

SEXUAL DIFFERENCES IN WILSON'S WARBLER MIGRATION

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Abstract.—Mist-netting was conducted in riparian habitat near the southern end of San Francisco Bay, California during the spring and fall migratory periods of Wilson's Warblers (*Wilsonia pusilla*) in 1987-1991. On the basis of banding records, spring migration started around 1 April and ran through late May, with a peak during mid-May. Fall migration occurred from 1 August through late October. No obvious peaks were apparent in the fall, although slight bimodality occurred with peaks in late August and mid-September. Males migrated significantly earlier in spring but not in fall than did females. Though males stayed longer (4 d) on average than did females (3 d), the length of stay on the site during spring migratory stopover did not differ significantly between the sexes. All but one of the birds staying longer than 5 d were males. No significant linear relationship was found between original arrival date and length of stay during the spring. The mean mass change during spring stopover was the same for males and females (0.4 g). The data presented here suggest that the timing of onset of migration rather than the rate of migration may be more important in establishing the earlier vernal migration of males.

DIFERENCIAS SEXUALES EN LA MIGRACIÓN DE *WILSONIA PUSILLA*

Síntesis.—Se atraparon aves con redes en hábitats riparios cerca del sur de la Bahía de San Francisco (37°20'N, 122°10'O) durante los periodos primaverales y otoñales de migración de *Wilsonia pusilla* entre 1987 y 1991. Según los registros de anillaje, la temporada de migración comienza para el 1° de abril y prosigue hasta fines de mayo, con un pico a mediados de mayo. La migración otoñal ocurrió entre el 1° de agosto y finales de octubre. No se detectaron picos en la migración otoñal, aunque se halló una pequeña bimodalidad en los picos de finales de agosto y mediados de septiembre. Los machos migraron significativamente antes que las hembras en la primavera pero no en el otoño. Aunque los machos permanecieron por más tiempo (4 días) que las hembras (3 días), el largo de la estadía en la localidad durante la parada migratoria de primavera no difirió significativamente entre los sexos. Todas menos una de las aves que permanecieron más de cinco días fueron machos. No se halló ninguna relación lineal significativa entre la fecha de la llegada original y la duración de la estadía durante la primavera. El promedio de cambio en masa durante la parada primaveral fué el mismo para ambos sexos (0.4 g). Los datos aquí presentados sugieren que el momento de comenzar la migración puede ser más importante que la tasa de migración para establecer la migración vernal de los machos.

Differential migration refers to the situation in which distinguishable classes of individuals (e.g., sex or age groups) differ with respect to timing or distance of migration (Terrill and Able 1988). Males of most migrant species precede females in arriving at the breeding grounds (Terrill and Berthold 1989). This differential pattern is also reflected along the migration route. For example, Yunick (1988) provided evidence for differential timing of spring migration of male and female Dark-eyed Juncos (*Junco heymanis*) in his studies at Schenectady, New York. Yunick found that migration occurred earlier for males than females during spring. An earlier passage of male wood warblers was observed by Francis and Cooke

(1986) in their work with 18 species of paruline warblers at Prince Edward Point, Ontario.

The Wilson's Warbler is a fairly common and widespread Neotropical migrant, especially in western North America (Bent 1953). It is well established that Wilson's Warblers exhibit differential timing of migration between the sexes (Francis and Cooke 1986). The western race (*Wilsonia pusilla chryseola*) breeds from southern British Columbia to southern California, primarily west of the mountain ranges (Bent 1953). On the basis of my banding records, most if not all, of the individuals of this race only pass through my area in migration (both spring and fall) and do not normally breed within the immediate vicinity of my banding station. Several breeding bird surveys (B. J. Katano, pers. comm.) and a 5-yr breeding bird atlassing effort (W. Bousman, pers. comm.) have failed to find any Wilson's Warblers breeding on the banding site. There is some evidence (i.e., a few males and females banded during the breeding season), however, that a few birds may occasionally attempt to breed here.

