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Timing of Breeding Range Occupancy Among High-latitude Passerine Migrants

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ABSTRACT.—The brief subarctic summer limits the
time available for birds to complete their reproduc-
tive activities, yet the temporal requirements of high-
latitude passerine migrants are not well understood.
Our analyses examined the timing of spring and au-
tumn migration among 18 passerine species to ob-
tain indirect estimates of the time they occupy their
breeding ranges in northwestern North America.
From 1992 to 1998, the Alaska Bird Observatory
(64°50′N, 147°50′W) banded 31,698 individuals dur-
ing the most intensive standardized mist-netting
study ever conducted in subarctic North America.
Among the migrants examined, the estimated num-

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ber of days that species were present in interior Alaska ranged from 48 days for adult Alder Flycatchers (*Empidonax alnorum*) to 129 days for American Robins (*Turdus migratorius*). Adults departed significantly later in autumn than immatures in 10 of 18 species we examined and significantly earlier than immatures in only one species, Alder Flycatcher. Breeding range occupancy of Nearctic–Neotropic migrants occurs in this region within the range of average frost-free temperatures in Fairbanks, Alaska, and is significantly shorter in duration than among Nearctic–Nearctic ("short-distance") migrants at this latitude.

The high latitudes of North America support a diverse avifauna, because during the summer months the region is characterized by a nutrient-rich environment, an extended photoperiod, and a hospitable climate. But summer at high latitudes is brief. For example, the average frost-free period in Fairbanks, Alaska was 105 days from 1905 to 1999 (from 20 May to 2 September; National Weather Service data). Birds that migrate to Alaska are therefore under greater temporal pressure to complete breeding-season activities (such as territory and mate acquisition, nest building, egg laying, incubation, care of young, and molt) than birds at lower latitudes. Yet, the total amount of time passerines spend completing the breeding effort is not well known. Few studies have been conducted over the entire breeding season at high latitudes, and those studies that have examined breeding chronology at northern locations (e.g. Rimmer 1988) may not accurately document departure from the breeding grounds because of small samples and postbreeding dispersal.

Studies sampling migrant passage during spring and autumn provide an indirect measure of time spent on the breeding grounds. The accuracy of that measure increases with proximity to a population's breeding area. We sampled migrants near the northern and western limits of their migrations during spring and autumn. Here we examine timing of passage at the species level in that region to obtain indirect estimates of the time birds occupy their breeding ranges in the northwestern extreme of North America. Additionally, we answer the following questions: (1) How compressed are breeding-season activities among high-latitude migrants? (2) Do Nearctic–Neotropic migrants differ from Nearctic–Nearctic ("short-distance") migrants in the timing of breeding-range occupancy?

Study area and methods.—The study area is located in Fairbanks, Alaska (64°5′N, 147°5′W), near the confluence of the Chena and Tanana rivers (elevation 130 m). The Tanana Valley is a well documented migration corridor for many species of birds, including Sandhill Cranes (*Grus canadensis*; Kessel 1984), many species of raptors (McIntyre and Ambrose 1999), waterfowl, shorebirds, and passerines (Cooper and Ritchie 1995).

TABLE 1. Net-hours of operation and total days of netting in spring and autumn at Creamer's Field Migration Station in Fairbanks, Alaska (1992–1998).

Year	Spring		Fall	
	Net-hours	Days	Net-hours	Days
1992	6,903	42	5,822	46
1993	10,552	43	13,472	50
1994	11,252	41	13,935	52
1995	12,731	45	13,944	57
1996	12,411	44	14,985	57
1997	7,548	42	14,617	66
1998	6,800	39	11,853	54
Total	68,196	296	88,627	382

The study site, at Creamer's Field Migration Station (CFMS), encompasses ~20 ha of the southwestern portion Creamer's Field Migratory Waterfowl Refuge (731 ha). It is owned by the State of Alaska and operated by the Alaska Department of Fish and Game. The northern portion of CFMS is dominated by mature willow (*Salix* spp.) and paper birch (*Betula papyrifera*) bordering a seasonally flooded wetland dominated by sedges (*Carex* spp.) and one grass species (*Calamagrostis canadensis*). The central section of the study area is characterized by late successional white spruce (*Picea glauca*) and balsam poplar (*Populus balsamifera*). The southern portion of the study area has trembling aspen (*Populus tremuloides*), balsam poplar, and willow growing near an agricultural field. Except for the agricultural field, that mosaic of habitat types is representative of the habitats occurring in the boreal forest floodplains of interior Alaska.

