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# DYNAMICS OF WARBLER ASSEMBLAGES DURING MIGRATION

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ABSTRACT.—We investigated among- and within-year community-level patterns in the phenology of wood-warblers (Parulidae) in old field/deciduous forest habitat in western Pennsylvania. The numbers of each of 29 species of warblers captured in mist nets were summed over six-day intervals from January 1981 to December 1985, and the data for spring and fall periods were analyzed separately by detrended correspondence analysis (DCA). Despite substantial annual variation in species abundances, patterns and rates of species turnover were consistent across years. However, within-year patterns differed qualitatively between seasons; in fall, species turnover was unidirectional (species replaced each other in sequence), whereas in spring it was bi-directional (community composition in late spring came to resemble that earlier in the season). Timing of migration was also associated with the general regions in which species either bred or wintered. DCA proved to be a powerful tool for analysis of dynamic community patterns. *Received 29 July 1998, accepted 8 January 1999.*

AVIAN MIGRATION is a dynamic phenological event: species come and go through time. But the fact that migration is a temporal phenomenon introduces complexities to the study of the migrant assemblage; unlike a community of breeding birds, which may remain relatively unchanged for months, the composition of an assemblage of migrants can change literally from day to day. Likewise, although particular species return to a site annually, due to vagaries of weather, for example (e.g. Richardson 1978), they may differ in their timing and abundance from the previous year. Thus, the composition of the migrant community includes both within- and between-year components of variation. Although attempts have been made to derive overall population-abundance measures for individual species (see Hussell 1981, Dunn and Hussell 1995), this obvious flux in numbers is at least part of the reason that more rigorous quantitative analyses of the composition of migration assemblages seldom have been pursued.

Our objective is to provide a quantitative description of the phenological dynamics of migration through time, both within and among years. We then answer several ecological questions: (1) How strong are these patterns? (2) Do patterns differ between spring and fall? (3) How much community turnover (species compositional change through time) do these patterns represent? (4) Are these patterns consistent through time, specifically, from one year to the next; and (5) are they related to the general location of species' wintering or breeding grounds? Below, we present a simple multivariate model that captures the essence of phenological patterns and then use it to describe the dynamics of community change in an assemblage of North American wood-warblers (Parulidae) during their migration at a site in western Pennsylvania. Because the technique we employ, and its specific application here, are likely to be unfamiliar to most ornithologists, we provide a detailed description of the procedure and a rationalization for its use.

## METHODS

*Site description and sampling methods.*—The migrant assemblage we analyzed was that of the Powdermill Nature Reserve, Westmoreland County, Pennsylvania, which is the field research station of the Carnegie Museum in Pittsburgh. Most of the immediate banding site was covered by old fields and other abandoned farm lands in various stages of succession, including nearly open meadow and fields with scattered shrubs and thickets. All of the more or less open habitat was surrounded by second-growth deciduous forest (including *Quercus, Acer,* and *Carya* as dominant overstory plants), with scattered *Alnus*-dominated wet areas. See Leberman and Wood (1983) for more details about the study area.

Our "censuses" consisted of counts of individuals captured in mist nets at specific times throughout the year. These individuals were captured as part of a

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TABLE 1. Summary of warbler species netted at Powdermill Nature Reserve, 1981 to 1985. Only species occurring on 25 or more censuses are shown. Codes appear in Figures 3 and 8.

| Species | Code | No. censuses | No. individuals | Breed[a] | Winter[b] |
|---|---|---|---|---|---|
| Blue-winged Warbler (*Vermivora pinus*) | BWWA | 34 | 55 | B | C |
| Golden-winged Warbler (*V. chrysoptera*) | GWWA | 33 | 66 | B | C |
| Tennessee Warbler (*V. peregrina*) | TEWA | 62 | 1,419 | H | C |
| Nashville Warbler (*V. ruficapilla*) | NAWA | 60 | 410 | B | C |
| Yellow Warbler (*Dendroica petechia*) | YWAR | 65 | 308 | B | C |
| Chestnut-sided Warbler (*D. pensylvanica*) | CSWA | 59 | 233 | B | C |
| Magnolia Warbler (*D. magnolia*) | MAWA | 65 | 1,788 | B | C |
| Cape May Warbler (*D. trigrina*) | CMWA | 41 | 837 | H | N, C |
| Black-throated Blue Warbler (*D. caerulescens*) | BTBW | 39 | 151 | B | C |
| Yellow-rumped Warbler (*D. coronata*) | YRWA | 54 | 2,605 | H | N |
| Black-throated Green Warbler (*D. virens*) | BTNW | 45 | 371 | B | C |
| Blackburnian Warbler (*D. fusca*) | BLBW | 28 | 74 | B | C, S |
| Prairie Warbler (*D. discolor*) | PRWA | 31 | 44 | L | N, C |
| Palm Warbler (*D. palmarum*) | PAWA | 30 | 122 | H | N, C |
| Bay-breasted Warbler (*D. castanea*) | BBWA | 30 | 412 | H | S |
| Blackpoll Warbler (*D. striata*) | BLPW | 33 | 184 | H | S |
| Black-and-white Warbler (*Mniotilta varia*) | BAWW | 59 | 122 | B | C |
| American Redstart (*Setophaga ruticilla*) | AMRE | 90 | 853 | B | C |
| Ovenbird (*Seiurus aurocapillus*) | OVEN | 80 | 515 | B | C |
| Northern Waterthrush (*S. noveboracensis*) | NOWA | 75 | 323 | B | C |
| Louisiana Waterthrush (*S. motacilla*) | LOWA | 42 | 113 | L | C |
| Kentucky Warbler (*Oporornis formosus*) | KEWA | 49 | 97 | L | C |
| Connecticut Warbler (*O. agilis*) | CONW | 25 | 113 | H | S |
| Mourning Warbler (*O. philadelphia*) | MOWA | 49 | 200 | B | C, S |
| Common Yellowthroat (*Geothlypis trichas*) | COYE | 105 | 1,836 | B | N, C |
| Hooded Warbler (*Wilsonia citrina*) | HOWA | 81 | 554 | L | C |
| Wilson's Warbler (*W. pusilla*) | WIWA | 48 | 253 | H | C |
| Canada Warbler (*W. canadensis*) | CAWA | 55 | 481 | B | S |
| Yellow-breasted Chat (*Icteria virens*) | YBCH | 26 | 56 | B | N, C |