In the following paper, I examine capture/recapture data obtained from mist-netting operations to determine if differential migration occurs in west-coast populations of Wilson's Warblers. I then examine length-of-stay and mass-change data to determine the importance of differential rate of passage in establishing differential migration.

STUDY SITE AND METHODS

Data were collected during mist-netting at Coyote Creek Riparian Station, Alviso, California (37°20'N, 122°10'W). The research site is located along the lower stretch of Coyote Creek approximately 9.2 km south of the point where the creek enters the southern end of San Francisco Bay. The site consists of three habitats: a planted revegetation site, a riparian woodland and a flood control overflow channel.

Revegetation area.—The Revegetation site, a former pear orchard cleared in 1982 and replanted in 1986, has been managed as a mitigation area for habitat lost along the creek during flood control work. The shrubs and trees in this area are dominated by western sycamores (*Platanus racemosa*), Fremont cottonwoods (*Populus fremontii*), blue elderberry (*Sambucus mexicana*) and willow (*Salix* spp.). There is also a dense understory of ripgut brome (*Bromus diandrus*), poison hemlock (*Conium maculatum*) and ryegrass (*Lolium perenne*). This area covers 1.9 ha of the site.

Riparian area.—The riparian area consists of existing creek-side habitat and is approximately 8–25 m in width. The nets used in this study were placed at intervals along a 2000 m stretch of this habitat. The overstory is dominated by Fremont cottonwood, California box elder (*Acer negundo*) and willow. The understory consists mostly of blackberry (*Rubus ursinus*), various grasses and poison hemlock.

Overflow channel.—The channel area sampled by our netting operations is approximately 25 × 400 m. The vegetation consists of an under-

story dominated by ox tongue (*Picris echioides*), mustard (*Brassica nigra*) and Russian thistle (*Cynodon dactylon*).

The over-flow channel was created in the fall of 1989 and the revegetation site was created in early spring of 1987. Prior to this time, these areas were open fields dominated by coyote brush (*Baccharis pilularis*) and poison hemlock.

Standard 32 mm or 36 mm nets were used. The nets were opened approximately 30 min before sun rise and closed at approximately 1100 hours PDT. Mist-nets were established in permanent locations on the site. A total of 64 nets (each 2 × 12 m) were established. These nets were run in a staggered fashion, with 20–45 nets run on any one day. Each of the 64 nets were opened at least twice during any 7-d period. The nets were opened daily unless weather or other emergencies required closures.

The nets were inspected every 60 min or less and individual birds were carefully removed from nets, placed in mesh bags and taken to a central processing area. Each bird was banded with a U.S. Fish and Wildlife band and released unharmed. Wing length, mass (to the nearest 0.1 g), time of capture, fat codes and molt characteristics were recorded for each bird.

The birds were sexed using the criteria of Pyle et al. (1987). Birds with shiny black caps with less than 5% greenish tipping and greater than 11 mm in length were considered males. Birds with crowns suffused with more than 20% greenish and black (or dark) caps less than 12 mm in length were considered females. Intermediate birds were not sexed (3% of spring and 12% of fall birds).

The data were subjected to four analyses. First, to establish the timing of migration on the site, the original capture records of Wilson's Warblers were pooled in 5-d increments for each of the 5 yr of the study and examined graphically.

Second, I tested whether there was differential timing of migration between the sexes. For each of the 5 yr, I broke the data into sex and season classes. I then plotted these data to see if any migratory patterns were evident. The pooled data for spring migration were tested for differences in male and female migration patterns using a Mann-Whitney *U*-test.

