

MIGRATION OF THE WILLOW FLYCATCHER ALONG THE MIDDLE RIO GRANDE

WANG YONG¹ AND DEBORAH M. FINCH¹

ABSTRACT.—We studied timing, abundance, subspecies composition, fat stores, stopover length, and habitat use of Willow Flycatchers (*Empidonax traillii*) during spring and fall stopover along the Middle Rio Grande, New Mexico. Spring migration started in mid-May and lasted about a month. Fall migration started in early-August and also lasted about a month. The most abundant subspecies was the Southwestern Willow Flycatcher (*E. t. extimus*), followed by *E. t. brewsteri*, *E. t. adastus*, and *E. t. traillii*. Nearly half of the Willow Flycatchers captured had no observable fat. Spring flycatchers had more fat stores than fall flycatchers. Willow habitat had the highest capture rate among the habitats sampled. Willow Flycatchers caught in willow habitat had higher fat stores than those caught elsewhere. Recaptured Willow Flycatchers had an average body mass gain of 1.6%/day with a short stopover length. Most Willow Flycatchers were unable to reach their destinations in a single flight, making it necessary for them to replenish their energy stores elsewhere en route. We suggest that the riparian woodlands of the middle Rio Grande provide important refueling sites for stopover flycatchers as they migrate between their breeding and wintering grounds. Received 3 July 1996, accepted 11 Dec. 1996.

The Willow Flycatcher (*Empidonax traillii*) breeds extensively from southern British Columbia east to Maine and south to California, Arkansas, and Virginia. It winters in Middle America from Veracruz and Oaxaca south to Panama (A.O.U. 1983, USFWS 1995). The species prefers thickets, scrubby and brushy areas, open second growth, swamps, and open woodland, breeding primarily in swampy thickets, especially of willow and buttonbush (A.O.U. 1983). In the southwestern United States, populations of the species have declined through the 20th century (Hubbard 1987, Unitt 1987, USFWS 1995), primarily due to loss of riparian habitat, water development, cattle grazing, brood parasitism by Brown-headed Cowbirds (*Molothrus ater*), and the invasion of riparian habitats by exotic tamarisk (*Tamarix* sp.) (USFWS 1995). The widespread reduction of riparian habitat essential for nesting and foraging is believed to have had the largest impact on the Willow Flycatcher's population (Remsen 1978, Harris et al. 1987, Unitt 1987). Owing to its severe population decline in the Southwest, the U.S. Fish and Wildlife Service listed the Southwestern Willow Flycatcher (*E. t. extimus*) as an endangered subspecies in 1995 (USFWS 1995).

This study provides basic information on migration biology, stopover

¹ USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, 2205 Columbia SE, Albuquerque, New Mexico 87106.

ecology, and use of riparian habitats by Willow Flycatchers during spring and fall migrations along the Rio Grande in central New Mexico. Our objectives were to (1) document seasonal and daily stopover patterns, (2) examine energy (fat) stores, (3) determine fat redeposition rate and stopover length, (4) investigate use of different stopover habitats, and (5) document variations in stopover ecology among subspecies.

METHODS AND STUDY AREA

We established two study sites at the Rio Grande Nature Center (RGNC, 35°07'N, 106°41'W), Bernalillo County, and at the Bosque del Apache National Wildlife Refuge (BNWR, 33°48'N, 106°52'W), Socorro County, New Mexico. Field data were collected in spring from 4 April to 15 June 1994 and from 3 April to 9 June 1995 and in fall from 1 August to 13 November 1994 and from 31 July to 12 November 1995. *F*-tests from ANOVA of differences between sites and years were not significant for most variables, so we combined data collected in 1994 and 1995 across both sites for most analyses.

We used 20 standard, nylon mist nets (12 × 2.6 m) to capture Willow Flycatchers. The netting area was about 30 ha (net density \approx 1.5 nets/ha) at each site. The nets were placed opportunistically at locations, such as brushy portions of wooded areas, forest edges or breaks, and near water, where birds could be captured most efficiently (Ralph et al. 1993). Unless rain, high winds, or temperature dictated a change, mist nets were opened 15 min before sunrise and operated approximately 6 h each banding morning. Each captured individual was weighed to the nearest 0.1 g using a digital electronic balance (ACCULAB V-333). Unflattened wing chord, tarsus, tail length, relative flight feather length (for wing formula calculation), presence of notch and emargination of the primaries, bill width, bill length, bill depth, lower mandible color, wing span, and tail shape were measured according to Svensson (1984) and Pyle et al. (1987). Skull ossification was examined in fall to identify age. Plumage color and relative contrast between parts of the body were recorded by referring to the color standards of Smithe (1975). Each Willow Flycatcher was banded with a numbered aluminum leg band.

