle Rio Grande, New Mexico.

TABLE 1.　Measurements of Wilson's Warblers ($\bar{x} \pm$ SD) captured during spring and fall migration along the middle Rio Grande River, central New Mexico. See text for estimation of amount of stored fat.

| Variable	Females			Males		
	Spring (all)	Fall (adult)	Fall (young)	Spring (all)	Fall (adult)	Fall (young)
Body mass (g)	7.03 ± 0.58	7.24 ± 0.49	7.11 ± 0.46	7.56 ± 0.73	7.56 ± 0.78	7.39 ± 0.53
Stored fat (g)	0.97 ± 0.01	1.00 ± 0.01	0.98 ± 0.01	1.05 ± 0.12	1.05 ± 0.01	1.03 ± 0.01
Wing chord (mm)	53.95 ± 1.79	54.93 ± 1.71	54.91 ± 1.39	56.48 ± 2.03	57.04 ± 1.59	56.82 ± 1.69
Tail length (mm)	46.81 ± 2.33	48.17 ± 2.11	48.24 ± 2.26	48.11 ± 2.53	49.34 ± 2.33	49.31 ± 2.22
Tarsus length (mm)	18.13 ± 0.99	18.09 ± 0.84	18.06 ± 0.98	18.14 ± 1.13	18.21 ± 1.00	18.02 ± 0.91
Sample size	188	334	594	403	594	670
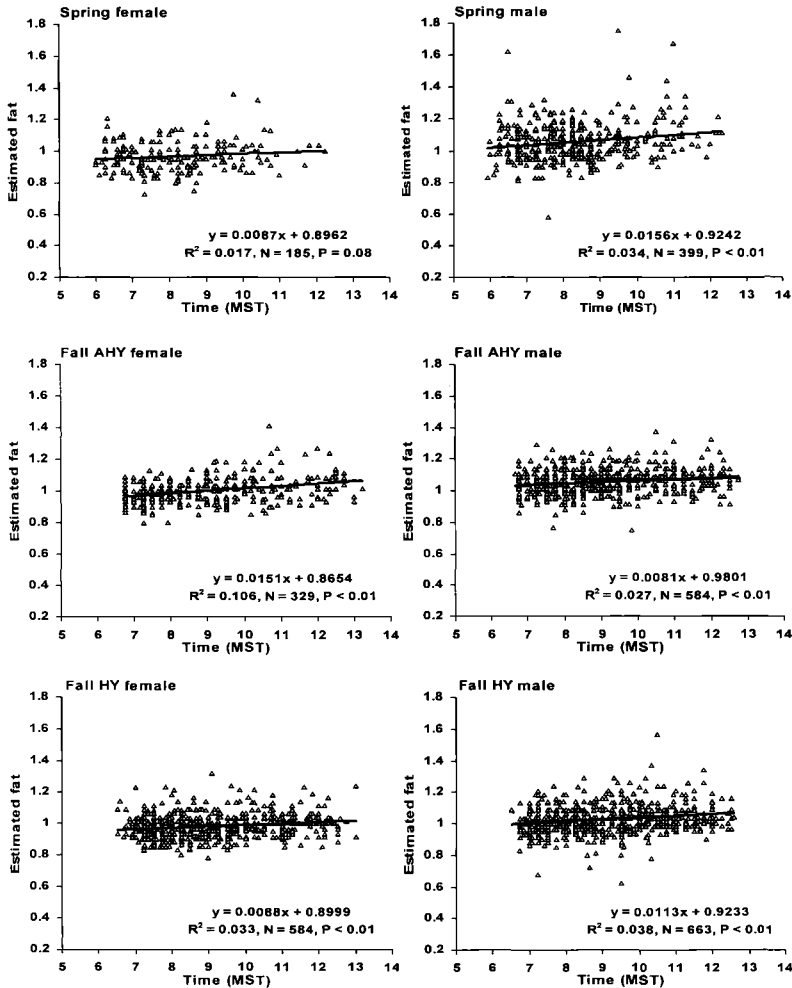
FIG 3.   Age- and sex-related daily body-condition change based on linear regressions between fat stores and capture time. Fat stores were estimated from body mass at capture minus fat-free body mass, which was estimated by $Y = 0.1878 + 0.8357X$, where Y is fat-free body mass in grams and X is body mass of captured individuals (Winker 1995). Sample sizes are in the parentheses.