Third, I examined the length of stay of individual birds on the site during spring migration. The number of days between initial and the final recapture was taken as a conservative estimate of each individual's minimum length of stay on the site (Cherry 1982, Loria and Moore 1990, Moore and Kerlinger 1987). This is a conservative estimate because the likelihood of capturing a migrant on its first and last day of stopover is very small (Moore and Kerlinger 1987). Birds that were not recaptured during the same season were assumed not to have stayed on the site (Cherry 1982, Loria and Moore 1990); these birds were given a length of stay of 0. The length of stay of individuals that had a length of stay of at least 1 d were then pooled over the 5-year period and divided into sex classes. These data were examined to determine if there were differences in length of stay between the sexes using a Mann-Whitney *U*-test.

Finally, I determined the mass change of individuals that stayed for

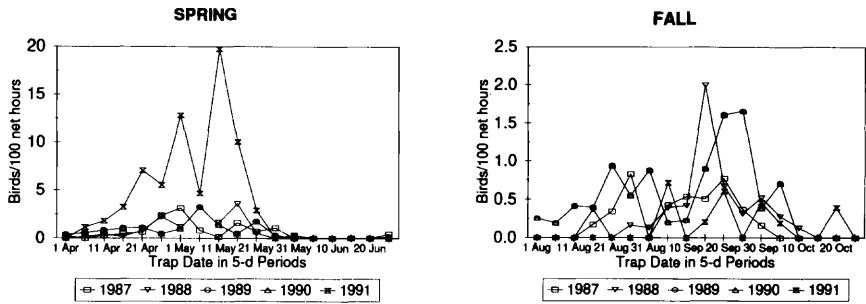


FIGURE 1. Rates of new captures of Wilson's Warblers.

more than a day. The mass change during stopover was calculated by subtracting the mass upon initial capture from the mass upon last capture. Some authors have shown that there are diel cycles of mass change in migratory birds (Collins and Bradley 1971, Loria and Moore 1990). Therefore, if comparisons of mass change are made from one capture to the next, the masses must be taken at the same time of day (Rappole and Warner 1976) or corrected to the same time by using the rate of mass gain during the daylight hours (Cherry 1982, Moore and Kerlinger 1987). All of the birds in this study were captured within a 4.5-h period 0630–1100, therefore the raw masses were used without correcting to a single time of day. The masses of birds that were captured two or more times during the same day were determined by taking the average of the masses obtained for each individual for that day. Changes in mass may reflect changes in flight musculature, water and material in the digestive tract, but essentially all the mass gain during stopover is due to accumulation of fat (Cherry 1982, Child 1969, Rogers and Odum 1964). Therefore, mass changes observed here were considered to be changes in fat content.

RESULTS

Timing pattern.—Spring migration began around 1 April and ran through late May, with a few individuals trickling through until mid-June (Fig. 1). There was generally a peak in numbers during early-May. Fall migration occurred from the first part of August through late-October. No obvious migratory peaks were apparent in the fall data, although slight bimodality occurred in late August and mid-September (Fig. 1). Capture rates in spring were much greater than in fall (Fig.1).

Difference between males and females in timing.—Male Wilson's Warblers appeared earlier in spring and numbers peaked earlier during spring migration relative to females (Fig. 2). In addition, males continued to appear after females had completed their migration. Males migrated significantly earlier than females (Mann-Whitney U -Test, $P < 0.001$). Males did not migrate significantly earlier than females in fall (Mann-Whitney U -Test, $P = 0.8$).