We estimated fat stores of each Willow Flycatcher by observing the subcutaneous fat deposits in the interclavicular fossa and abdomen according to a six-point scale developed by Helms and Drury (1960). Estimates of body mass change during stopover were calculated as the difference in body mass between initial capture and last capture, and as the correlation between condition index (mass-wing⁻³) and time of capture for all individuals captured (following Winker et al. 1992). The maximum potential flight ranges were estimated according to Pennycuik (1989) using a wing span of 210 mm (Yong and Finch, unpubl. data), energy density of 31 kJ/g fat (Biebach 1992), still air, and air density of 1.23 kg-m⁻³. Flight range estimates are valuable for generating migratory strategy predictions (Alerstam and Lindström 1990). Birds with zero observable fat could have internal fat detectable via lipid extraction analysis, so we estimated fat-free body mass by subtracting 3% (Berthold 1975) from the average body-mass of fat class zero birds.

Vegetation data from each net location were collected in 1995 based on a modified method of Daubenmire and Daubenmire (1968) and Daubenmire (1970). Habitats were characterized based on a riparian/wetland vegetation community classification developed by Durkin et al. (1996). We identified four major vegetation types: willow, agriculture field, cottonwood-Russian olive, and cottonwood-other vegetation.

The Willow Flycatcher has long been recognized for being geographically variable with four to five races recognized as valid (Phillips 1948, Phillips et al. 1964, Wetmore 1972,

Oberholser 1974, Hubbard 1987, Unitt 1987, Browning 1993). The breeding ranges of the widely distributed *E. t. traillii* and *E. t. campestris* extend across the northern United States and southern Canada, from New England and Nova Scotia west, through northern Wyoming and Montana, and into British Columbia. Hubbard (1987) and Unitt (1987) treated *E. t. campestris* as synonymous with *E. t. traillii*, but Browning (1993) considered them separate subspecies. The subspecies *E. t. adastus* breeds from Colorado west of the plains, west through the Great Basin States and into the eastern portions of California, Oregon and Washington. The breeding range of *E. t. brewsteri* extends from the central California coast north, through western Oregon and Washington to Vancouver Island. The breeding range of the Southwestern Willow Flycatcher, *E. t. extimus*, includes southern California, southern Nevada, southern Utah, Arizona, New Mexico, and western Texas (Hubbard 1987, Unitt 1987, Browning 1993, USFWS 1995).

These subspecies are distinguished primarily by subtle differences in color and morphology. In this study, we adopted the four-subspecies classification system of Hubbard (1987) and Unitt (1987). Subspecies identity using this system is based on measurements of wing, tail, wing formula (relative length of flight feathers), coloration of the head and neck and its contrast with the back, and the contrast between the breast-band and the throat (see Phillips 1948, Hubbard 1987, Unitt 1987, Browning 1993). Given morphological overlap and hybridization among subspecies, complete accuracy in identifying subspecies is not achievable.

All statistical analyses were performed with SPSS/PC + (SPSS 1994). Normality and homogeneity were examined prior to applying parametric tests, and nonparametric tests were used when these assumptions were violated. For sparse contingency tables we used Exact Test, a powerful method for obtaining accurate results when the data set is small (SPSS 1994).

RESULTS

For the two years combined, we operated 59,870 net-hours, and a total of 84 Willow Flycatchers (14 birds/10,000 net-h) were captured during spring ($N = 42$) and fall ($N = 42$) migrations. Spring passage started in mid-May, with first and last captures on May 13 and June 8, respectively. Fall migration started in mid-August with the first capture on August 9 and the last capture on September 16. The mean Julian capture dates of spring and fall migrations were day 148 (May 28) and day 241 (August 29), respectively. While spring migration peaked in the last week of May, no peak was observed in the fall based on weekly captures (Fig. 1). In fall, adults tended to migrate through earlier (Julian date 238 ± 11 , $\bar{x} \pm \text{SD}$; $N = 25$) than hatching-year birds (Julian date 245 ± 11 , $N = 17$, $t = 1.96$, $P = 0.06$). The daily timing of captures peaked around 08:00 (MST) in spring and around 09:00 in fall and the difference was not significant between seasons. About 70% of birds were captured between 07:00 and 09:00.

Fifty percent of the Willow Flycatchers captured did not have any observable subcutaneous fat stores (fat class 0) (Fig. 2), and only 11% had fat stores ranked at fat class two or higher. The average body mass was 12.7 ± 1.2 g with a range of 10.3 to 15.9 g. Body mass was signif-