A standardized mist-netting protocol was conducted at CFMS from 1992–1998 using an array of 22–50 standard mist nets (30 mm mesh, 2.6 × 12 m). Nets were arranged in a north–south direction, perpendicular to the Tanana Valley migration corridor, and operated daily from 0600 to 1300 (Alaska) during spring migration (25 April–15 June). During autumn migration (15 July–30 September), nets were opened at approximately sunrise and closed 7 h later. Sampling at the ends of both seasons (10–15 June and 25–30 September) was limited to every other day. Nets were closed during inclement weather. Fewer nets were operated in 1992, 1997, and 1998 than in other years (Table 1), and nets were not operated between 17 July and 2 August 1992.

Birds were banded with U.S. Fish and Wildlife Service bands, and data were collected to determine age (autumn only, using degree of skull ossification), and breeding condition (spring only, using incubation patches in females and enlarged cloacal protuberances in males). During autumn migration, estimates of the percentage of juvenal plumage were recorded for first-year individuals.

To ensure independence of records in those analyses, we used only initial captures of individuals (all subsequent captures of individuals were eliminated). We also excluded local breeders on the basis of the following criteria: females with incubation patches, individuals captured more than seven days from first capture, and birds captured in one season and recaptured in another. First captures of individuals were also removed if they were later recaptured with breeding characteristics. Finally, we excluded first-year birds with >30% of their body in juvenal plumage, because we considered them nonmigratory at that time.

We defined Nearctic–Neotropic migrants as those species with all or part of their populations breeding north of the Tropic of Cancer and all or part of the same populations wintering south of that line (Rappole et al. 1983). We defined Nearctic–Nearctic migrants as those species whose breeding and wintering populations are primarily north of the Tropic of Cancer. Those species are often categorized as short-distance migrants.

A maximum estimate of time spent on breeding grounds was obtained from the difference between median dates of spring and autumn passage. We did not standardize numbers of birds captured by unit of netting effort for two reasons. First, net hours (nh) were uniformly distributed among days when all years were combined during spring (Kolmogorov-Smirnov-test, $Dmax = 0.08$, $n = 68,196$, $P > 0.10$) and autumn (KS-test, $Dmax = 0.07$, $n = 87,627$, $P > 0.10$). Second, standardizing captures by unit of netting effort can impart bias by artificially inflating or deflating sample sizes. For example, 18 birds captured during 80 nh could provide sample sizes of 22.5 birds/100 nh, 225 birds/1,000 nh, or .225/ nh. Thus, an arbitrary number of net-hours used to standardize captures directly affects sample size, which affects the power in statistical tests. Finally, manipulating sample size in our study was not necessary given the uniformity of net-hours within seasons.

Differences in timing of passage were present among years for some species (Benson 2000). Here we combined all years to increase sample sizes because that provides the best species-level estimate of the duration of breeding-range occupancy. Additionally, variation in the netting effort in earlier years was minimized when years were pooled because nets were operated uniformly among days within each season when all years were combined.

We tested for differential timing of migration between adults and immatures during autumn using the Mann-Whitney U test. Differences in timing of migration between age classes could affect species-level estimates of the median date of autumn passage, because most autumn captures at that study site are first-year birds.