trends for mass change except AHY males in agriculture field/edge habitat, HY males in cottonwood/saltcedar habitat, and HY females in willow habitat, where a nonsignificant negative trend characterized the data (Table 3). When fall captures were combined by habitat type, the rate of mass gain differed among habitats based on an ANCOVA test on the equality of slopes of the regression equations between estimated fat stores and capture time ($F = 4.11$, df = 3 and 2,007, $P < 0.01$); birds from agriculture field/edge habitat had the lowest rate of mass gain.

The small sample of recaptured birds pre-cluded analysis among age/sex classes across habitat types for some of the variables. However, female recapture rate in spring (19%) was higher than that of males (10%; $G = 5.56$, df = 1, $P < 0.05$) in the willow habitat, where we had a relatively large recapture sample of birds ($n = 40$). In fall, the recapture rate tended to be habitat dependent ($G = 9.92$, df = 5, $P < 0.08$) but was not related to sex or age class ($G = 4.18$, df = 3, $P = 0.24$). In fall, the recapture rate was lowest (6.3%) in willow habitat, followed by agriculture field/edge (7.5%), cottonwood/Russian olive (8.8%), cottonwood/native understory (12.0%), and cottonwood/saltcedar (12.2%).
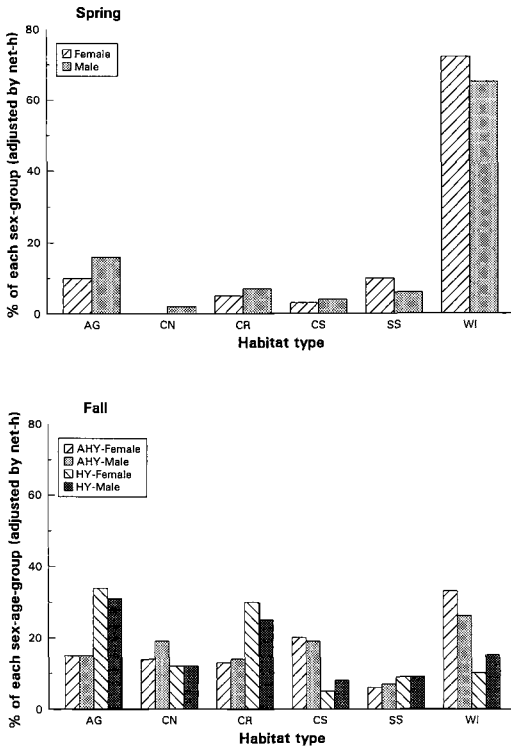
FIG. 4.   Relative distributions of Wilson's Warblers among habitats during spring and fall stopover along the middle Rio Grande, New Mexico. The relative abundance of each age/sex class in each habitat was calculated by dividing the capture number of each age/sex class in each habitat by net hours in the corresponding habitat; the results were then divided by the capture rate of each age/sex class across all habitats and multiplied by 100. See Table 2 for sample size of each age/sex class.

Saltcedar habitat had the highest recapture rate (25%). The length of stopover based on recaptured birds varied among habitats (Kruskal-Wallis test, $\chi^2 = 14.63$, df = 5, $P < 0.05$); birds initially captured in agriculture field/edge tended to have longer stopover (3.16 ± 2.39 days) than those initially captured in other habitats (2.16 ± 1.92 days). In spring, 88% of the recaptures (113) were from the same habitats where the birds were initially captured, and the probability of being recaptured at the initial capture site did not differ between the sexes (Fisher's Exact Test, $P = 0.68$). In fall, only 53% of the recaptured birds (343) were in the same habitats as the initial capture sites, and again, the probability of being recaptured in

the initial habitat did not differ between age classes (Fisher's exact test, $P = 0.46$).

