The Wilson Journal of Ornithology 118(4):547–551, 2006

DIFFERENTIAL TIMING OF WILSON'S WARBLER MIGRATION IN ALASKA

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ABSTRACT.—We examined age- and sex-related differences in the timing of Wilson's Warbler (*Wilsonia pusilla pileolata*) migration at four locations in Alaska: Fairbanks, Tok, Mother Goose Lake, and Yakutat. We captured Wilson's Warblers with mist nets for ≥5 years during spring (northbound) and autumn (southbound) migration. In spring, males passed through our two northernmost sites—Tok and Fairbanks—earlier than females. During autumn, timing of adult migration did not differ by sex, but immatures passed through earlier than adults at all four sites. During previous studies of autumn passage sampled at lower latitudes, the lack of age-related differences in migration timing could be attributed to adults migrating faster than immatures (i.e., if immatures from higher latitudes began migration earlier than the adults, then the adults may have caught up to them at lower latitudes) or to the mixing of breeding populations from different locales. Autumn migration of adults and immatures netted at our two southernmost sites, both coastal locations, preceded migration at our two interior sites. These site-specific differences in the timing of autumn migration are likely the result of our coastal stations sampling birds that breed farther south and arrive earlier than birds breeding in more northerly regions of Alaska (and sampled at our interior stations). Early-arriving populations are likely able to complete their breeding season activities earlier and, subsequently, initiate their autumn migration earlier. *Received 29 July 2005, accepted 5 May 2006.*

Age- or sex-related differences in timing of migrant passage have been documented at several locations in North America (see reviews by Gauthreaux 1982, Woodrey 2000). Analyses of between-sex variation in the timing of spring migration have shown that males of several North American passerine species migrate prior to females (Francis and Cooke 1986, Yunick 1988, Otahal 1995, Yong et al. 1998, Swanson et al. 1999). Studies documenting age-class differences in the timing of autumn migration have revealed varied patterns. Immature Wilson's Warblers (*Wilsonia pusilla*) preceded adults by 9 days in southwestern Idaho (Carlisle et al. 2005a); 10 days at Yakutat, Alaska (Andres et al. 2005); and 13 days at Fairbanks, Alaska (Benson and Winker 2001). The autumn migration timing of adult and immature Wilson's Warblers did not differ in South Dakota (Dean et al. 2004) or in the riparian forest of the middle Rio Grande in New Mexico (Yong et al. 1998).

We selected the Wilson's Warbler to examine differential migration timing because it is a relatively abundant migrant and is sexually dichromatic. Wilson's Warblers breed throughout Alaska and winter in the southern United States, Mexico, and Central America (Ammon and Gilbert 1999). *W. p. pileolata* is the only subspecies known to range into Alaska (American Ornithologists' Union 1957, Gibson and Kessel 1997).

The geographic location of Alaska, relative to the continental landmass, provides an opportunity to study the passage of migrants near where they terminate their spring migration and initiate their autumn migration. Our objectives were to use data from four widely dispersed migration banding stations in Alaska to examine differences in the timing of Wilson's Warbler migration. Our specific objectives were to determine (1) between-sex differences in the timing of spring migration, (2) between-age differences in the timing of autumn migration, and (3) among-site differences in the timing of autumn migration.

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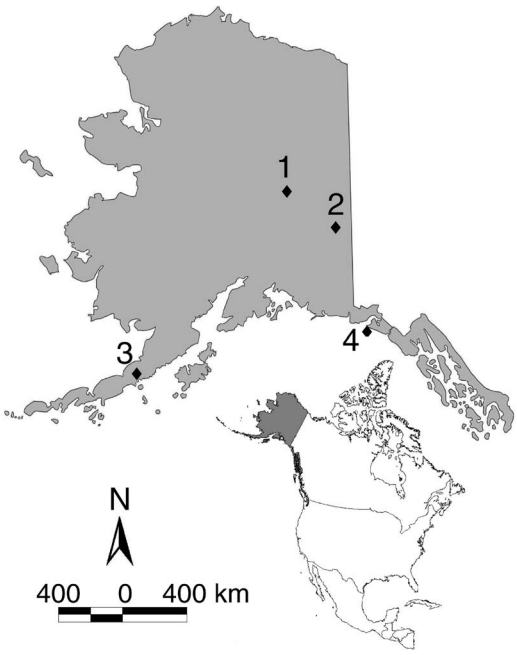

FIG. 1. Location of four migration monitoring stations in Alaska: (1) Fairbanks, (2) Tok, (3) Mother Goose Lake, and (4) Yakutat, 1992–2000.

