Timing of Songbird Migration in the St. Croix River Valley, Minnesota, 1984 – 1986

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"It must be kept constantly in mind...that no complete and scientific study of the..[speed at which birds migrate]...is as yet possible, and that the present records are given merely because they are the best now obtainable, and because they may furnish some material for the use of the future student." Cooke (1888:13).

Introduction

Despite more than a century of interest, we still know little about the nonbreeding movements of nearctic songbird migrants. Timing of passage in particular has received little more than casual attention since the early days of nearctic migrant research. The early work of Wells W. Cooke (1888) synthesized a large effort to map the passage of migrants northward through the Mississippi Valley in spring. Cooke presented data showing the rates of movement for many species for the first time but, as he recognized, the timing of arrival of the first individuals of a species or the dates of the last departures really tell us little about the timing of individual movements.

Ideally, the timing of migratory movement should be investigated by following specific individuals throughout their migratory journeys. At present, this is not feasible for small passerines (but see Cochran et al. 1967). Secondarily, timing of seasonal movements could be investigated by monitoring all individuals passing particular geographic points and then comparing timing among these points. Although this is difficult to implement, one approach to this goal is to place mist nets in the same position season after season to sample migrants as they pass. Mist nets, in effect, are observers with a relatively constant bias, especially when set in the same places and kept open for as much time as possible. The strength of this approach lies in capturing large numbers of passing individuals by maximizing sample effort. One can have most confidence in the results generated by the most commonly captured species.

Why is timing so important? Consider these questions: How fast are birds traveling? Where are the demands for resources being met? Long distance migrants are generally unable to carry enough fat to migrate the complete distance between breeding and wintering grounds, and are therefore dependent upon "refueling" stops along the way (see Tucker 1974, Bairlein 1987, Winker et al. 1992a). Species showing very rapid movement are likely to place a high demand on the resources at daily stopover sites (most of these birds migrate at night). Little is known about "refueling" strategies, timing, or route selection in migrant songbirds. Understanding these things will help in conservation efforts as well as in addressing an array of evolutionary questions.

Techniques

Mist nets and the aluminum band are two important tools for studying migration, despite having proven largely ineffective in addressing long distance questions because band recoveries in nongame species are so rare. Capture allows birds to be measured, sexed (when possible), aged, weighed, and examined for fat level and molt status. These data allow us to address various demographic and physiological questions regarding birds in passage. What are the age and sex ratios of the transient populations? Are they feeding? Are they molting? How much fat are they carrying? Capture also allows an estimate of abundance when captures are standardized for sample effort. In studies using mist nets, the sample unit is the "net hour": one 12m x 2.6m net open for one hour. Banding enables the investigator to determine which birds are new to an area and which are remaining. By disregarding recaptures, we can look more certainly at the movements of transients—birds that will neither breed nor winter in an area.