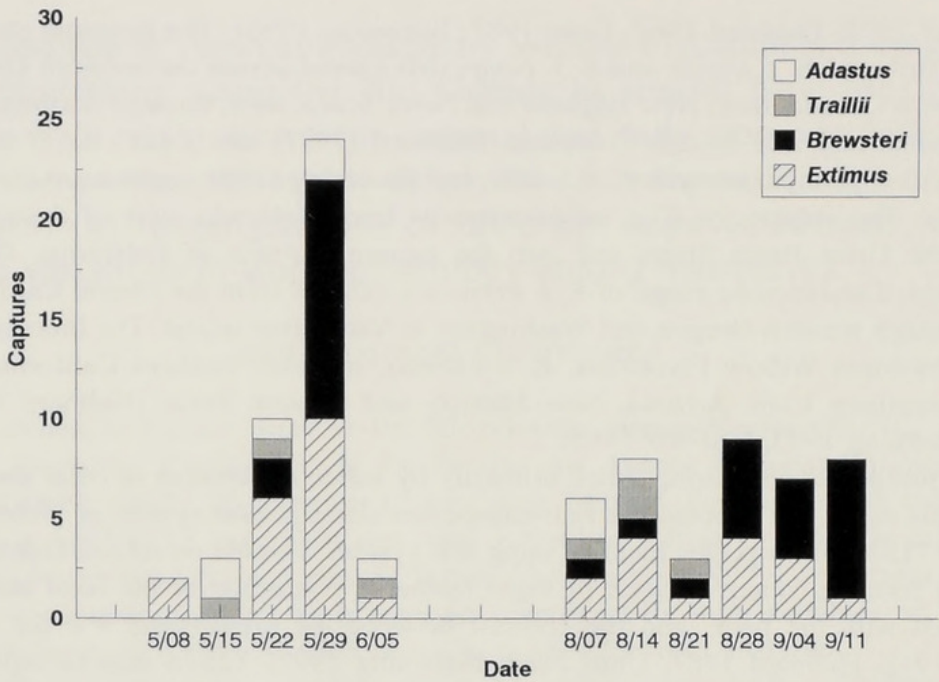


FIG. 1. Seasonal capture patterns of Willow Flycatcher (*Empidonax traillii*) during spring and fall migrations along the middle Rio Grande.

icantly different among fat classes ($F_{2,81} = 18.2$, $P < 0.001$, Fig. 2). The average body mass of birds in fat class zero was 12.3 ± 0.9 g ($N = 41$). The estimated average fat-free mass of Willow Flycatchers was 11.9 g. Average body mass of flycatchers in fat classes one and \geq two were 12.9 ± 1.1 g ($N = 32$) and 14.3 ± 0.75 g ($N = 10$), respectively. This translates to 1.0 g (8% fat-free body-mass) and 2.4 g (20% fat-free body-mass) fat stores, respectively. Average potential flight range was 225 km for all captures, 257 km for birds in fat class one, and 404 km for birds in fat class \geq two (see Fig. 3 for depiction of relationship).

Body mass did not vary by capture date during spring and fall migrations. Wing length was negatively correlated with capture date in both spring and fall (Fig. 4a and 4b). Condition index increased during spring migration ($r = 0.39$, $P < 0.05$) but not during fall migration (Fig. 4c and 4d). Body mass of Willow Flycatchers captured in spring (13.2 ± 1.1 g, $N = 41$) was significantly higher ($t = 14.42$, $P < 0.01$) than that of the fall captures (12.3 ± 1.0 g, $N = 42$). The ANOVA test detected body mass differences ($F_{2,81} = 7.62$, $P < 0.01$) among adult birds captured in spring (13.2 ± 1.1 g, $N = 41$), adult birds captured in fall (12.4 ± 1.2 g, $N = 25$), and hatching-year birds in fall (12.1 ± 0.8 g, $N = 17$). The multiple range tests suggested the difference was between spring birds and fall after-hatching year birds and between spring birds and fall hatching year birds (Tukey Test, $P < 0.05$). The difference between the two age groups in the fall was not significant.