DISCUSSION

Stopover patterns.—The timing of spring passage among Wilson's Warblers in relation to age and sex was consistent with our predictions. Males migrated through our study sites earlier than females, although overlap between the sexes was evident. This pattern was also reported for Wilson's Warblers at other locations (e.g. Ontario [Francis and Cooke 1986]; Veracruz, Mexico [Ramos 1988]; Alviso, California [Otahal 1995]). The female/male capture ratio was about 1:2 during spring migration. We do not believe that this pattern was caused by our sampling effort because we sampled evenly throughout the period of Wilson's Warbler migration. Biased population structure, different migratory routes, disproportionate use of riparian habitat and upland habitat during passage, or other behavioral differences between sexes (see Remsen and Good 1996) could have contributed to a sex-biased capture rate.

We detected no age- or sex-related differences timing of passage during fall migration. This is inconsistent with earlier studies that suggested: (1) adults migrate earlier than immatures in fall (Stewart et al. 1974), (2) immatures migrated earlier than adults (Nilsson 1970), (3) males migrated earlier than females (Ramos 1988), or (4) vice versa (Kjellén 1992). However, our results were consistent with Murray (1966) and Lebeman and Clench (1970), who reported that in many passerine species in eastern North America, adults and immatures travel at approximately the same time during fall migration. Otahal (1995) also found no difference in timing of fall migration between male and female Wilson's Warblers.

Our results suggest that several stopover parameters (e.g. stopover length, recapture rate, and rate of fat deposition) are consistent with sex-specific time constraints in spring and age-specific constraints in fall. The higher fat stores, lower recapture rate, and higher rate of mass gain for male Wilson's Warblers in spring suggest that they migrate earlier and faster than females, although Otahal (1995) found that mass change and length of stay were the same for males and females during spring migration at Alviso, California. This discrepancy may be

TABLE 2. Body mass of Wilson's Warblers captured in different habitats (centered in bold) during spring and fall migration along the middle Rio Grande River, central New Mexico. Values are $\bar{x} \pm$ SD in g, with n in parentheses.

Spring		Fall			
Females	Males	AHY females	AHY males	HY females	HY males
Agriculture field/edge					
6.89 ± 0.68 (8)	7.32 ± 0.76 (27)	7.17 ± 0.36 (52)	7.53 ± 0.49 (95)	7.30 ± 0.40 (181)	7.29 ± 0.48 (188)
Cottonwood/native understory					
—	8.35 ± 0.40 (4)	7.40 ± 0.44 (21)	7.59 ± 0.49 (52)	7.17 ± 0.48 (27)	7.31 ± 0.51 (33)
Cottonwood/Russian olive					
7.30 ± 0.71 (27)	7.92 ± 0.79 (71)	7.37 ± 0.59 (88)	7.65 ± 0.46 (179)	7.12 ± 0.45 (315)	7.45 ± 0.52 (303)
Cottonwood/saltcedar					
7.20 ± 0.54 (6)	7.60 ± 0.59 (21)	7.27 ± 0.49 (65)	7.56 ± 0.52 (109)	7.42 ± 0.73 (23)	7.50 ± 0.61 (49)
Saltcedar					
7.10 ± 0.27 (3)	7.30 ± 0.72 (4)	7.03 ± 0.38 (3)	7.32 ± 0.57 (6)	7.24 ± 0.62 (7)	7.41 ± 0.60 (8)
Willow					
6.99 ± 0.54 (144)	7.47 ± 0.69 (276)	7.11 ± 0.43 (105)	7.47 ± 0.46 (153)	7.15 ± 0.48 (50)	7.34 ± 0.60 (88)
F-value[a]					
1.83	6.12*	3.47	2.46	3.54	2.46

[a] ANOVA among habitats within age and sex classes; *, $P < 0.001$.

due to different study locations, different races being sampled, or both. Most Wilson's Warblers captured during our study belong to *W. pusilla pileolata* and were still on their migratory journey in spring. In contrast, birds captured by Otahal (1995) belonged to the *W. p. chryseola* subspecies and were already at or near their breeding grounds when captured.