METHODS

Study sites.—We analyzed data from four migration stations operated for ≥5 years during 1992–2000. Fairbanks and Tok were operated in spring and autumn, and Yakutat and Mother Goose Lake were operated only in the autumn. The Fairbanks banding station, operated by the Alaska Bird Observatory on the Creamer's Field Migratory Waterfowl Refuge (64° 50′ N, 147° 50′ W), and the Tok banding station (63° 22′ N, 143° 12′ W), operated by the Tetlin National Wildlife Refuge, are located in interior Alaska in the Tanana River Valley (Fig. 1). The Yakutat station, operated by the U.S. Fish and Wildlife Service, is on the Gulf of Alaska coastline ~300 km northwest of Juneau (59° 30′ N, 139° 40′ W; Fig. 1). The Mother Goose Lake station (57° 11′ N, 157° 15′ W), operated by the Alaska Peninsula/Becharof National Wildlife Refuge Complex, lies west of the Aleutian Mountain Range in southwestern Alaska, ~165 km southwest of King Salmon (Fig. 1).

We used 2.6- × 12-m nets with 30-mm mesh at all stations; specific operation details are provided in Table 1. The netting period at all stations spanned the entire duration of Wilson's Warbler migration. Our studies were designed to capture a wide suite of passerine species, many of which pass through study sites earlier and depart later than Wilson's Warblers.

Ageing and sexing.—At all locations during fall migration, age was determined by degree of skull ossification (Pyle 1997). During spring at Fairbanks and Tok, and during fall at Yakutat and Mother Goose Lake, birds were sexed by plumage and morphometric characteristics (Pyle 1997). During autumn at Fairbanks and Tok, birds were sexed using the following discriminant function, developed from known-age Alaskan birds (Weicker and Winker 2002), whereby 96% of known-age birds were classified correctly:

$$D = 0.9189 \text{ cap category} + 0.1800 \text{ cap length} + 0.0977 \text{ tail length} + 0.0938 \text{ wing chord} - 13.9426,$$

where D is the discriminant function, cap category separates caps into one of four classes (ranging from solid olive-green to solid

TABLE 1. Spring and autumn mist-netting efforts to capture migrant Wilson's Warblers at four banding stations in Alaska, 1992–2000.

Station	Season	Years	Period	No. nets	Time	Total net hr
Fairbanks	Spring	1992–2000	25 Apr–15 Jun	22–50	06:00–13:00	81,736
	Autumn	1992–2000	15 Jul–30 Sep	22–50	sunrise + 7 hr	114,053
Tok	Spring	1994–1998	late Apr–early Jun	20–24	sunrise + 6 hr	22,707
	Autumn	1993–2000	early Aug–late Sep	20–24	sunrise + 6 hr	49,322
Mother Goose Lake	Autumn	1994–2000	1 Aug–22 Sep	10–15	sunrise + 6 hr[a]	11,018
Yakutat	Autumn	1994–1999	1 Aug–5 Oct	10–15	sunrise + 6 hr	23,256

[a] Nets were opened 0.5 hr after sunrise.

TABLE 2. Median passage dates of Wilson's Warbler at four locations in Alaska: Fairbanks (1992–2000), Tok (1993–2000), Yakutat (1994–1999), and Mother Goose Lake (1994–2000).

		Adult between-sex differences					Between-age-class differences				
		Males		Females			Immatures		Adults		
Season	Site	Date[a]	*n*	Date[a]	*n*	*z*	Date[a]	*n*	Date[a]	*n*	*z*
Spring											
	Fairbanks	143	105	148	143	4.40**[b]					
	Tok	142	771	150	450	18.33**					
Autumn											
	Fairbanks	243	58	253	28	1.56	230	1,009	243	105	9.52**
	Tok	242	195	240	36	1.29	230	1,185	241	616	17.71**
	Yakutat	228	73	228	38	0.70	222	374	228	111	5.60**
	Mother Goose Lake	234	160	234	50	0.32	225	10,481	235	287	17.29**

[a] Median Julian date of passage.
[b] Double asterisk indicates $P < 0.001$.

black), and cap length is the extent of black feathers from the front to the back of the head. For our analyses, we included only records with ≥75% probability that individuals were sexed correctly.

Definition of migrants.—In analyses for all sites, we included only first captures of birds. Based on two criteria, we eliminated individuals that may not have been migrating at the time of capture: (1) birds recaptured >7 days after first capture and (2) locally fledged birds (i.e., birds retaining >60% of their juvenal plumage). We did not specifically remove females with brood patches because this could potentially bias the retention of males and elimination of females, and affect our between-sex comparisons. No females with brood patches were captured at Fairbanks, Tok, or Yakutat, and only nine such individuals were captured and included in the data set from Mother Goose Lake. It is possible that birds not migrating at the time of capture were included in our analyses, resulting in an early-biased median date of autumn passage. However, considering the relatively few birds netted in summer compared to the vast numbers captured during the brief and intense migration pulse, we suspect the numbers of breeding birds included in these analyses were small. If some non-migratory birds were included in these analyses, they likely affected the data from each station and, therefore, should not have affected our among-site comparisons.