	SPRING								AUTUMN										
Species	S1	S2	S3	S4	S5	S6	Range	Median	A1	A2	A3	A4	A5	A6	A7	A8	A9	Range	Median
American Woodcock	2	1	1	0	2	2	121-147	-	0	0	1	1	2	0	1	0	1	233-264	-
Ruby-throated Hummingbird	0	1	12	23	32	18	128-148	140	0	34	79	83	70	54	48	17	2	227-265	241
Olive-sided Flycatcher	0	0	0	1	1	0	135-140	-	0	3	8	20	15	6	0	0	0	229-251	241
Eastern Wood-Pewee	0	0	0	2	2	4	137-147	142-3	0	5	15	24	18	12	8	6	9	229-264	243
Yellow-bellied Flycatcher	0	0	0	1	3	24	138-148	146	0	12	45	79	56	22	5	10	7	229-264	240
"Traill's" Flycatcher	0	2	3	9	7	20	125-149	143	0	20	26	74	44	27	5	6	5	229-264	240
Least Flycatcher	4	26	141	97	36	22	118-148	133	0	11	18	29	41	21	13	10	10	229-265	242
Eastern Phoebe	2	1	0	1	0	0	119-138	-	0	0	2	2	6	2	3	0	6	232-266	247
*Great Crested Flycatcher	0	2	0	4	3	5	127-147	140	0	10	12	2	3	4	1	1	1	227-262	235-6
Red-breasted Nuthatch	1	1	2	3	0	0	119-138	-	0	0	3	1	6	7	3	8	7	235-265	-
Brown Creeper	3	2	3	1	0	0	122-134	-	0	0	0	0	1	8	1	4	13	242-267	-
*House Wren	15	18	17	24	17	4	118-148	-	2	26	18	11	21	11	6	4	6	226-266	238
Winter Wren	3	0	0	0	0	0	118-123	-	0	0	0	0	0	3	7	7	23	248-267	-
Ruby-crowned Kinglet	121	31	62	26	1	0	118-139	-	0	0	0	0	1	1	14	34	47	243-267	-
Golden-crowned Kinglet	0	0	0	0	0	0	-	-	0	0	0	0	0	0	1	0	9	255-265	-
*Blue-gray Gnatcatcher	1	1	2	3	2	1	121-147	134-5	0	3	2	0	1	0	0	0	0	229-244	-
Veery	2	2	1	23	11	6	120-146	136	0	6	11	12	11	13	4	5	5	229-267	243
Gray-cheeked Thrush	0	23	71	23	27	5	124-148	132	0	0	0	4	2	6	12	12	12	238-265	256-7
Swainson's Thrush	1	53	71	59	111	51	119-148	138	0	9	19	49	52	138	140	176	80	229-267	254
Hermit Thrush	6	1	3	2	0	0	119-137	-	0	0	1	0	0	0	0	0	2	232-264	-
*Wood Thrush	0	1	13	7	15	7	125-147	139	0	1	1	10	2	2	7	5	3	231-266	251
*American Robin	9	2	8	4	7	8	118-147	134	0	7	10	8	7	7	2	2	10	229-266	243
*Gray Catbird	0	7	22	84	82	38	125-148	-	7	39	69	62	60	68	35	29	32	222-267	-
Cedar Waxwing	49	149	59	5	6	23	119-148	-	0	18	26	47	19	12	5	2	7	229-266	-
Solitary Vireo	2	2	47	44	3	1	122-145	133	0	0	1	7	15	19	31	31	33	233-267	255
Yellow-throated Vireo	0	0	0	0	0	0	-	-	0	2	2	1	5	1	0	1	1	230-266	242

Table 1. Distribution of migrants through time in the lower St. Croix River Valley (Valley Creek, Washington Co., Minnesota), displayed as total individuals captured during particular time periods (summed, 1984–1986). Recaptures are excluded. All migrant species with more than ten individuals captured are included. Spring (Julian Days 118–149) is divided into six periods, and autumn (Julian Days 222–268) into nine. The first and last periods of each season have six days, the rest have five. In non-leap years, 15 May = Day 135 (second day in S4), and 1 Sep = Day 244 (third day in A5). An asterisk indicates a species with a resident breeding population. Median dates are given only when the data suggest that the majority of the migratory period was sampled. Common names follow AOU (1983).