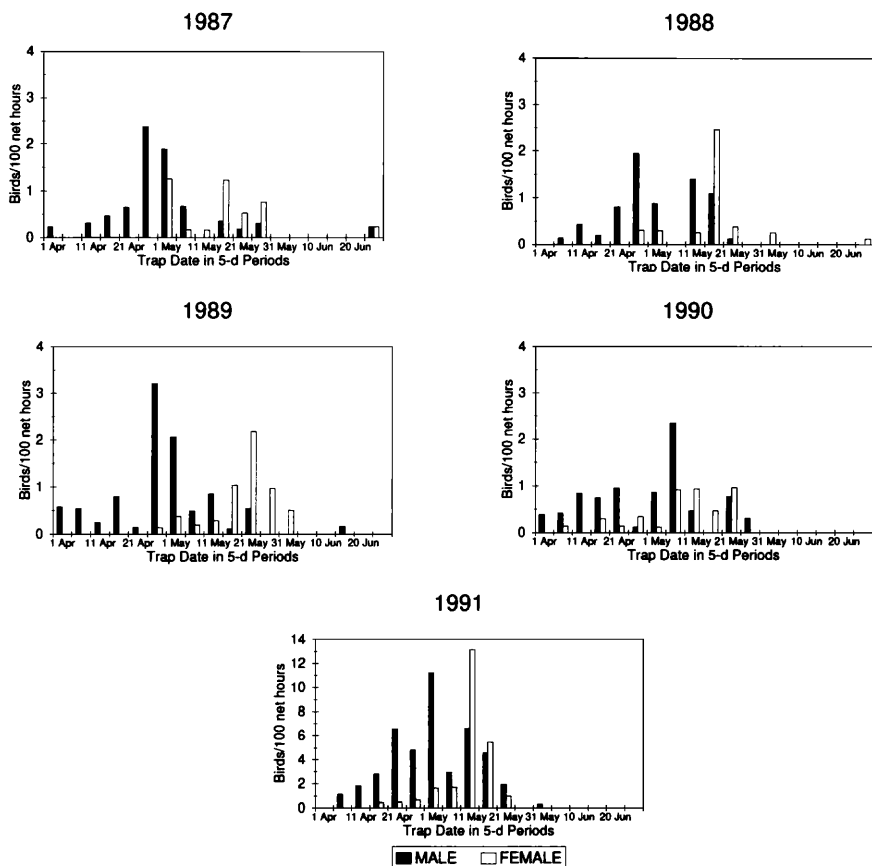


FIGURE 2. Capture rates of male and female Wilson's Warblers during spring migration (new captures only).

Length of stay and mass change.—Fifty-one of 416 males (12.3%) and 22 of 226 females (9.7%) stayed at least 1 d during spring migration. No significant difference (Mann-Whitney U -Test, $P = 0.2$) was found in the length of stay between males and females (Fig. 4). There was no significant difference between the likelihood of males stopping over as compared to females (Chi-squared, $P = 0.10$). There was no significant (Bartlett Chi-squared Statistic, $P = 0.33$) linear relationship between original arrival date and length of stay of individuals in spring. The mean mass change during stopover for males (mean = 0.4, SD = 0.74) was the same as that of females (mean = 0.4, SD = 0.74) during spring.

DISCUSSION

Male Wilson's Warblers pass through this site earlier than do females during spring migration. The same pattern is not observed in fall migra-

tion in that males and females move through the area at the same time. The first of these findings is consistent with findings reported by Ramos (1988) in his studies of Wilson's Warblers on their wintering grounds in Veracruz, Mexico. The second result, however, is counter Ramos's findings that males migrated earlier than females in fall in his study. This discrepancy may be due to the fact that Ramos was working with two different races (*P. p. pusilla* and *P. p. pileolata*) from the one in this study (*P. p. chryseola*). No statistically significant differences were found in the duration of stopover or mass change between males and females.

Males appearing after the females' peak migration in spring may not be actual migrants. These birds may be attempting to breed locally. Each year, one or more individuals were captured during the breeding season (nine males and four females over 5 yr of banding), which indicates that there may be some attempts at breeding in the area. If these birds are not local birds searching for territories, they may be first-year birds that, in some parulid warblers, migrate after adult males and females (Francis and Cooke 1986). Further study is needed to address this question.

Somewhat different selective pressures may act on males and females with respect to timing of migration and arrival on the breeding grounds (e.g., Francis and Cooke 1986). It may be advantageous for males to arrive on the breeding grounds as soon as food resources and climatic conditions are adequate for survival, whereas, females arrive later when conditions are optimal for nesting. Birds arriving on the breeding grounds early may be exposed to many risks such as reduced food supplies, cooler weather and storms. Males that arrive early on the breeding grounds, however, may have a better chance of acquiring high-quality territories than males arriving later. Thus, the natural selective advantages of early arrival may outweigh the costs of early arrival by males.