Results.—During 1992–1998, staff of the Alaska Bird Observatory accumulated 68,196 nh during spring and 88,627 nh during autumn (Table 1). During those seven years, 31,698 birds of 58 species were banded. We examined the timing of passage of 25,718 individuals among 18 passerine species. Judging from capture distributions (Benson 2000), the netting periods spanned the entire spring and autumn migration periods for all species analyzed except Alder Flycatcher. Spring netting was truncated shortly after peak passage of that species. Therefore, for that species median spring passage dates may be slightly later than presented here.

There were significant differences in median dates of autumn passage between adults and immatures in 11 of 18 species (Table 2). The Alder Flycatcher was the only species in which the departure date of adults preceded that of immatures; that difference averaged 13 days (Table 2). In Ruby-crowned Kinglets, Swainson's Thrushes, American Robins, Orange-crowned Warblers, Yellow-rumped Warblers, Yellow Warblers, Blackpoll Warblers, Wilson's Warblers, American Tree Sparrows, White-crowned Sparrows, and Dark-eyed Juncos, immatures preceded adults (Table 2). The largest significant age-related differences in passage dates occurred among Wilson's Warblers and Dark-eyed Juncos; in both species, adults migrated on average 13 days later than immatures. In 6 of 18 species, there were no significant differences between adults and immatures in median dates of passage. Because there were significant age-related differences in departure dates in several species, and because inference of departure is conflated by large numbers of immatures (lowering accuracy; Table 2), immatures were eliminated from all subsequent analyses.

Estimates of the period that adults occupied their breeding ranges were more condensed for Nearctic–Neotropic migrants ($n = 12$) than for Nearctic–Nearctic migrants ($n = 6$; Mann-Whitney $U = 71.0$, $P < 0.05$; Table 2, Fig. 1). The mean period of breeding-range occupancy for all Nearctic–Neotropic migrants was 90.6 days (SE = 4.4 days), or <25% of the annual cycle. Nearctic–Nearctic migrants averaged 119.8 days (SE = 3.4 days), or 33% of the annual cycle.

The estimated number of days that adults were present in interior Alaska ranged from 48 days for Alder Flycatchers to 129 days for American Robins (Fig. 1). The next-briefest times occurring between median dates of spring and autumn passage in Yellow Warblers, Hammond's Flycatchers, and Northern Waterthrushes, which spent 84, 86, and 86 days, respectively, on their breeding ranges, or ~23% of the annual cycle.

Discussion.—The later departure dates of adults in many species may be explained by the timing of molt in adults, which, unlike immatures, replace flight feathers in autumn. Differences in timing of passage between adult and immature Swainson's Thrushes, although present here, were not at Long Point, Ontario, western Pennsylvania, or coastal Alabama in

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TABLE 2. Timing of migration during spring and autumn, and differences in passage dates between adults and immatures during autumn among passerine species in Fairbanks, Alaska (1992–1998).