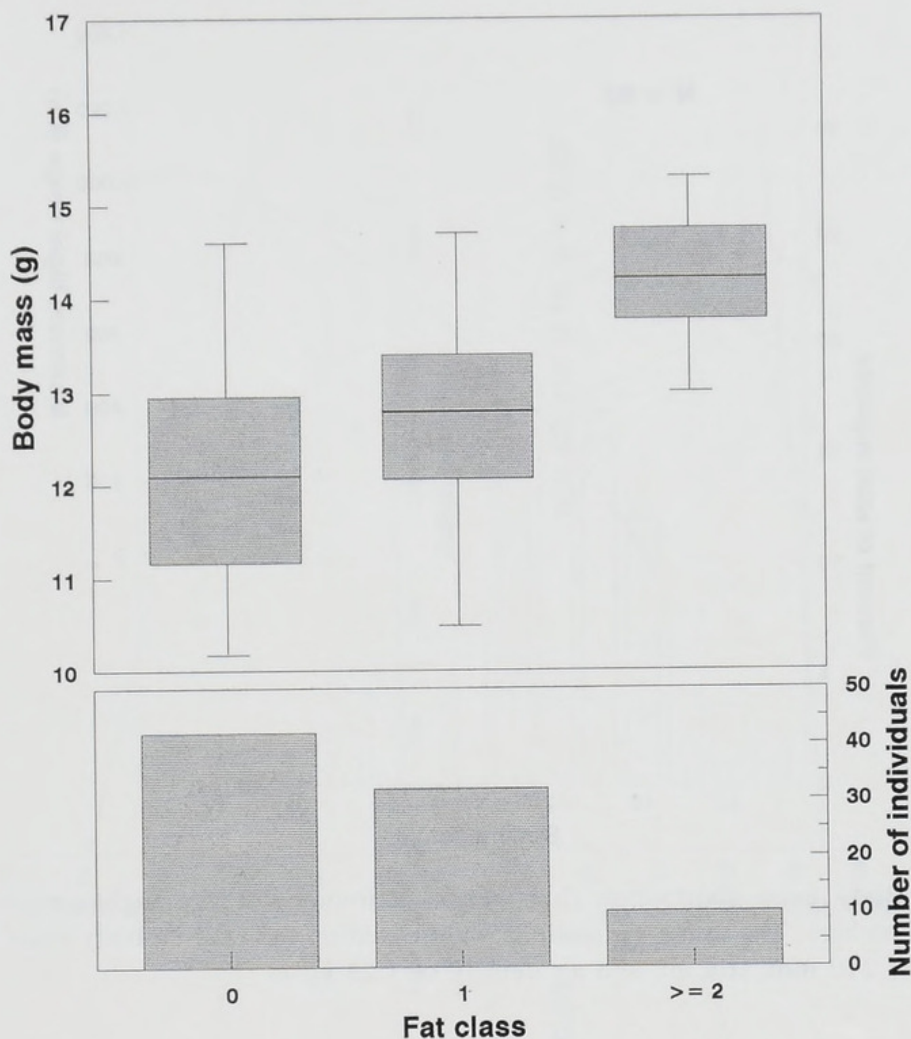


FIG. 2. Fat distribution and its relationship with body mass of Willow Flycatchers captured during spring and fall migrations along the middle Rio Grande.

Only seven Willow Flycatchers (8% total captures) were recaptured during the two-year field seasons. All recaptures occurred within one day after initial capture. Average body mass of recaptures was 12.4 ± 0.8 g at initial capture and was 12.6 ± 1.00 g at last capture, or an average change of 1.6% body mass/day. Body mass tended to be positively associated with daily time of capture in spring ($r = 0.28$, $P = 0.08$) and in fall ($r = 0.30$, $P < 0.05$). However, the partial correlation between daily time of capture and body mass, controlling for wing size variation, was not significant, suggesting that daily body mass change was due to the effect of smaller birds caught earlier in the day. Daily fat store accumulation estimates based on correlation between daily time of capture and condition index were not significant.

The capture rate of flycatchers among habitats deviated significantly from expected frequencies by net efforts ($\chi^2 = 30.67$, $df = 3$, $P < 0.001$, Table 1). Willow habitat had the highest capture rate (34.1 birds/10,000

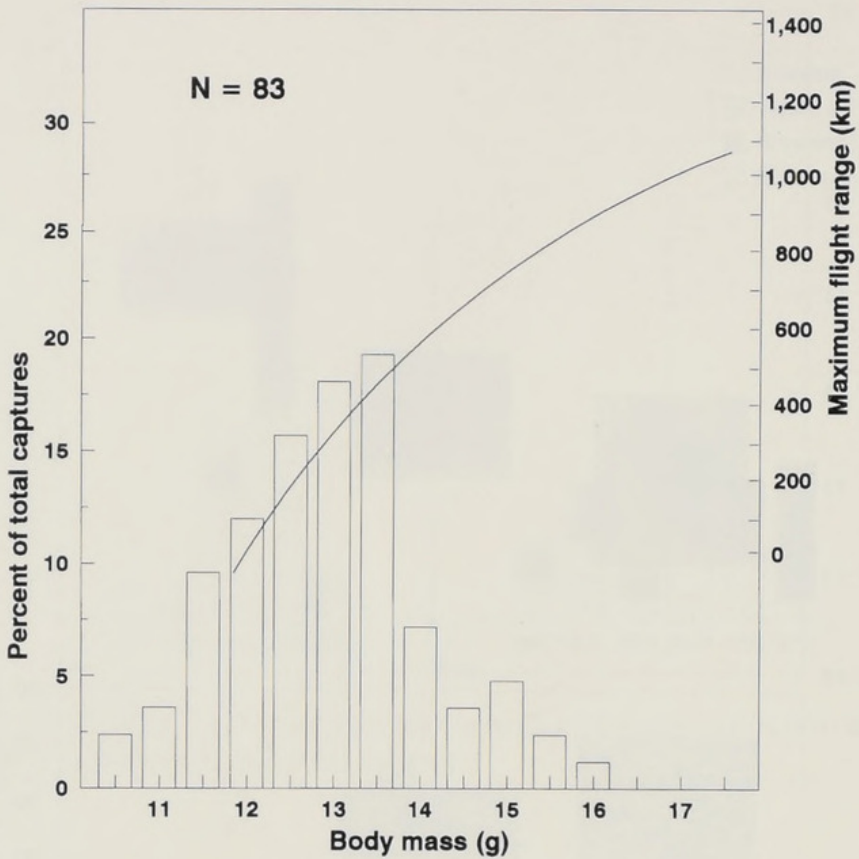


FIG. 3. Body mass distribution (bars) and maximum potential flight ranges (line) of Willow Flycatchers. The range estimations were based on the fat-free body mass of 11.9 g, wing span of 210 mm, still air, and air density of 1.23 kg-m^{-3} .

net-h), followed by cottonwood-Russian olive (16.0 birds/10,000 net-h), and agriculture (12.9 birds/10,000 net-h). The cottonwood-other habitat had the lowest capture rate (4.5 birds/10,000 net-h). The Exact Test suggested that the frequencies of occurrence of subspecies were independent of the frequencies of habitat type, suggesting that variation in habitat use was not subspecies related.