Some authors argue that data on the differential timing of passage at sites along migration routes are ambiguous with respect to whether the sexes actually differ in onset or rate of migration. Chandler and Mulvihill (1990) suggest that differential timing may stem from three distinct causes: differential onset of migration, differential rate of travel, and/or differential geographic origin of the sexes. There was no statistically significant difference in the mean length of stay of male and female Wilson's Warblers during spring migration, which suggests that the differential rate of migration is not important in establishing the spring differential migration pattern, that is if this is the typical pattern seen at all stopover sites.

Some authors suggest that males may be taking on more fat during stopover and thus be able to make fewer stops than females after leaving this site (C. R. Chandler, pers. comm.). The data presented here do not support this line of argument. I found that males and females, on average, put on the same amount of fat.

Differences in the distance each of the sexes travel could influence the timing of arrival (Chandler and Mulvihill 1990, Francis and Cooke 1986). For example, it has been shown that there is clinal distribution of Dark-

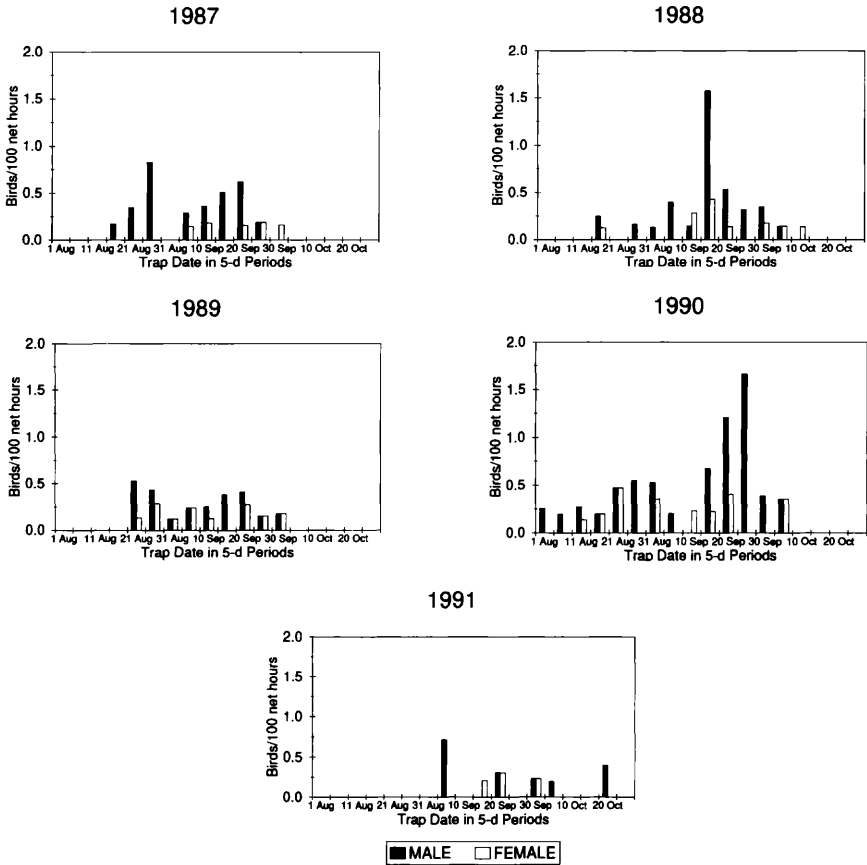


FIGURE 3. Capture rates of male and female Wilson's Warblers during fall migration (new captures only).