Species	Status[a]	Spring migration			Autumn migration						Z[c]	Days[d]
		n	Range	Date[b]	Adults			Immatures				
					n	Range	Date[b]	n	Range	Date[b]		
Alder Flycatcher (*Empidonax alnorum*)	L	39	154–167	161	83	196–237	209	342	204–256	222	8.81**	48
Hammond's Flycatcher (*Empidonax hammondii*)	L	58	115–166	138	19	198–259	224	226	196–249	216	1.66	86
Ruby-crowned Kinglet (*Regulus calendula*)	S	46	116–143	130	107	226–269	253	846	198–273	245	4.32**	123
Gray-cheeked Thrush (*Catharus minimus*)	L	102	135–159	144	45	199–265	242	187	211–261	239	2.76*	98
Swainson's Thrush (*Catharus ustulatus*)	L	283	132–159	145	82	224–270	240	675	198–268	232	7.24**	95
American Robin (*Turdus migratorius*)	S	217	121–167	137	77	235–271	266	198	205–272	249	6.66**	129
Orange-crowned Warbler (*Vermivora celata*)	L	252	130–164	143	582	196–266	245	3,378	196–270	237	8.63**	102
Yellow-rumped Warbler (*Dendroica coronata*)	L	539	117–163	136	376	208–268	244	5,663	196–266	234	5.49**	108
Yellow Warbler (*Dendroica petechia*)	L	149	135–167	151	94	199–264	235	734	196–260	227	7.42**	84
Blackpoll Warbler (*Dendroica striata*)	L	69	135–160	142	37	223–266	236	359	209–256	231	4.07**	94
Northern Waterthrush (*Seiurus noveboracensis*)	L	210	133–159	143	12	221–237	229	221	197–252	227	1.15	86
Wilson's Warbler (*Wilsonia pusilla*)	L	242	129–162	144	90	207–271	242	822	198–271	229	9.58**	98
American Tree Sparrow (*Spizella arborea*)	S	88	117–153	131	501	236–271	257	3,224	224–274	256	3.53**	126
Savannah Sparrow (*Passerculus sandwichensis*)	L	197	126–167	143	30	198–268	235	536	197–270	231	2.55*	92
Fox Sparrow (*Passerella iliaca*)	S	48	115–147	131	64	228–264	247	221	199–269	244	2.44*	116
Lincoln's Sparrow (*Melospiza lincolnii*)	L	71	124–167	139	60	196–269	235	1,259	196–273	229	1.28	96
White-crowned Sparrow (*Zonotrichia leucophrys*)	S	93	123–156	135	37	198–266	240	416	204–271	230	4.98**	105
Dark-eyed Junco (*Junco hyemalis*)	S	213	116–166	135	231	221–272	256	2,710	197–272	246	4.12**	121

[a] L = Nearctic–Neotropic migrant, S = Nearctic–Nearctic migrant.
[b] Median Julian dates of passage.
[c] Results from Mann-Whitney *U* tests for differences in passage dates between adults and immatures in autumn.
[d] Maximum estimate of the average number of days adults occupy breeding range (difference between median dates of spring and autumn passage).
* *P* < 0.05, ** *P* < 0.003 (significance with Bonferroni corrections).
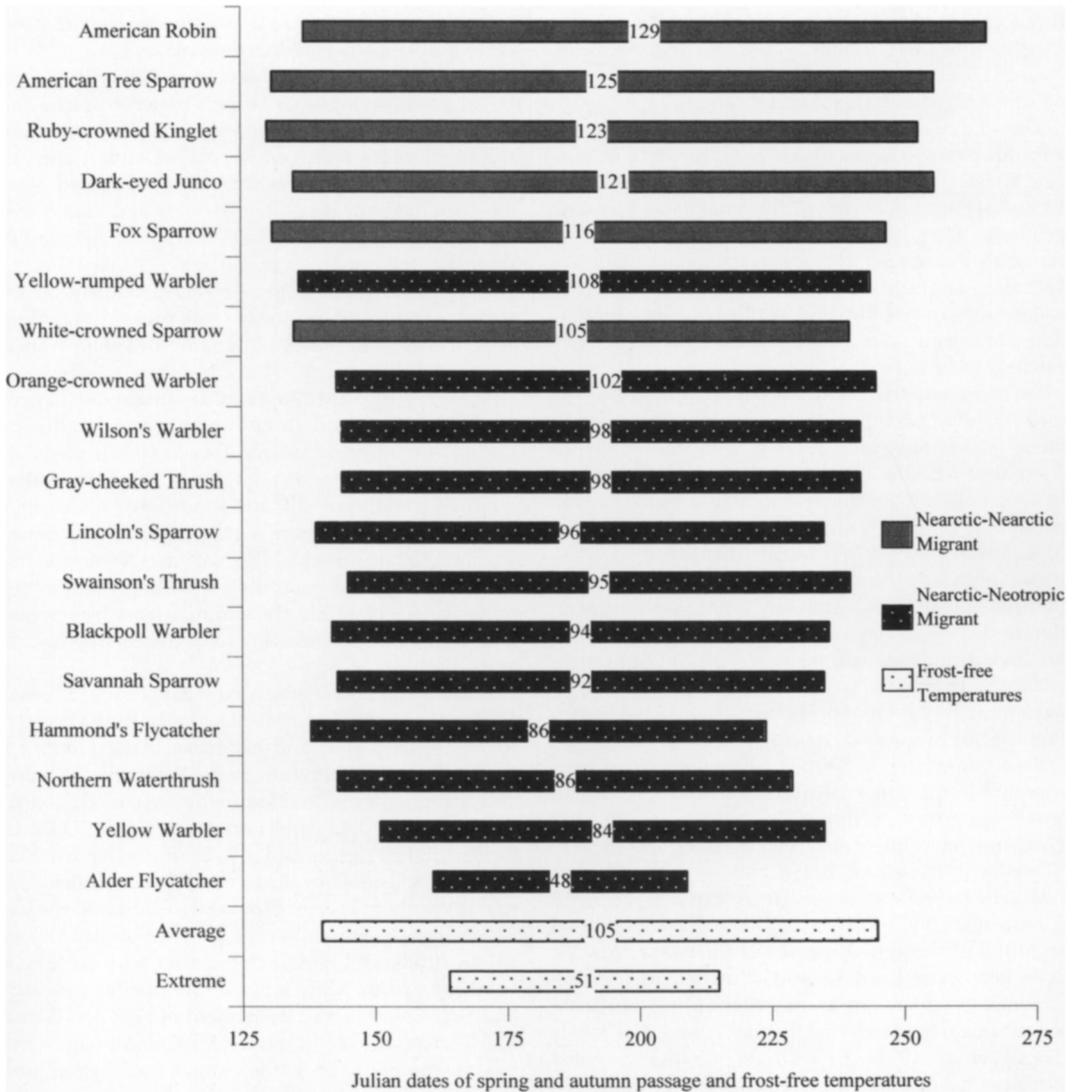
FIG. 1. Species-level estimate of the number of days passerine migrants occupy breeding ranges in Alaska using median dates of spring and autumn passage. Number of frost-free days are calculated from temperature records (n = 95 years) in Fairbanks, Alaska.