Body mass of flycatchers tended to be habitat dependent ($F_{3,80} = 2.26$, $P = 0.08$): birds captured in willow habitat had the highest average body mass, while birds from agricultural fields had the lowest average body mass (Table 1). The amount of observable fat stores of birds captured from different habitats tended to be different (Kruskal-Wallis Test, $\chi^2 = 6.20$, $df = 3$, $P = 0.10$), and the trend was perfectly correlated with the body mass variations among habitats (Spearman Correlation between average body mass and fat class of each habitat, $r_s = 1.00$, Table 1).

FIG. 4. Seasonal changes of wing length and condition index (mass-wing⁻³) of Willow Flycatchers captured during spring and fall migrations along the middle Rio Grande.

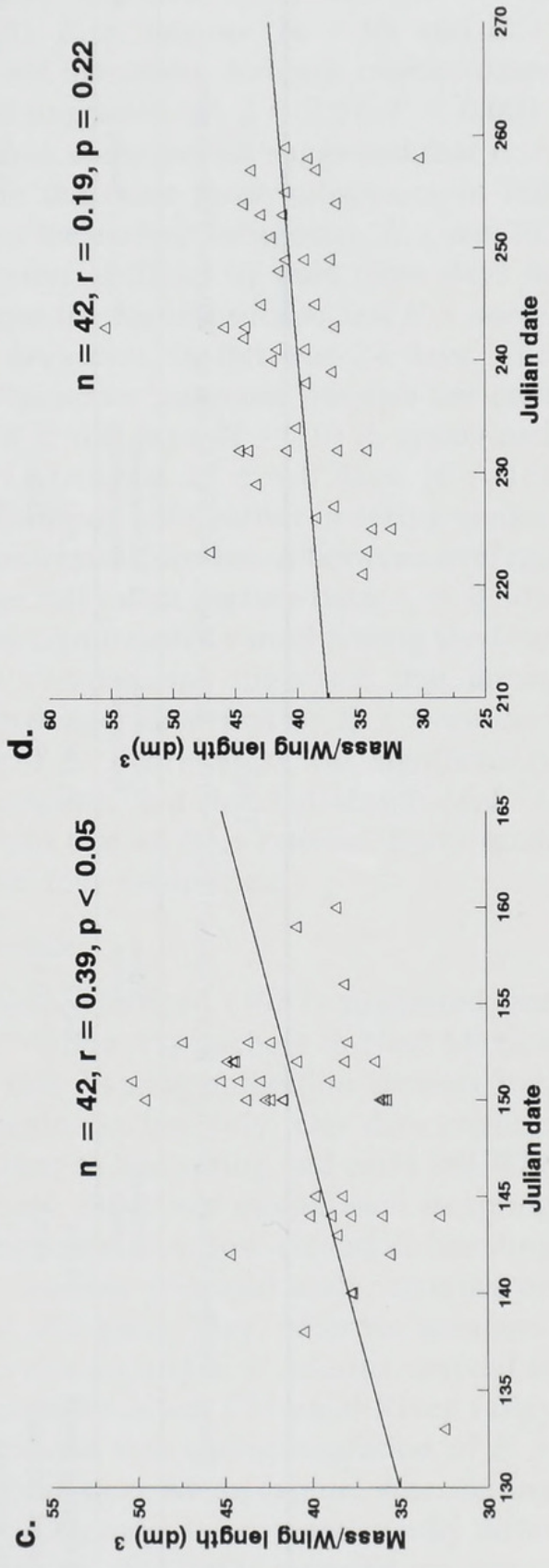
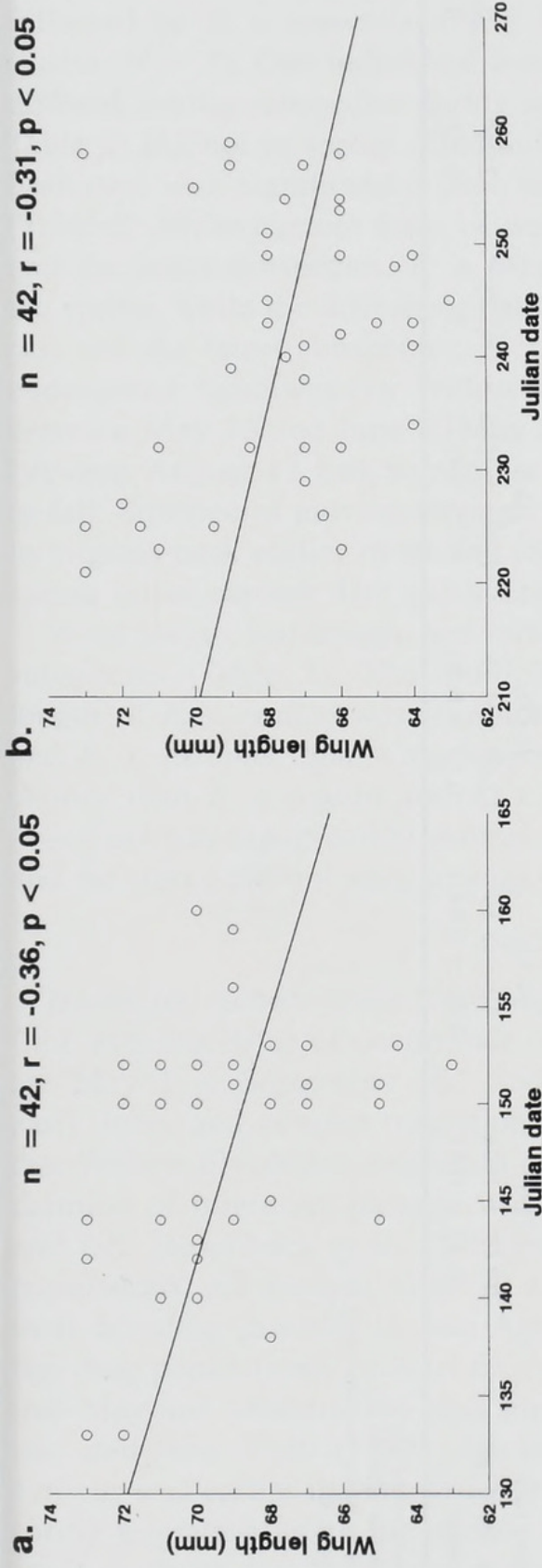