Data analysis.—We tested for age-, sex-, and site-related differences in median passage dates by using Mann-Whitney *U*-tests. For two reasons, we did not standardize by unit of netting effort. First, standardizing by unit of effort can artificially inflate or deflate sample sizes, which, in turn, can affect the power of a test (see examples in Benson and Winker 2001). Second, standardizing by unit of effort was not necessary in these analyses because even in Fairbanks, where there were some netting-effort inconsistencies in earlier years, net hr over a given season had a uniform distribution when all years were combined (see Benson and Winker 2001).

RESULTS

During spring migration, males preceded females by 5 days at Fairbanks ($Z = 4.40$, $n = 248$, $P < 0.001$; Table 2) and by 8 days at Tok ($Z = 18.33$, $n = 1{,}221$, $P < 0.001$; Table 2). In autumn, we found no between-sex difference in the timing of adult migration at any location (Table 2). However, immatures consistently preceded adults at all locations: by 13 days at Fairbanks ($Z = 9.52$, $n = 1{,}114$, $P < 0.001$), 11 days at Tok ($Z = 17.71$, $n = 1{,}801$, $P < 0.001$), 6 days at Yakutat ($Z = 5.60$, $n = 485$, $P < 0.001$), and 10 days at Mother Goose Lake ($Z = 17.29$, $n = 10{,}768$, $P < 0.001$; Table 2). Passage of both adults and immatures was significantly earlier at the two coastal sites than at the two interior sites (all $Z \geq 7.84$, $P < 0.001$). Wilson's Warblers also passed through Yakutat significantly earlier than they did at Mother Goose Lake (all

$Z \geq 5.23$, $P \leq 0.001$). There was no significant difference between the passage dates at Fairbanks and Tok.

DISCUSSION

Basic patterns in the timing of migration were similar at all four migration stations in Alaska. In spring, the earlier passage of male Wilson's Warblers, compared with females, was similar to results found by Francis and Cooke (1986) and Yong et al. (1998). These results were expected because of the selective pressures that favor males to arrive early and obtain a high-quality territory, whereas females likely benefit by arriving later when resources are more predictable (see review by Francis and Cooke 1986).

Immature Wilson's Warblers migrate southward from Alaska significantly earlier than adults, most likely because they do not undergo the full prebasic molt that adults must complete before migration (Dwight 1900). Adults, however, compensate for their later migration by migrating with greater mass and fat stores (Andres et al. 2005, Benson and Winker 2005). The differences in age-related migration timing among Wilson Warblers in fall may not be detectable at lower latitudes (e.g., Yong et al. 1998, Dean et al. 2004) because immatures may migrate at slower rates due to their inability to forage as efficiently as adults. During fall migration in New Mexico, immature Wilson's Warblers had lower fat scores than adults, but age-class differences in mass and rates of mass gain have not been detected at other locations for this species (Jones et al. 2002, Carlisle et al. 2005b).

The among-site differences in median dates of autumn passage were not surprising. The onset of winter can vary substantially throughout the large and mountainous state of Alaska, and populations originating from regions with briefer summers are likely to depart earlier. Stopover ecology of Wilson's Warblers is also influenced by habitat (Hutto 1985, Skagen et al. 1998), but we did not measure the effect of this variable at the locations studied.

We currently lack sufficient information for defining the breeding ranges of populations sampled at our four study sites; however, we hypothesized that samples from interior sites represented different populations than those sampled at coastal sites because large mountain ranges separate the southern coast of Alaska from the state's interior. Isotopic ratios of Wilson's Warblers breeding in western North America indicate that coastal breeders overwinter in western Mexico and those that breed farther inland and at higher elevations overwinter in eastern Mexico (Clegg et al. 2003). However, a few recoveries of birds banded at Mother Goose Lake indicate that birds occurring at that site may represent populations that winter in both eastern and western locations.

ACKNOWLEDGMENTS

Funding for this project was provided by the Alaska Bird Observatory, Alaska Department of Fish and Game, Alaska Peninsula/Becharof National Wildlife Refuge, Earthwatch Institute, Tetlin National Wildlife Refuge, and U.S. Fish and Wildlife Service (Region 7) Migratory Bird Management, and Alaska Department of Natural Resources. These studies would not have been possible without the many staff and volunteers that contributed countless hours capturing and banding birds. We especially thank B. Browne, T. J. Doyle, A. R. Ajmi, C. Adler, T. Burke, K. Convery, C. R. Davis, D. Dewhurst, N. DeWitt, R. C. Egan, T. Eskelin, J. Foster, N. Gregory, R. I. Frey, J. Klima, A. L. Lancaster, K. W. Larson, M. Margulies, R. C. Means, J. Melton, R. Moore, H. Moore, R. K. Papish, T. H. Pogson, G. Ruhl, M. Sardy, D. Shaw, K. M. Sowl, S. K. Springer, H. K. Timm, L. Wells, and D. L. Williams. We also thank G. Collins for preparing the map and P. J. Heglund for reviewing an earlier version of the manuscript. Many thanks to D. L. Swanson and an anonymous reviewer for comments that improved the manuscript.

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