FALL MIGRATION PATTERNS OF WOOD WARBLERS IN THE SOUTHERN APPALACHIANS

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The large scale banding projects carried out during the fall migration of passerine birds have drawn attention to the patterns of migration of these species. Four questions among others have occupied those who have studied this phenomenon: (1) What is the ratio of first-year birds (HY) to older birds (AHY)? (2) Do the two age classes migrate synchronously, and if not, which comes first? (3) Do the males and females migrate synchronously, and if not, which comes first? (4) What is the shape of the curve representing the migration pattern?

A series of papers by Hussell, Clench, and others (references given in Hussell 1980) has discussed the lack of age-class synchrony in the *Empidonax* flycatchers. Questions (1) and (2) have been discussed for a wide variety of species by Murray (1966), Ralph (1971), Leberman and Clench (1973) and Stewart et al. (1974) using banding data, and by Taylor (1973) using tower-kill data. King et al. (1965) and Leberman and Clench (1971) have discussed question (3). The results from various locations have not always agreed.

In 22 years of operation, over 40,100 warblers of 33 species have been banded at the Allegheny Front Migration Observatory located in the mountains of northern West Virginia. Some of these species have been handled in very large numbers, as for example in 1977 31% of the Blackburnian Warblers and 27% of the Black-throated Blue Warblers (scientific names in Table 1) reported to the Banding Laboratory were banded at this station. Descriptions of this banding station and of the migratory phenomena taking place there have been given by Hall and Bell (1981). Of the 33 warbler species, 12 have been handled in large enough numbers to warrant analysis.

METHODS

The data analyzed here are from birds banded at the Observatory during the autumn migrations of 1973, 1974, 1976, and 1977. (In 1975 a substantial fraction of the birds were not aged.) During these years the station was operated from 24 August to 10 October. On a few days in these periods inclement weather forced the station to close, but in general banding was conducted on every day. Birds were caught in mist nets, banded, and aged by examination of the degree of pneumatization of the skull. Several banders over the 4-year period collected the data, and some error does exist in the age-class data due to errors in skull examination. Additional error may have been introduced late in the season when some young birds of some species could have completed the pneumatization process.

In order to smooth out the irregularities due to the weather factors which varied from year to year, the data for all 4 years were pooled, and tabulated in 5-day periods. These data were then plotted against



FIGURES 1 and 2. Migration patterns. Number of birds banded plotted against dates, except for Cape May Warbler which is plotted against days before and after the median point of the migration. Solid line = HY, and dashed line = AHY birds.

the date. In the case of the Cape May Warbler, this plot showed a marked bimodal distribution. This was produced by the occurrence of a heavy early migration in one year. To smooth these data the mid-point of each year's migration was determined, the data were clumped in 5-day periods before and after the mid-point, and the data for the 4 years



were then combined. This resulted in the curve shown, which was essentially unimodal. This method was then carried out with all species, but in no case was the essential picture obtained from the original plot altered.

In order to test more sensitively the synchrony of the migration of the 2 age classes, the data for all species were plotted on probability graph paper using the method developed by Preston (1966). A synchronous migration gives a single line on a probability plot (Figure 3A) while in an asynchronous migration the 2 age classes plot as distinct lines (Figure 3B).

RESULTS AND DISCUSSION

The data for all 12 species are plotted in Figures 1 and 2. Figure 3 shows the probability paper plot for 2 species. Table 1 gives a summary of the conclusions drawn from these graphs.

Ratio of age classes.—Table 1 gives the percentages of AHY birds for the several species. With the exception of the Blackpoll Warbler, the values all lie close to the 33% which would be the result from a southbound migration of a pair of adults and 4 fledged young. These results contrast sharply with those from coastal stations. On the New Jersey coast Murray (1966) reported that for 7 of these same species the percentage of AHY birds averaged only about 10.5 and that most were 5% or less, while in coastal California 5 warblers averaged 9% AHY (Stewart et al. 1974). The data agree with those from most inland stations. For example, in inland California, 5 species of warblers averaged 41% AHY (Stewart et al., loc. cit.). In Pennsylvania, only about 130 km north of the Alleghenv Front station, in 11 of the 12 species we studied, the average percentage of AHY was only 16.7 (Leberman and Clench 1973), while Florida tower-kills of 2 species (Cape May and Black-throated Blue) averaged about 60% AHY. The high percentage of adult Blackpoll Warblers at the Allegheny Front station may well reflect the near absence of AHY birds along the coast, or may be related to the fact that this station lies almost at the southern edge of the migratory pathway of this species (Nisbet 1970).

