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Sexual differences in Wilson's Warbler Migration

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SEXUAL DIFFERENCES IN WILSON'S WARBLER
MIGRATION

A Thesis

Presented to

The Faculty of the Department of Biological Sciences
San Jose State University

In Partial Fulfillment
of the Requirement for the Degree
Master of Sciences

By

Christopher Dale Otahal

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ABSTRACT

SEXUAL DIFFERENCES IN WILSON'S WARBLER MIGRATION

by Christopher Dale Otahal

The migratory stopover behavior of Wilson's Warblers (*Wilsonia pusilla chryseola*) was studied using mist-netting in a riparian system near the southern end of San Francisco Bay, California. Spring migration started around 1 April and ran through late May and fall migration occurred from 1 August through late October. Males migrated significantly earlier in spring but not in fall than did females. The length of stay during spring stopover did not differ significantly between the sexes. There was no significant linear relationship 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. 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.

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INTRODUCTION AND LITERATURE REVIEW

General Background on Differential Migration

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 pattern is also reflected along the migration route. For example, Yunick (1988) provided evidence for differences in the timing of spring migration of male and female Dark-eyed Juncos (*Junco heymalis*) 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.

Species Background

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 differences in the 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). Based upon the station's banding records, most if not all, of the individuals of this race only pass through this site in migration (both spring and fall) and do not normally breed within the immediate vicinity of the 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.

Scope of this Investigation

In the following study, capture/recapture data were obtained from mist-netting operations to determine if differential migration occurs in west-coast populations of Wilson's Warblers. Length-of-stay and mass-change data were compared between the sexes to determine the role these variables may play in establishing migration patterns.

STUDY SITE

General Characteristics

Data were collected during mist-netting at Coyote Creek Riparian Station, Alviso, California. 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.

Study Area Habitats

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 the netting operations is approximately 25 x 400 m. The vegetation consists of an understory dominated by ox tongue (*Picris echinoides*), mustard (*Brassica nigra*) and Russian thistle (*Cynodon dactylon*). The overflow 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.

MATERIALS AND METHODS

Chronology

Data for this study were collected almost daily during the spring and fall migratory periods of Wilson's Warblers (Table 1). Data were pooled for the years 1987 through 1991.

Mist-netting and Banding

A total of 64 standard (2 x 12 m) mist-nets were used to capture the birds for study. The mist-nets were established in permanent locations and where operated in a staggered fashion, with 20-45 nets opened on any one day. The nets were opened approximately 30 min. before sun rise and closed at approximately 5 hours after opening. Each net was 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.

Table 1. Summary of Captures and Capture Effort
SPRING CAPTURE EFFORT

Period = 1 April to 29 June (90 Total Days)

1 Net Hour = One 2 X 12 meter net operated one hour)

YEAR	DAYS BANDING	PERCENT COVERAGE	NET HOURS	BIRDS BANDED	BIRDS PER 100 NET HOURS
1987	80	89	8714	62	0.7
1988	89	99	12805	101	0.8
1989	90	100	12930	110	0.9
1990	85	94	12718	87	0.7
1991	83	92	6352	247	3.9

FALL CAPTURE EFFORT

Period = 1 August to 29 October (90 Total Days)

1 Net Hour = One 2 X 12 meter net operated one hour)

YEAR	DAYS BANDING	PERCENT COVERAGE	NET HOURS	BIRDS BANDED	BIRDS PER 100 NET HOURS
1987	88	98	10388	25	0.2
1988	88	98	12033	38	0.3
1989	89	99	12379	30	0.2
1990	77	86	8532	43	0.5
1991	84	93	7298	10	0.1

Sex Determination

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).

Establishing Migratory Periods

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. Since there is little evidence of on site breeding (see introduction), all birds captured in this study were assumed to be migrants. Arrival dates and apparent peaks in migration were determined by visual examination of the graphs.

Establishing Differential Migration

The presence or absence of differences in the timing of migration between the sexes was determined. For each of the 5 yr., the data were divided into sex and season classes. These data were then plotted to determine if any migratory patterns were apparent by visual examination. The

spring and fall data were pooled over the five years of the study to increase sample size (after Ramos 1988) then subjected to Mann-Whitney U-tests (see references in Wilkinson 1989) to determine if there was a statistically significant difference between male and female migration.

Determination of Length of Stay

The length of stay of individual birds on the site during spring migration was analyzed. The number of days between initial and the final recapture was used 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) and were assigned a length of zero. The length of stay of individuals that had a length of stay of at least 1 d (that were recaptured at least once) were then pooled over the 5-yr. period and divided into sex classes. A Mann-Whitney U-test was used to determine if there were differences in length of stay between the sexes.