eyed Juncos (*Junco hyemalis*), with the percentage of females increasing towards the south in wintering populations in the eastern United States (Ketterson and Nolan 1976, 1979). Yunick (1988) provided evidence for differential timing of spring migration of male and female juncos, with males passing through his site earlier than females. Chandler and Mulvihill (1990) suggested that the winter distribution of juncos may account for part of this observed migration pattern. They suggest that even if the males and females initiated migration at the same time, the males could pass through earlier in spring simply because they have a shorter distance to travel. There is little evidence that male and female paruline warblers differ in their wintering ranges (Francis and Cooke 1986). Ramos (1988) found no statistically significant differences in the percentage of male (48%) and female (44%) Wilson's Warblers in his study of Wilson's War-

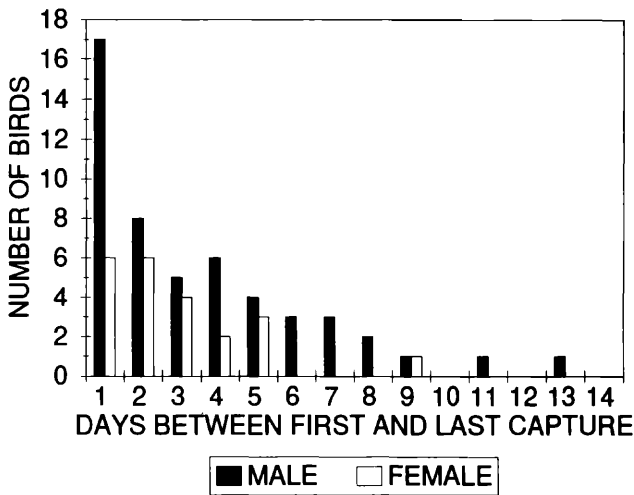


FIGURE 4. Minimum length of stay (time between original capture and last recapture) of Wilson's Warblers stopping over during spring.

blers in Veracruz, Mexico, indicating that the sexes may not be segregating geographically (8% of the birds were not sexed). Therefore the winter distribution hypothesis probably does not play a large role in establishing the observed migration pattern in Wilson's Warblers. More work needs to be undertaken on the wintering grounds to address this issue.

In combination, these data indicate that the differential timing of migration of Wilson's Warblers between the sexes in spring is probably due to differential onset of migration. Differential onset of migration from the wintering grounds has been found in other bird species. For example, Nisbet and Medway (1972), working with Eastern Great Reed Warblers (*Acrocephalus orientalis*) in Malaysia found that males depart on spring migration before females from areas where they winter together.

A lack of differential migratory behavior between the sexes with respect to timing of autumn migration may indicate that different selective pressures act on the timing of the autumn migration relative to spring migratory behavior. One factor important in selection for arrival time on the wintering grounds may involve the establishment of winter territories (which are widely documented in a number of wood warblers, including congeners of Wilson's Warblers, for example, see Morton [1990] and Mabe and Morton [1992]). If both males and females are competing for winter territories, selection for timing of arrival on the wintering grounds may be similar for all individuals regardless of sex. Bent (1953), in his description of Wilson's Warbler behavior, offers anecdotal evidence that indicates that Wilson's Warblers on their wintering grounds are solitary and defend individual territories. This could account for the lack of differential migration in the fall; if both sexes establish territories on the

wintering grounds, there would be equal pressure for early fall migration among the sexes.

There are two other interesting results from my data that I cannot explain fully, but that deserve additional attention. First is the relatively low capture rate seen during fall migration (Figs. 2 and 3). This is a rather surprising result because capture rates should be much higher in the fall due to the large number of young birds augmenting the migration at that time. Ramos (1988) reported capturing much larger numbers of Wilson's Warblers in fall than in spring during his studies in Veracruz, Mexico. Wilson's Warblers may use a different migratory route in spring and fall as is known in other species of migrants (e.g., see Curry-Lindahl 1981) or this may be a site-specific phenomenon related to as yet undetermined factors.