Migration patterns.—The graphs in Figures 1 and 2 can be classified in 3 patterns. Seven species show a near normal distribution, both on the seasonal graphs, and on the probability plots. The Magnolia Warbler shows a curve with a broad, ill-defined maximum. Two species, Blackburnian and Chestnut-sided warblers, show curves greatly skewed to the right. This corresponds to a migration in which there is no gradual build up to a peak, but rather a sudden appearance of many birds. Such a "wave migration" is quite common in warblers in the spring, but is comparatively rare in the fall. White-throated Sparrows (Zonotrichia albicollis) and Dark-eyed Juncos (Junco hyemalis) often exhibit this behavior in the fall. Both of the warblers showing this "wave migration" are ones whose migration is early in the season. When this result was first noted from the analysis of one year's data for the Blackburnian Warbler, it was thought that it was likely an artifact of not having started the operation early enough. However, the inclusion of additional data, and the examination of data from years not included in this analysis, suggest that the effect is real. The American Redstart may also show this, but the numbers handled are too low to draw definite conclusions. Two other early migrants through this station are Golden-winged (Vermivora



FIGURE 3. Probability paper plot. Cumulative fraction of birds banded plotted against 5day interval time periods. $\times = HY$ and $\bigcirc = AHY$ birds. A. Blackpoll Warbler; B. Black-throated Blue Warbler.

chrysoptera), and Mourning warblers (Oporornis philadelphia) but these have not been handled in numbers sufficient for analysis. At Powdermill Nature Reserve in Pennsylvania Chestnut-sided Warblers show this "wave migration" (M. H. Clench, pers. comm.).

		%	Pat-	
Species	N	AHY	tern ¹	Timing ²
Tennessee (Vermivora peregrina)	3191	28.7	n.	syn.
Nashville (Vermivora ruficapilla)	196	25.6	n.p.	syn.
Magnolia (Dendroica magnolia)	767	35.9	b.p.	ΉΥ
Cape May (Dendroica tigrina)	2582	33.3	n.	AHY
Black-throated Blue (Dendroica caerulescens)	2237	31.6	n.	HY
Black-throated Green (Dendroica virens)	991	29.5	n.	HY
Blackburnian (Dendroica fusca)	1071	36.7	skwd.	syn.
Chestnut-sided (Dendroica pensylvanica)	121	23.1	skwd.	syn.
Bay-breasted (Dendroica castanea)	1267	34.8	n.	syn.
Blackpoll (Dendroica striata)	3436	48.8	n.	syn.
Wilson's (Wilsonia pusilla)	144	35.6	n.p.	syn.
American Redstart (Setophaga ruticilla)	192	29.1	skwd.	syn.

TABLE 1. Summary of migration patterns of warblers.

¹ Migration patterns: n. = normal distribution, n.p. = no pronounced peak, skwd. = skewed distribution, b.p. = broad peak distribution.

² Synchrony of migration: syn. = age classes move together, HY = first year birds come earlier than old birds, AHY = old birds come earlier than first year birds.

Nashville and Wilson's warblers show a migration for which there is a steady movement of small numbers throughout the season. This may well result from the low numbers handled. At a station handling larger numbers a more typical curve, but perhaps one with a broad peak might result. The increase in AHY Nashville Warblers in October may be due to incorrectly aged birds, since some individuals of this species complete the pneumatization process quite early.

Synchrony of movement of age classes.-In 8 species, the 2 age classes migrate at essentially the same time. This is most clearly shown on the probability plots, e.g., Figure 3A. In the Cape May Warbler the AHY birds precede the HY, but in Magnolia, Black-throated Blue (Figure 3B), and Black-throated Green warblers, the HY birds precede the AHY. This is evident for the Black-throated Blue without any analysis since it is rare to find an AHY bird before mid-September. These results are in some disagreement with those from other stations. Murray (1966) found all these species to have a synchronous migration on the New Jersey coast, but his small number of AHY birds may be responsible for the lack of difference between age classes. In Florida tower-kills, Taylor (1973) found a synchronous migration for Cape May and Black-throated Blue warblers. In western Pennsylvania Leberman and Clench (1973) agree with our results for 5 species. In 2 cases, Tennessee and Magnolia warblers, where their sample size was comparable to ours, there was agreement.

It is not clear why different stations should show differences in the synchrony of the different age classes. These differences may result from differences in the populations sampled. The coastal station handles mostly HY birds that have drifted out over the ocean during the night. The Pennsylvania station handles birds which are feeding through the valley, and are not actively migrating when caught, while the Allegheny Front station handles birds that are actively migrating in a diurnal phase of the migration (Hall, unpublished data). Alerstam (1979) has suggested that perhaps because of the difference in navigational system used, the HY birds and the AHY birds react differently to wind drift, and this may result in slightly different populations occurring at these stations.

Synchrony of the sexes.—In only 3 of these species, Cape May, Blackthroated Blue, and Blackburnian warblers can the sexes be distinguished without error, and for all of these the sexes move together. There is a slight tendency for late stragglers of both Cape May and Blackburnian warblers, both early migrants, to be HY females.

SUMMARY

The autumn migration of 12 warbler species was analyzed with respect to the ratio of age classes, migration pattern, synchrony of ageclass migration, and synchrony of sex migration. Most species showed a synchronous migration by age class, but in Black-throated Blue and Black-throated Green warblers the HY birds preceded the AHY birds, while in the Cape May Warbler the reverse was true. There was no asynchrony of migration by sex for the 3 species analyzed. The percentage of AHY birds ranged from 23 to 48, substantially greater than at the coastal banding stations.

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