TABLE 1
TOTAL NETTING HOURS, CAPTURE RATE (BIRDS/10,000 NET-H), BODY MASS, AND FAT CLASS OF WILLOW FLYCATCHERS

	Agriculture fields	Willow habitat	Cottonwood- Russian olive	Cottonwood- other vegetation	df	Statistic	P
Total netting hours	9336	6457	26,236	17,841			
Expected captures	13.1	9.1	36.8	25.0			
Actual captures	12	22	42	8	3	30.67 ^a	<0.001
Capture rate	12.85	34.1	16.00	4.5			
Body mass (g) ^d	12.09 ± 0.94	13.12 ± 1.19	12.69 ± 1.18	12.91 ± 0.95	3,79	2.26 ^b	0.08
Fat class ^d	0.42 ± 0.51	0.95 ± 0.84	0.55 ± 0.80	0.75 ± 0.71	3	6.20 ^c	0.10

^a Goodness-of-Fit (χ^2).
^b One-Way ANOVA (F).
^c Kruskal-Wallis One-Way ANOVA (χ^2).
^d Mean ± SD.

Of the 84 Willow Flycatchers we sampled, the Southwestern Willow Flycatcher (*E. t. extimus*) was the most abundant subspecies ($N = 34$), followed by *E. t. brewsteri* ($N = 33$), *E. t. adastus* ($N = 9$), and *E. t. traillii* ($N = 7$). One individual was not identified. Average capture dates differed among subspecies during fall migration ($F_{3,37} = 7.51$, $P < 0.001$, Table 2) but not in spring. The multiple comparisons suggested that *E. t. brewsteri* was significantly later than the other three subspecies in fall (Table 2). Mean capture dates between the earliest subspecies, *E. t. traillii*, and the latest subspecies, *E. t. brewsteri*, differed by only three days in the spring, while the difference between the earliest subspecies, *E. t. adastus*, and the latest subspecies, *E. t. brewsteri*, in fall was 24 days. The endangered Southwestern Willow Flycatcher migrated through the area between May 13 and June 8 ($\text{May } 28 \pm 6.8 \text{ days}$, $N = 19$) in spring and between August 13 and September 11 ($\text{August } 27 \pm 9.8 \text{ days}$, $N = 15$) in fall. Subspecies moving through the study sites earlier in spring tended to migrate back earlier in the fall (Spearman Correlation between average spring julian capture date and average fall julian capture data, $r_s = 0.80$).

Wing length, tail length, and tarsus significantly varied among the four subspecies (Table 2). The multiple comparisons suggested that tarsus length of *E. t. traillii* was significantly longer than that of *E. t. brewsteri* and *E. t. extimus*, that wing length of *E. t. brewsteri* was significantly shorter than *E. t. traillii* and *E. t. adastus*, and that tail length of *E. t. brewsteri* was significantly shorter than that of *E. t. extimus*. Body mass and fat stores did not vary among the four subspecies.