Species	S1	S2	S3	S4	S5	S6	SPRING Range	SPRING Median	A1	A2	A3	A4	A5	A6	A7	A8	A9	AUTUMN Range	AUTUMN Median
Warbling Vireo	0	1	2	1	5	1	127-146	140	0	0	1	2	5	1	1	1	1	235-263	244
Philadelphia Vireo	0	1	3	4	2	1	127-145	135	0	1	3	24	19	52	26	27	14	230-266	249
*Red-eyed Vireo	0	0	2	8	11	16	130-148	142	0	10	40	230	199	144	52	35	35	229-267	243
Blue-winged Warbler	0	1	8	7	2	6	127-146	134-5	0	2	4	0	1	1	0	0	0	229-250	236
Golden-winged Warbler	0	1	4	6	1	0	127-140	135	0	0	7	9	12	11	1	4	2	234-263	244
Tennessee Warbler	0	7	10	15	11	1	127-144	134	1	56	120	238	233	73	14	21	21	226-266	240
Orange-crowned Warbler	11	14	12	11	0	0	118-135	-	0	0	0	0	0	1	1	2	7	251-266	-
Nashville Warbler	3	38	29	66	6	1	120-147	134	0	28	63	118	120	108	71	84	123	229-267	248
Northern Parula	0	0	0	0	0	0	-	-	0	0	0	1	3	6	3	0	0	239-253	249
Yellow Warbler	0	1	5	13	5	2	124-147	135	0	1	0	0	2	0	0	0	0	230-244	-
Chestnut-sided Warbler	0	0	6	11	11	3	130-147	138	0	16	52	99	112	53	23	15	16	229-267	242
Magnolia Warbler	0	1	27	43	21	13	126-149	137	0	25	56	199	238	149	42	32	37	229-267	242
Cape May Warbler	0	0	0	0	0	0	-	-	0	2	11	25	7	1	0	0	1	229-262	238
Black-throated Blue Warbler	0	0	0	0	0	0	-	-	0	0	0	1	4	0	3	3	0	240-261	252
Myrtle Warbler[a]	25	14	35	10	0	0	118-135	-	0	1	0	0	1	2	2	1	8	229-266	-
Black-throated Green Warbler	0	0	3	4	0	0	132-137	135	0	0	6	18	25	20	6	4	3	233-264	244
Blackburnian Warbler	0	0	0	2	0	1	135-145	-	0	1	10	14	25	3	2	0	2	229-265	242
Palm Warbler	5	5	5	0	0	0	118-133	-	0	0	0	0	0	2	0	0	1	250-263	-
Bay-breasted Warbler	0	0	0	0	0	0	-	-	0	7	24	28	44	44	11	7	19	229-266	245
Blackpoll Warbler	0	0	0	8	0	0	135-138	136-7	0	0	0	0	0	2	3	2	0	249-261	255
Black-and-white Warbler	0	3	42	34	3	2	125-146	133	1	2	29	63	100	39	18	13	10	226-265	242
American Redstart	0	3	16	24	31	20	125-148	139-40	0	19	65	134	167	91	18	13	20	229-267	242
*Ovenbird	4	35	27	64	27	8	120-148	135	0	31	54	111	117	141	69	72	63	229-267	247
Northern Waterthrush	45	116	98	121	42	9	118-148	132	0	15	16	34	58	53	22	22	13	227-265	245
Connecticut Warbler	0	0	0	0	2	2	141-146	-	0	1	6	13	9	9	3	3	3	230-263	243
Mourning Warbler	0	0	0	15	38	35	135-148	142-3	0	4	14	41	27	19	2	7	9	230-264	242
*Common Yellowthroat	1	13	28	68	87	48	121-148	139	11	20	37	37	34	34	22	12	10	222-267	242
Wilson's Warbler	0	2	28	50	24	15	126-147	138	0	10	9	45	45	20	19	5	5	229-264	243
Canada Warbler	0	1	1	9	16	18	124-148	145	0	15	46	58	54	27	12	6	4	229-266	240
*Scarlet Tanager	0	0	0	4	8	5	134-148	140	0	0	1	4	7	2	2	2	3	233-267	245
*Rose-breasted Grosbeak	0	9	15	29	19	11	125-148	135	1	8	42	40	61	49	26	17	17	226-267	244
*Indigo Bunting	0	4	2	13	29	24	125-149	142	2	4	17	6	2	4	2	2	4	226-265	236
*Chipping Sparrow	1	6	6	9	6	4	121-149	-	0	0	0	1	0	2	0	0	0	-	-

(Table continued on page 137)

Aside from Cooke's early efforts (1888, 1915), very little has been done to illuminate broad geographic patterns of passerine migration in both time and space. This lapse in activity is probably due to a lack of adequate data: there are very few detailed summaries of bird movements at specific sites. This paper was developed in part to address this problem, and it is hoped that others studying migration will find it useful to compare their data with ours.