During fall migration, variation in stopover parameters in Wilson's Warblers is related to age. The similar passage times between age classes, in combination with higher fat stores upon initial capture, lower recapture rate, and shorter stopover for adults, suggest that hatching-year birds migrate at a slower pace than adults in fall. Woodrey and Moore (1997) found that adults carried significantly higher fat stores than young birds on the coast of Alabama during fall migration for several species, namely Swainson's Thrush (*Catharus ustulatus*), White-eyed Vireo (*Vireo griseus*), and American Redstart (*Setophaga ruticilla*). Veiga (1986) and Ellegren (1991) found that adults had lower recapture rates and shorter stopover times in some Old World passerines. Morris et al. (1996) reported that immatures passerines captured at Appledore Island during fall migration had lower fat stores, lower initial mass, and higher recapture rates than adults, and they suggested that age-specific recapture rates were a func-

tion of hesitation to migrate over the Atlantic Ocean by immatures because they lack experience or are physiologically weaker than adults (see Stewart et al. 1974).

Our study sites are not associated with a major ecological barrier, and stopover habitat is relatively continuous along the migratory route of the Wilson's Warbler. We suspect that the higher recapture rate, lower fat stores, and longer stopovers of immatures during fall migration resulted because these birds were in poorer migratory condition than adults. Several factors might contribute to poor migratory condition. For example, young Wilson's Warblers have shorter and more rounded wings than adults (Yong and Finch unpubl. data) and might consume more energy during a migratory flight, which would require the accumulation of larger fat stores during stopover (or more frequent stopovers). Immature Wilson's Warblers also may forage less efficiently than adults (cf. Moreno 1984, Jansen 1990). Adult birds generally are socially dominant to immatures (e.g. Terrill 1987), which may enable them to use higher-quality habitat during stopover or experience less interference during foraging. Furthermore, if immatures are less efficient than adults at extracting energy and nutrients (see Karasov 1990), it would take longer

TABLE 3. Daily change in amount of stored fat (g) by habitat and age/sex class of Wilson's Warblers. The variables b and a are from $y = ax + b$, where y is estimated fat mass (g) at capture, x is time of capture (hours), b is the y-intercept, and a is the slope. The r-values measure the strength of the relationship between stored fat and time, and the F-values indicate how well the linear model fits the data. Daily changes are based on the average day length during banding operations (following Morris et al. 1996). The analysis was performed for each age/sex class with sample size ≥ 20 and combined at the habitat level otherwise.

Habitat	Group	b	a	r	F	n	Daily change
		Spring					
Agriculture field/edge	All birds	1.03	−0.0035	0.04	0.04	34	0.05
Cottonwood/Russian olive	All birds	0.93	0.0173	0.21	4.52*	96	0.24
Cottonwood/saltcedar	All birds	0.84	0.0236	0.42	5.23*	27	0.33
Willow	All birds	0.97	0.0071	0.08	2.86	419	0.36
	Females	0.91	0.0065	0.10	1.37	143	0.09
	Males	0.98	0.0075	0.09	2.02	276	0.11
		Fall					
Agriculture field/edge	All birds	0.97	0.0032	0.06	1.68	507	0.04
	AHY females	0.93	0.0070	0.17	1.52	52	0.10
	AHY males	1.15	−0.0110	0.19	3.37	93	−0.15
	HY females	0.94	0.0030	0.07	0.82	175	0.04
	HY males	0.94	0.0088	0.15	4.13	188	0.12
Cottonwood/native understory	All birds	0.92	0.0108	0.21	5.99*	132	0.15
	AHY females	0.84	0.0190	0.47	5.24	21	0.27
	AHY males	0.99	0.0070	0.13	0.89	52	0.10
	HY females	0.86	0.0130	0.29	2.23	27	0.18
	HY males	0.94	0.0083	0.16	0.80	33	0.12
Cottonwood/Russian olive	All birds	0.89	0.0137	0.24	52.09**	861	0.19
	AHY females	0.76	0.0280	0.47	23.10**	85	0.39
	AHY males	0.96	0.0112	0.24	10.25*	174	0.16
	HY females	0.87	0.0116	0.23	16.46**	305	0.16
	HY males	0.94	0.0106	0.19	10.76*	298	0.15
Cottonwood/saltcedar	All birds	0.99	0.0055	0.10	2.27	242	0.08
	AHY females	0.92	0.0086	0.21	2.75	64	0.12
	AHY males	1.00	0.0062	0.12	1.42	109	0.09
	HY females	0.86	0.0189	0.23	1.06	22	0.26
	HY males	1.10	−0.0055	0.07	0.23	49	−0.08
Saltcedar	All birds	0.92	0.0112	0.18	0.69	22	0.16
Willow	All birds	0.94	0.0087	0.15	9.25*	394	0.10
	AHY females	0.92	0.0069	0.14	2.19	105	0.10
	AHY males	0.97	0.0088	0.16	3.83	153	0.12
	HY females	1.01	−0.0029	0.05	0.14	49	−0.04
	HY males	0.85	0.0184	0.29	7.99*	88	0.26