DISCUSSION

Based on records from New Mexico, Hubbard (1987) suggested that "the extreme dates of occurrence of Willow Flycatchers in New Mexico are May 1 to September 16" and that "spring migration persists into early June, and autumn migration begins in late July. Our data confirm that Willow Flycatcher migration occurs in late spring and early fall. The duration of migration passage was only about one month each in spring and fall. Rosenberg et al. (1991) suggested that low-elevation breeding populations, all thought to be *E. t. extimus*, migrated early, arriving on their breeding grounds in late April and early May, whereas montane-breeding populations, such as *E. t. brewsteri* and *E. t. adastus*, arrived in mid-May and continued to pass through the lower Colorado River valley into mid-June. Unitt (1987) also indicated that spring migration of *E. t. extimus* was earlier than that of *E. t. brewsteri*. Mean capture dates during spring migration along the middle Rio Grande did not statistically differ among subspecies. Similarly, Suckling et al. (1992) reported no strong differentiation among subspecies spring arrival dates on the breeding

TABLE 2
MORPHOLOGICAL MEASUREMENTS AND CAPTURE DATE ($\bar{x} \pm \text{SD}$) OF SUBSPECIES OF THE WILLOW FLYCATCHERS

	Subspecies					df	F
	<i>adastus</i>	<i>brewsteri</i>	<i>extimus</i>	<i>traillii</i>			
N	9	33	34	7			
Mass (g)	13.31 \pm 1.19	12.59 \pm 1.13	12.73 \pm 1.16	13.07 \pm 0.84	3,78	1.27	
Wing length (mm)	70.67 \pm 2.12	67.29 \pm 2.70	68.46 \pm 2.44	70.00 \pm 2.24	3,79	5.55**	
Tail length (mm)	58.00 \pm 1.58	56.15 \pm 2.97	57.82 \pm 2.38	58.29 \pm 2.81	3,79	3.11*	
Tarsus (mm)	16.53 \pm 0.78	16.52 \pm 0.71	16.79 \pm 1.00	17.73 \pm 1.80	3,79	3.19*	
Fat class	0.78 \pm 0.44	0.82 \pm 0.92	0.59 \pm 0.74	0.14 \pm 0.38	3	5.63 ^a	
Spring capture date ^b	146.83 \pm 8.35	149.86 \pm 2.82	147.68 \pm 6.76	146.67 \pm 8.33	3,38	0.55	
Fall capture date	223.67 \pm 3.06	247.42 \pm 10.39	238.93 \pm 9.79	232.00 \pm 5.72	3,37	7.51***	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

^a Kruskal-Wallis One-Way ANOVA.

^b = Julian date.

grounds. Difference in timing of fall passage was more obvious among subspecies in our study: the Pacific subspecies, *E. t. brewsteri* migrated through the study sites latest, while the Southwestern Willow Flycatcher had a relatively broad passage period.

Wing length, tail length, and tarsus varied among subspecies. In contrast, body mass did not vary by subspecies but did differ between seasons. In many passerine species, wing length and body size vary in relation to age and sex (Pyle et al. 1987). We speculated that flycatcher body mass may have been significantly lower in fall than in spring if hatching-year birds weighed less than adults. Although body mass of young fall birds significantly differed from that of spring adults, it did not differ from fall adults. Therefore age only partially explained body mass variation between spring and fall.

Body mass did not vary within each migration season, but declines in wing length through spring and fall and increases in condition index through spring suggest that flycatcher condition and wing size may be related to departure times (and travel distances) of different groups of flycatchers. Spring capture dates did not vary by subspecies (although fall capture dates did), so subspecies alone does not explain within-season variation in condition and wing length. Such variation may be related to sex or age, or interactions of sex with age or subspecies. Interpretation of other breeding studies suggests that arrival and departure times of Willow Flycatchers vary in relation to sex and age, and consequently such factors are likely to contribute to changes in mass within and between migration periods. For example, male Willow Flycatchers are reported to arrive on the breeding grounds ahead of females, based on behavioral observations (Bent 1942, Walkinshaw 1966). Males of other passerine species are also reported to migrate before females (e.g., Francis and Cooke 1986, Morton 1992), possibly due to competition among males for high-quality territories, ability to tolerate harsher weather than females, and differences between males and females in travel distances to breeding and wintering areas. Thus, some of the changes in body condition and wing length that we detected during spring and fall migrations may be related to variation in departure times of sexes, with males leaving before females in both seasons. In spring, females may prepare in advance for the high energy costs of egg-laying by depositing more fat in proportion to wing length than males.

In addition to differences in departure time between sexes and among subspecies in fall, adult Willow Flycatchers are reported to head south earlier than hatching-year birds (Unitt 1987), thus further complicating interpretation of intra-seasonal changes in body size and condition during migration. Adult Willow Flycatchers can start migrating earlier in fall

than young birds because they delay molting (postnuptial or prebasic) until they reach their wintering ground in Central and South America. By contrast, young flycatchers molt into their first winter (basic) plumage prior to migration, which adds to the length of their stay on the breeding grounds (Unitt 1987, Hubbard 1987). Our results showed that hatching-year birds tended to migrate through the Rio Grande valley later than adults, suggesting that age-related departure time may be a complicating factor in explaining seasonal decreases in wing length in fall. Interaction effects of age with subspecies and sex may have masked fall variation in attributes such as body mass and condition between adults and hatching-year birds.