1990 (Woodrey and Chandler 1997). The same was true for 1991, with the exception of Long Point, where the median date of passage of adults was significantly earlier than immatures (Woodrey and Chandler 1997).

The Alder Flycatcher was the only species in our study in which adults preceded immatures in autumn. We estimated that adult Alder Flycatchers departed 13 days earlier than immatures, which is similar to previous results from Long Point, Ontario where a 14 day difference was found (Hussel 1991a). The lack of molt

in adults of that species prior to autumn migration (Dwight 1900) probably accounts for this difference.

Studies at lower latitudes have suggested that the duration of the breeding season for some Nearctic–Neotropic migrants is brief. Winker et al. (1992) studied passerine migration in Minnesota at ~45°N and concluded that many species spend <30% of their annual cycle on their breeding grounds. In this study, at 64°5′N and much nearer to the final destinations of high-latitude migrants, we estimated that populations of Nearctic–Neotropic migrants cap-

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tured at our study site occupy their breeding ranges for <25% of their annual cycles, and that Nearctic–Nearctic migrants average 33% of their annual cycles on those high-latitude breeding ranges.

The 48 day difference between median spring and autumn passage dates of Alder Flycatchers in interior Alaska suggests that that species spends just 13% of its annual cycle on those northern breeding grounds. That is the shortest period of breeding range occupancy yet documented for a population or species of migratory passerine. In comparison, a lower-latitude study estimated 73 days between median dates of spring and autumn passage of Alder Flycatchers (adults only; Hussel 1991a, b).

We estimated that some Alaska populations of Yellow Warblers occupied their breeding range for 84 days, which suggests decided compression when compared with the 104 days estimated to be required to accomplish breeding-season activities in Manitoba, at 50°1′N (Busby and Sealy 1979). Other studies of Yellow Warblers also indicate that breeding activities at high latitudes are indeed compressed. Studies by Briskie (1995) and Rimmer (1988) provide an estimate of 79–115 days required by Yellow Warblers for breeding range activities at other high-latitude sites, and that is concordant with our estimate of 84 days for completion of breeding season activities for this species in interior Alaska.