Effects of Sex on The Probability of Stopping Over

A contingency table was developed which relates sex to the probability of stopping over. First, the observed capture data were divided into two classes: stopping birds (with a stay of one day or greater) and non-stopping birds (birds with a stay of zero days). These classes were then further divided into sex classes. Expected values for these four classes, assuming no special relationship between sex and stopover probability, were then determined. To illustrate this determination process, the expected number of males not stopping over will be used. Since males (n=442) make up 65% of all captured birds (n=680) the expected value of non-stopping males would be 395 (65% of the 607 non-stopping birds). A similar process was used to calculate each of the remaining expected values. These data were then subjected to a Yates Corrected Chi-square test (Scheffler 1980) to determine if there is a statistically significant difference between the likelihood of males stopping over as compared to females.

Effects of Arrival Date on Length of Stay

A graph relating length of stay to arrival date (date of first capture) of individuals was developed (all five years of data were pooled to increase sample size). For the purposes of this graph the original capture time was assigned a "trap date" by converting the capture date into a

numerical equivalent (e.g. 1 April was assigned the trap date 1, 2 April was assigned the trap date 2 and so on through the 90 day sample period). A linear regression line was fitted to these data and the Bartlett Chi-square Statistic (see references in Wilkinson 1989) was used to test for goodness of fit.

Determination of Mass Change of Individuals

The mass change of individuals that stayed for more than a day was determined. 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.

RESULTS

Timing Pattern

Spring and fall captures were plotted to establish migratory periods (Fig 1). Spring migration began around 1 April and ran through late May, with a few individuals trickling through until mid-June. 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. Capture rates in spring were much greater than in fall.

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). Also, males continued to appear after females had completed their migration. Males migrated significantly earlier in spring than females (Mann-Whitney $\underline{U}$ -Test, $\underline{p} < .001$, $n=589$). Males did not migrate significantly earlier than females in fall (Mann-Whitney $\underline{U}$ -Test $\underline{p} = .8$, $n=129$) (Fig. 3).

Figure 1. Rates of new captures of Wilson's Warblers during spring and fall of 1987-1991.

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

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

Length of Stay and Mass Change in Spring

Fifty-one of 391 males (13.0%) and 22 of 216 females (10.2%) stayed at least 1 d during spring migration. No significant difference (Mann-Whitney U-Test, $P = .2$) was found in the length of stay between males and females (Fig. 4). There was no significant difference (Yates Corrected Chi-square Test, $P > .25$) between the likelihood of males stopping over as compared to females (Table 2). There was no significant (Bartlett Chi-square Statistic, $P = .33$) linear relationship between original arrival date and length of stay of individual (Figure 5). Also, the average mass gain of males and females was found to be equal (0.4 grams) in spring.

Figure 4. Minimum length of stay (time between original capture and last recapture) during spring stopover.

Table 2. Contingency table relating stopover probability with the sex of captured birds.

	STAY = 0 DAYS		STAY > 0 DAYS	
	OBSERVED	EXPECTED	OBSERVED	EXPECTED
MALE	391	395	51	47
FEMALE	216	212	22	26

Expected values are based upon the assumption that there is no special relationship between sex and the likelihood of stopping over.

Figure 5. A graph showing the length of stopover as it relates to original capture dates of individuals.

DISCUSSION

General Overview of Pattern

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

Spring Migration

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. 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, Francis and Cook (1986) suggest that the advantages of early arrival may outweigh the costs of early arrival by males.

The advantages of early arrival on the breeding grounds by females may be less than those achieved by males (e.g., Francis and Cooke 1986). If the benefits of early arrival are less significant for females, factors such as food availability and the risk of poor weather become more important (Francis and Cooke 1986). Thus, it may be advantageous for females to arrive later when conditions are optimal for breeding.

Some authors argue that data on the 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 these variations in timing may stem from three distinct causes: migration at different times, different rates of travel, and/or different 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 different rates of migration is not important in establishing the spring this migration pattern at our study site.

Some authors suggest that males may be acquiring 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. It was found that males and females, on average, acquire the same amount of mass. 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, since mass changes were equal, it is assumed that males and females acquire the same amount of fat during spring stopover.

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 geographic variation in the sex ratio of winter populations of Dark-eyed Juncos (*Junco hyemalis*) in the eastern United States (Ketterson and Nolan 1976, 1979). In this case the percentage of females increases towards the south. 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 Warblers 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 pattern of migration Wilson's Warblers show in spring is probably due to differences in the onset of migration between the sexes. Differences in the 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.

Fall Migration

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, Mabey 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 some 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, since both sexes may be establishing territories on the wintering grounds; there would be equal pressure for early fall migration among the sexes.

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