Study Site and Methods

This study was conducted near Afton, Minnesota (Washington Co.), in the St. Croix River Valley, approximately 2 km from the river itself (44°55'N 92°48'W) for three years (1984–1986). Mist nets were placed in five wooded habitat types and kept open as much as possible during the peaks of spring and autumn migration. Birds were captured, examined, banded, and released. Netting periods for all years combined spanned Julian days 118–149 (spring) and days 222–268 (autumn). In non-leap years, these days correspond to 28 April – 29 May and 10 August – 25 September. These periods encompass the bulk of woodland associated migration in this area (see Winker et al. 1992b). Although many songbird species show considerable movements at this latitude outside of these periods, these species tend to be short-distance (nearctic-nearctic), rather than long distance (nearctic-neotropic) migrants. The study accumulated 71,398 net hours in spring and 65,799 net hours in autumn.

Work on the timing of migration was part of a larger project in which we examined habitat preferences, individual performance, species-level differences in daily mass gain, and regional differences in migration routes (see Winker et al. 1991, 1992a,b). Here we report on the temporal distributions of most of the migrants captured.

Considering Temporal Distributions

When examining individuals out on the edges of a distribution—the few first or last birds passing—there is a danger in attributing characters to a species (in this case timing) based on only a few individuals. When the bulk of the passage of common species has been sampled, however, missing a few individuals on either end of the temporal distributions will have little effect on the placement of the median individual because the overall distribution of a large number of sample points is hardly affected by the addition or subtraction of a few. The median date of passage is therefore more robust than the first or last date of passage, although its "firmness" in time is related to the number of individuals it describes. Stone (1889) recognized this, and suggested that graphing daily censuses of birds would illuminate arrival times and peaks. Cooke (1908) later dealt with the vagaries of arrival dates by averaging them. His methods still relied, however, on the appearance of one or a few individuals.

Preston 1966 considered passage to be largely normal in distribution ("normal" in this case is a mathematical expression; see Preston 1966:376). From normal curves one can calculate "peaks" (in this case essentially population means) and standard deviations. While Preston's (1966) technique may be useful for some purposes, it does have problems. First, there is a considerable degree of annual variation in the distributions of migrant individuals. Preston (1966:376) noted this problem in passing; it was strikingly evident when examined statistically in migrant flycatchers in south Texas (Winker and Rappole 1992). Secondly, even several years of data often reveal strikingly non-normal distributions (skewed, bimodal, and multimodal), for which discerning a "peak" is often not possible. For example, see Fig. 1, which shows a skewed, bimodal distribution in Gauss' Nightjar, a fictitious migrant in which males precede females in spring. Real examples can be found in the spring and autumn passage of Swainson's Thrush (*Catharus ustulatus*) at our study site in Minnesota (Winker et al. 1992a).

When distributions are not normal, the median can be a more representative statistic of the movements of the entire sampled population than the mean (see Sokal and Rohlf 1981:44). Fig. 2 demonstrates why peaks, first, and last days of passage are not as useful for describing migratory movements as median dates. Median dates denote when half of all captured individuals have occurred. Note that Gauss' Nightjars (Fig. 1) and the equally fictitious Dark Barstanders (Fig. 2) have different temporal distributions, but the same first and last dates of occurrence, the same number of captured