In anticipation of the high energy demand of migration, small landbird migrants deposit fat stores before their long-distance flight. Nonmigratory birds have lipid contents of only 3–5% of lean body mass, whereas migratory birds can deposit fat stores of up to 30–50% of lean body mass (Berthold 1975). However, small landbird migrants, especially Neotropical long-distance migrants, generally do not deposit enough fat to fly nonstop between breeding and wintering grounds. In this study, about 50% of the Willow Flycatchers had no fat stores, which is lower than that reported for other species (e.g., Cherry 1982, Bairlein 1985, Biebach et al. 1986, Moore and Kerlinger 1987, Winker et al. 1992, Yong 1993).

Low fat stores in Willow Flycatchers could be caused by depletion of fat stores during nocturnal migration. Moore and Kerlinger (1987) found that arrival condition, as indexed by amount of fat stores, of trans-Gulf migrants was significantly related to wind direction and precipitation. Ålerstam and Lindström (1990) proposed that low fat stores in stopover migrants could be a behavioral response to minimize energy needed for migration: lighter birds keep flight costs lower than heavier birds by storing only enough fat to reach the next stopover site. Maintaining a low body mass could also help to reduce the energetic cost of foraging during stopover, especially in wing-foragers such as the Willow Flycatcher. In any case, owing to low fat stores, Willow Flycatchers are seemingly constrained to feed at stopover sites such as our study area to make progress toward their breeding or wintering destination.

The condition index estimates failed to show daily increases in body mass during stopover. Although our analysis of recapture data was hampered by relatively small sample size, recaptured Willow Flycatchers had higher average body mass, which suggests increase of fat stores during stopover. Additional data are required to confirm this pattern. Rate of body mass gain (1.6% of initial body mass) of the Willow Flycatchers is similar to estimates for other species (Cherry 1982, Bairlein 1985, Biebach et al. 1986, Moore and Kerlinger 1987, Winker et al. 1992). Based

on the results of low recapture rate and short duration between capture and recapture (birds were recaptured only within one day after initial capture), we conclude that stopover length of Willow Flycatchers at our study sites was relatively brief. Proportional gain of body mass and short stopover length suggest that Willow Flycatchers were able to find food quickly and efficiently in stopover habitats to redeposit energy stores for migration.

Previous research has shown that landbird migrants use specific habitats and select among alternative vegetation types during stopover (e.g., Bairlein 1983, Moore et al. 1990, Winker et al. 1992, Mabey et al. 1992), presumably in response to differential suitability among habitats (Hutto 1985, Moore and Simons 1992). We evaluated whether variation in capture rates among mist-nets was related to kinds of habitats that nets were erected in. Mist-net locations that had relatively high captures of Willow Flycatchers in our study were characterized by a relatively open overstory and dense mid-/and low-stories, close proximity to water, and presence of willows or Russian olives. Net sites in willow captured the greatest proportion of stopover Willow Flycatchers, followed by net sites in dense young cottonwood-Russian olive stands. In addition to plant species composition, vegetation structure may influence capture rates (Remsen and Good 1996), i.e., flycatchers may be captured more frequently in habitats with dense shrub vegetation than in open, shrubless habitats (e.g., cottonwood-other or agriculture), regardless of cottonwood presence or absence. Hirsch and Segelquist (1978) found that Willow Flycatcher numbers were positively correlated with willow volume during breeding season.

During this study, we observed Willow Flycatchers actively foraging within dense willow habitat, taking insects on the wing and gleaning from foliage. Densities of arthropods are high in willows relative to other vegetation (Yong and Finch, unpubl. data). We hypothesize that migrating Willow Flycatchers stop more frequently in willow habitats than in other habitat types because willows contain more arthropod food that flycatchers favor. We recommend that this hypothesis be tested through experimental manipulations of food supply, habitat, and flycatcher foraging behavior in willow versus other habitat types. For example, arthropods could be experimentally removed from individual willows and other plant species by fogging with a stunning solution, then observers could monitor flycatcher foraging responses to fogged and unfogged plants.

Up until now research and conservation efforts pertaining to the Willow Flycatcher have focused on its breeding grounds. The energetic consequences of flycatcher migration and the need for suitable en route habitat for refueling are largely overlooked as factors affecting the survival of adult and hatching-year Willow Flycatchers. Our results, however, suggest

that riparian woodlands along the middle Rio Grande are important as stopover sites for resting and fat redeposition by the Willow Flycatcher during its spring and fall migrations. If migrating Willow Flycatchers cannot periodically replenish their fat stores and do so quickly, the probability of a successful migration is reduced. We recommend that flycatcher stopover habitats, especially native shrubs such as coyote willow, be actively monitored, maintained, and preserved to protect endangered Southwestern Willow Flycatchers.

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