*, $P < 0.05$; **, $P < 0.001$.

for them to replenish depleted fat stores before continuing their migration.

Habitat use.—Capture rates were disproportionately high in willow habitat in spring and less variable among habitats in fall. Although our results may be affected by sampling bias associated with mist netting (Remsen and Good 1996), we argue that the observed variation in capture rate reflects differential use of habitats for the following reasons: (1) our analyses are based on a single species, so the effect of behavioral variation among species is not an issue; (2) our between-season comparisons provide an experimental control (i.e. if capture rates were biased in certain habitats, then consistent patterns would be expected between seasons for the same age or sex class, but this was not the case); (3) the structural composition of habitats was relatively stable during the study period so that variation caused by change in habitat was limited; (4) netting effort was continuous throughout the entire migration season in both spring and fall; and (5) we exercised caution when establishing nets, checking nets, and handling birds (cf. Dunn et al. 1997).

Although migratory songbirds use specific habitats and select among alternative vegeta-

tion types during stopover (Moore et al. 1995), only a few studies have documented shifts in habitat use between seasons (Hutto 1985a, b; Winker et. al 1992). We documented age- and sex-related habitat distribution of transient birds. The shift in use of habitat that we observed could be the result of changes in relative resource availability among habitats between seasons, so that birds settle in habitats on the basis of relative suitability (Fretwell and Lucas 1970). Winker et al. (1992) found that Northern Waterthrushes shifted their distribution among swamp, floodplain, and willow habitats, whereas Swainson's Thrushes shifted from drier habitats in spring toward wetter sites in autumn. Hutto (1985a, b) found seasonal habitat shifts among foliage-gleaning insectivorous migrants and also provided convincing evidence that food availability was the intrinsic factor in the birds' assessment of habitat quality during the nonbreeding season. He suggested that the use of direct or indirect cues enabled birds to settle such that their densities matched resource abundance. We observed Willow Flycatchers (*Empidonax traillii*) actively gleaning insects from foliage within dense willow habitat. Densities of arthropods are high in willows relative to other vegetation, especially in spring. We believe that migrating Wilson's Warblers stop more frequently in willow habitats than in other habitat types in spring because willows contain more arthropods, food that Wilson's Warblers favor.

Because the breadth of habitat types occupied by a species could be directly related to its population size (Fretwell and Lucas 1970), the observed shift in habitat use also could have resulted from changes in bird population structure and size between seasons. We captured nearly four times the number of Wilson's Warblers during fall migration than during spring. In addition, more than half of the fall captures were immature birds. The large number of birds in fall may magnify the potential for competition among individuals for high-quality habitats, which may force immatures to use less-favorable habitats by virtue of their lower social status and lack of experience (Carpenter et al. 1993). Although we did not collect resource data, the age-related distribution among habitats during fall was consistent with these expectations. More adults were captured in the willow habitat, whereas more immatures were captured in the agriculture field/edge. Moreover, birds in the agriculture field/edge were associated with lower rates of fat deposition and longer stopover times.

In contrast to high habitat fidelity observed during spring stopover, fall recapture data suggest that Wilson's Warblers were more likely to switch habitats after initial captures. These patterns are consistent with less-experienced immatures being forced to leave more preferred willow habitat, where they initially tried to settle. In addition, because initial body condition (the amount of fat stores) was similar among age and sex classes across habitats, we hypothesize that the initial settlement among habitats was not affected by the physiological condition of the birds. These patterns may support the hypothesis that distribution among habitats was affected by the social status of individuals (Carpenter et al. 1993). However, we detected no sex-biased or age-biased habitat shifts in spring or fall. Shifts among habitats by individuals may raise concern about an analysis based on initial capture data. However, our analysis is justified because: (1) most Wilson's Warblers stopped over briefly (more than 90% of the birds were not recaptured), and a shift in habitat would be less likely among these birds; (2) most (88%) of the recaptures in spring did not show a shift in habitat; and (3) our analysis of body-mass change was based on the entire age/sex sample rather than solely on recaptured birds.