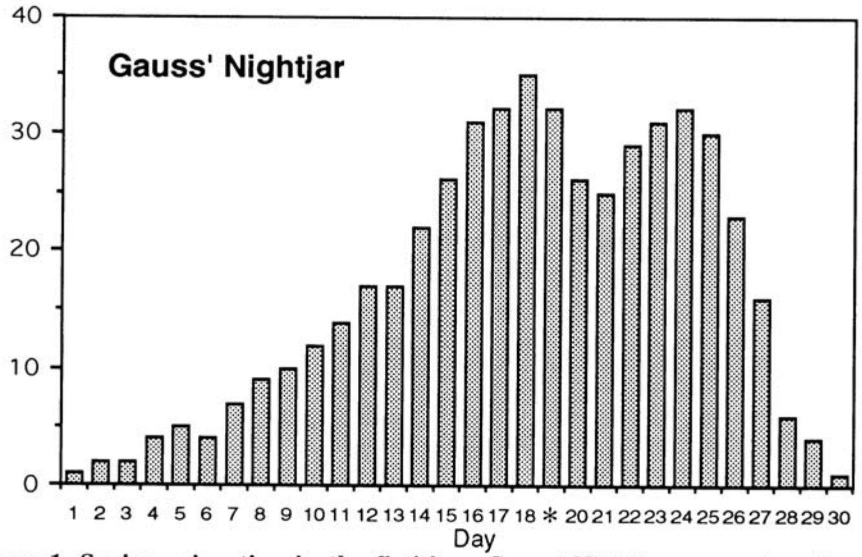

Figure 1. Spring migration in the fictitious Gauss' Nightjar, a species where males precede females. The species shows no "peak", but is rather skewed and bimodal in temporal distribution. Its timing of passage is best described by its median date of passage, which occurs on day 19 (*).

individuals, and the same median dates. Because of the advantages of median dates over other descriptors of temporal distribution, we have chosen to represent migratory movements as median dates of passage. In cases where samples are small we can have less confidence in the temporal rigidity of this figure as a species-level characteristic at this site. For those species or seasons where we do not feel that the migratory period was adequately sampled we do not give a median date.

Results and Discussion

Table 1 gives the temporal distribution of migrants at our study site for those species with more than ten individuals captured. Another aspect of movement important in the development of a geographic summary of migration can be derived from this table. The mean "density" of migrants occurring at this site during the sample periods can be estimated by dividing the total number of birds by sample effort (given above). Each season is the sum of three years' work (this has a damping effect on between-year variability).

The median dates of passage of all birds captured at our site occurred on Julian days 134 and 243, which correspond to 14 May and 31 August in non-leap years (see Winker et al. 1992b). Once again, although migratory movements occur outside of our sample periods, these individuals tend to be short distance (largely nearctic-nearctic) migrants. These dates, then, are roughly the median dates of nearctic-neotropic woodland passerine migration at this site. Four species showed a difference between spring and autumn median dates of 95 days or less: Yellow-bellied Flycatcher, Least Flycatcher, Canada Warbler, and Indigo Bunting. Eighteen species showed a difference of 105 days or less. This means that approximately 53% of the migrants whose movements were adequately sampled by our study spend less than 30% of their annual life cycle on their breeding grounds. For these species, about 70% of each year is spent on neotropical wintering grounds and in migration. It is no wonder, then, that conservation and research efforts are beginning to focus on these parts of the migrant's annual cycle.