The second interesting result is the unusually high number of Wilson's Warblers captured in the spring of 1991 (Fig. 1). This greatly increased spring capture rate was also seen in the Swainson's Thrush (*Catharus ustulatus*) and Orange-crowned Warblers (*Vermivora celata*) passing through this area (Otahal, unpub. data). At the same time Yellow Warblers (*Dendroica petechia*) and Pacific-slope Flycatchers (*Empidonax difficilis*) suffered substantial decreases in capture numbers (Otahal, unpub. data). I have no explanation to account for this unusual year.

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LITERATURE CITED

- BENT, A. C. 1953. Life histories of North American wood warblers. U.S. Natl. Mus. Bull. 203.
- CHANDLER, C. R., AND R. S. MULVIHILL. 1990. Interpreting differential timing of capture of sex classes during spring migration. J. Field Ornithol. 61:85-89.
- CHERRY J. D. 1982. Fat deposition and length of stopover of migrant White-crowned Sparrows. Auk 99:725-732.
- CHILD, G. I. 1969. A study of nonfat weights in migrating Swainson's Thrushes (*Hyalocichla ustulata*). Auk 86:327-338.
- COLLINS, C. T., AND R. A. BRADLEY. 1971. Analysis of body weights of spring migrants in southern California: part 2. Western Bird Bander 46:48-51.
- CURRY-LINDAHL, K. 1981. Bird migration in Africa. Vol. 1 and 2. Academic Press, London, United Kingdom, 662 pp.
- FRANCIS, C. M., AND F. COOKE. 1986. Differential timing of spring migration in wood warblers (Parulinae). Auk 103:548-556.
- KETTERSON, E. D., AND V. NOLAN, JR. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering dark-eyed juncos (*Junco hyemalis*). Ecology 57:679-693.
- , AND ———. 1979. Seasonal, annual, and geographic variation in sex ratio of wintering populations of Dark-eyed Juncos (*Junco hyemalis*). Auk 96:532-536.
- LORIA, D. E., AND F. R. MOORE. 1990. Energy demands of migration on red-eyed vireos, *Vireo olivaceus*. Behav. Ecol. 1:24-35.
- MABEY, S. E., AND E. S. MORTON. 1992. Demography and territorial behavior of wintering

- Kentucky Warblers in Panama. Pp. 329–336, in J. M. Hagan III and D. W. Johnston, eds. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C.
- MOORE, F., AND P. KERLINGER. 1987. Stopover and fat deposition by North American wood warblers (Parulinae) following spring migration over the Gulf of Mexico. *Oecologia* 74: 47–54.
- MORTON, E. S. 1990. Habitat segregation by sex in the hooded warbler: experiments on proximate causation and discussion of its evolution. *Am. Nat.* 135:319–333.
- NISBET, I. C. T., AND L. MEDWAY. 1972. Dispersion, population ecology and migration of Eastern Great Reed Warblers *Acrocephalus orientalis* wintering in Malaysia. *Ibis* 114:451–494.
- PYLE, P., S. N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, California. 278 pp.
- RAMOS, M. A. 1988. Eco-evolutionary aspects of bird movements in the northern neotropical region. *Proc. XIX Intern. Ornithol. Cong.* 1:251–293.
- RAPPOLE, J. H., AND W. WARNER. 1976. Relationship between behavior, physiology and weather in avian transients at a migration stopover site. *Oecologia* 26:193–212.
- ROGERS, D. T., JR., AND E. P. ODUM. 1964. Effect of age, sex, and level of fat deposition on major body components in some wood warblers. *Auk* 81:505–513.
- TERRILL, S. B., AND K. P. ABLE. 1988. Bird migration terminology. *Auk* 105:205–206.
- , AND P. BERTHOLD. 1989. Experimental evidence for endogenously programmed differential migration in the blackcap (*Sylvia atricapilla*). *Experientia* 45:207–209.
- YUNICK, R. P. 1988. Differential spring migration of Dark-eyed Juncos. *J. Field Ornithol.* 59: 314–320.

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