Breeding-season activities begin later in Alaska compared with other latitudes. For example, in Palomarin County, California, juvenile Swainson's Thrushes have been observed as early as 15 May (Johnson and Geupel 1996), and juvenile Wilson's Warblers have been observed as early as 15 April (Chase et al. 1997). The median date of spring arrival of adults of those two species in Fairbanks, Alaska, does not occur until 15 May. Further, in Orange-crowned Warblers, nest construction has been observed in early March on Channel Island, California (Sogge et al. 1994). In contrast, Orange-crowned Warblers do not arrive in central Alaska until ~75 days later.

The latest date on which freezing temperatures have occurred in spring in Fairbanks was 13 June (1922), and the earliest date of freezing temperatures in autumn was 3 August (1944; based on a 95-year National Weather Service record). At the extreme, therefore, that region has the possibility of delivering only 51 consecutive days of temperatures greater than 0°C. In that region, Alder Flycatchers arrive near the record last date of frost in spring and leave before the record first date of frost in autumn (Fig. 1). That is probably not a coincidence. It is well known that flying insect availability is negatively affected by frosts, and that would seem to provide strong selection against Alder Flycatchers' occupation of their breeding grounds during times of potential frost. Other insectivorous birds probably forage on a more diverse prey base when flying insects

are not available and are therefore able to withstand early and late frosts in extreme years.

Summer at high latitudes is brief. Nearctic–Nearctic migrants averaged 119.8 days between spring and autumn median dates of passage, and Nearctic–Neotropic migrants averaged 90.6 days. All but one Nearctic–Neotropic species, the Yellow-rumped Warbler, appeared to time their arrivals and departures to occur within the long-term average of 105 days of frost-free temperatures in Fairbanks, Alaska (Fig. 1). Nearctic–Neotropic migrants rely primarily on insects for food, and are likely to be present as that resource waxes, becomes abundant, and then wanes. Conversely, most of the Nearctic–Nearctic species we studied rely on a seed- or fruit-dominant diet in winter, accounting for their ability to be present during periods of frost and indeed frozen conditions. Further, Nearctic–Nearctic migrants may be better adapted to adverse climatic conditions, which they may also experience on wintering areas. In northwestern North America, the Nearctic–Neotropic migrants we studied time their breeding-range occupancy to occur within the summer frost-free period and complete their annual reproductive cycle in a brief temporal window.

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Growth Rate and Energetics of Arabian Babbler (*Turdoides squamiceps*) Nestlings

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ABSTRACT.—Arabian Babblers (*Turdoides squamiceps*) are territorial, cooperative breeding passerines that inhabit extreme deserts and live in groups all year round. All members of the group feed nestlings in a single nest, and all group members provision at similar rates. Nestlings are altricial and fledge at about 12 to 14 days, which is short for a passerine of its body mass. Because parents and helpers feed nestlings, we hypothesized that the growth rate of nestlings is fast and that they fledge at a body mass similar to other passerine fledglings. Using a logistic growth curve, the growth rate constant (k) of nestlings was 0.450, which was 18% higher than that predicted for a passerine of its body mass. Asymptotic body mass of fledglings was 46 g, which was only 63% of adult body mass, a low percentage compared to other passerines. Energy intake retained as energy accumulated in tissue decreased with age in babbler nestlings and amounted to 0.29 of the total metabolizable energy intake over the nestling period. However, energy content per gram of body mass increased with age and averaged 4.48 kJ/g body mass. We concluded that our hypothesis was partially confirmed. Growth rate of babbler nestlings was relatively fast compared to other passerine species, but fledgling mass was relatively low.

Deserts are characterized by unpredictable rainfall and unpredictable, often sparse, food availability

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