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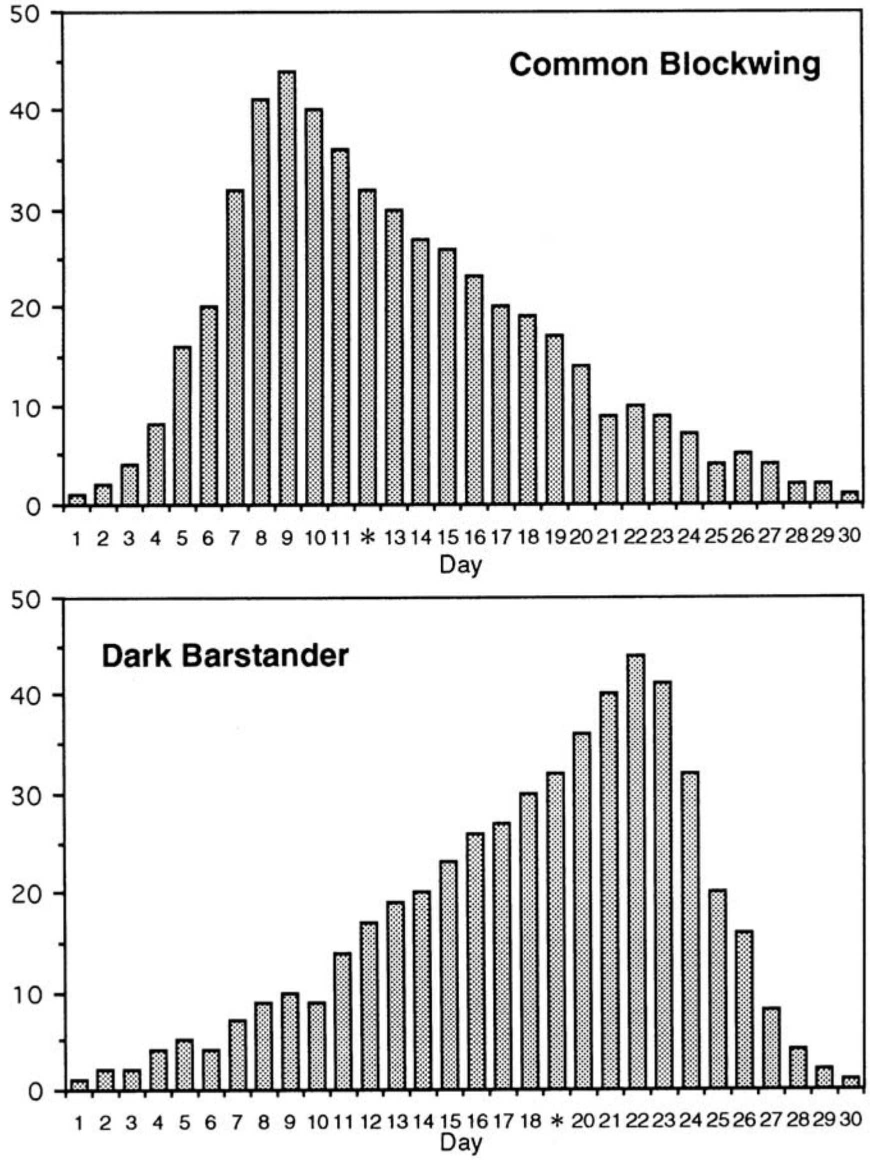

Figure 2. The passage of two hypothetical migrant species, the Common Blockwing and Dark Barstander. They have the same date of first arrival and last departure (days 1 & 30), and the same number of individuals are encountered or captured (505). They have different passage timing, however. Their respective peaks occur 13 days apart (days 9 vs. 22), but peaks can be altered by the movements of relatively few individuals, and are thus not reliable species-level characteristics. Median dates (days 12 & 19, marked with " * ") occur seven days apart, and in these cases are the best descriptors of movement at the species level. We conclude from these samples that Common Blockwings pass through this site one week earlier than both Dark Barstanders and Gauss' Nightjars (Figure 1).

	SPRING								AUTUMN											
Species	S1	S2	S3	S4	S5	S6	Range	Median	A1	A2	A3	A4	A5	A6	A7	A8	A9	Range	Median
*Field Sparrow	1	2	0	1	1	0	121-141	-	0	0	1	0	1	1	1	0	6	235-267	-
*Song Sparrow	14	14	6	5	8	11	118-148	-	5	21	26	27	12	15	7	6	3	222-264	-
Lincoln's Sparrow	2	7	15	5	2	1	122-146	131-2	0	0	0	0	0	1	4	1	9	250-267	-
Swamp Sparrow	41	43	40	11	2	1	118-145	-	0	0	0	0	0	3	6	1	3	250-265	-
White-throated Sparrow	80	66	58	16	4	0	118-141	-	0	1	0	3	0	31	29	30	61	229-267	-
*Brown-headed Cowbird	0	1	5	2	2	2	127-148	-	0	0	0	0	0	0	0	0	0	-	-
*Baltimore Oriole[b]	0	0	1	9	6	6	133-149	140-1	0	2	8	8	2	0	0	0	0	230-244	237
Purple Finch	1	2	0	0	0	0	122-128	-	0	2	7	52	40	53	19	19	11	231-264	-
*Pine Siskin	5	1	0	13	1	1	119-145	-	0	0	0	0	0	4	2	3	0	249-259	-

*Denotes migrants with resident breeding populations.
[a]*Dendroica c. coronata*; [b]*Icterus g. galbula*.

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