The acquisition of adequate food to replenish fat stores may be the greatest constraint during migration (Moore et al. 1995). The significant relationship between body mass and initial capture time in both spring and fall suggests that Wilson's Warblers gained mass at the study sites during the day (see Winker et al. 1992). Based on the ideal-free distribution model (sensu Fretwell and Lucas 1970), we expect that birds in favorable habitats would deposit fat at higher rates during stopovers. Our results are consistent with this prediction to some extent. In spring, birds from agricultural field/edge habitats tended to lose body mass, whereas those captured in other habitats tended to gain mass. In fall, although all habitats sampled had positive trends, the rate of fat gain was slower among birds captured in the agricultural field/edge habitat and was statistically significant only among birds captured in cottonwood/na-

tive understory, cottonwood/Russian olive, and willow habitats. Caution should be exercised when interpreting our results because variation in mass gain was large within a given habitat, even within the same age and sex classes. Besides, birds in cottonwood/Russian olive and cottonwood/saltcedar habitats in spring, and birds in cottonwood/native understory and cottonwood/Russian olive habitats in fall, obtained a higher rate of mass gain than birds captured in willow habitat in spring and fall. Habitat preferences of Wilson's Warblers could be preprogrammed or influenced by previous experience, which could affect where birds settle during stopovers (see also Hutto 1985a).

CONSERVATION IMPLICATIONS

The pattern of stopover and use of habitat varied between spring and fall passage and variation was age- and sex-specific in the Wilson's Warblers we studied. Wilson's Warblers appeared to prefer native willow habitat along the middle Rio Grande during spring migration. They were able to deposit fat stores and resume migration in a short period of time. On the other hand, more birds used agricultural field/edge habitat during fall migration, and most of these birds were immatures. The agricultural field/edge habitat may have represented "sink habitat" because birds in these habitats tended to have lower rates of fat deposition and longer stopovers. Young birds may be particularly vulnerable to habitat disturbances during the en-route period. Management of stopover habitats for migratory songbird should be conducted with an awareness of age differences in habitat use.

Historically, riparian habitat along the middle Rio Grande (and the western United States in general) has been altered by water management, agricultural conversion, urban development, livestock grazing, and recreational use (Ohmart 1994). In addition, exotic woody species such as saltcedar and Russian olive have encroached in most riparian zones. Lake/marsh and scrubland along the middle Rio Grande has decreased by 150% and 50%, respectively, whereas urban and agricultural land has increased 270% and 14% between 1935 and 1989 (Finch and Yong 1998), according to National Wetland Inventory data. Breeding populations of some songbird species have

been dramatically affected by such changes (DeSante and George 1994). The decline of the endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*) largely is the result of conversion of willow and other native habitats into less-suitable habitats (USFWS 1995, Yong and Finch 1997b). Our data suggest that habitat alteration also might negatively influence populations of Wilson's Warbler during the stopover period—a species that has experienced a continent-wide negative population trend in the last two decades (Sauer et al. 1997, Yong and Finch 1997a). To counteract loss and conversion of native riparian habitats, restoration programs should focus on native vegetation, especially along major migration routes (such as the Rio Grande) in the western United States.

Finally, our findings of sex- and age-specific habitat use and variation between spring and fall periods are important vis-a-vis the establishment of management policies for migratory songbirds. Management policies based on a single season alone are likely to be ineffective and possibly detrimental. For example, the agricultural field/edge habitats were used most often by Wilson's Warblers in fall; yet, birds in these habitats tended to be immatures that were not able to resume migration in a timely manner. When deciding which habitats are important during migration and how to manage for migrant birds at this time, consideration should be given to variation between seasons and among age and sex classes.

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Associate Editor: R. L. Hutto