[a] General breeding range. H = north of 45°N; L = south of 45°N; B = straddles 45°N.

[b] General wintering range. N = southern North America; C = Central America; S = South America.

long-term banding project operated by the reserve. The banding station operated 45 mist nets in 15 lanes scattered around the reserve headquarters, covering an area of roughly 10 ha (see Leberman and Wood 1983 for more details). Their standardized design consisted of six days on and one day off throughout the entire year, except for a two-week break in winter. To smooth out day-to-day irregularities in numbers of birds netted owing to short-term variation in weather, we pooled into a single census (an "observation" or unit of analysis) the total number of individuals of each species captured during a six-day period. To ensure that we were dealing primarily with the migrating fraction of the assemblage, we counted only new birds, not recaptures. We confined our analysis to one taxonomic group, the wood-warblers, 29 species of which made up the bulk of the individuals captured (Table 1). We selected this group primarily because it was speciose and abundant in the sample of captured birds.

We examined five consecutive years of data, 1981 through 1985. These particular years were chosen because of the ready availability of summarized netting records. Because there were two obvious peaks in the data, we analyzed the spring and fall migration periods separately. We fixed both periods at 75 days duration to enable us to compare them directly. The spring period was from mid-April through the end of June (days 101 to 175, counting from 1 January), and the fall period was from mid-August through the end of October (days 226 to 300).

Following Hagen et al. (1991), we determined each species' general breeding and wintering range. Breeding regions were classified as mostly north of, south of, or straddling 45°N latitude. Wintering localities were categorized as southern USA and northern Mexico, Central America, or South America, plus two intermediate categories (Mexico and northern Central America; Central America, the Caribbean, and northern South America). For species in our samples but not in Hagen et al. (1991), we used information in AOU (1998).

*Statistical model.*—Phenological patterns of abundance of migrant species display specific characteristics. Typically, a species appears (or is present in relatively low numbers), increases in abundance to a peak, and then declines, often disappearing at a later time. Thus, within a season, abundance patterns often are unimodal. This structure is typical of a variety of ecological data, particularly those that describe the distribution of species abundances along environmental gradients. Common examples include plant species abundances along an elevational transect or a soil-moisture gradient (e.g. Whittaker 1967, ter Braak and Prentice 1988). This implies that we should look to the quantitative tools developed for ecological gradient analysis, those multivariate models devised for ordination studies, in analyzing migration data. Here, we emphasize the importance of using a quantitative model whose assumptions fit the structure of our data.

The multivariate model that best fit data such as these is detrended correspondence analysis (DCA; Hill and Gauch 1980), also known as reciprocal averaging. This model assumes that species abundances are distributed unimodally (most often a "Gaussian," or bell-shaped, distribution, but any unimodal distribution is appropriate) along some underlying ecological gradient (see Pielou 1984, ter Braak 1985, ter Braak and Prentice 1988). In the case of migration data, the underlying gradient is time. This assumption of unimodality, of a species rising *and* falling, is in sharp contrast to the use of principal components analysis (PCA) in ordination, which assumes linearity (Pielou 1984). For such a linear model to be applicable, each species would either rise *or* fall through time. Indeed, applying PCA to primarily unimodal data such as these can result in substantial distortions of the underlying patterns (Pielou 1984).

Recent critiques of DCA (e.g. Austin 1985, Wartenberg et al. 1987) have focused on this explicit assumption about the structure of species' distributions. However, phenological data such as these may represent the closest conformity to those assumptions that any community is likely to approach (Rotenberry 1990). Indeed, for data taken from more or less continuous, unimodal species' distributions along gradients, DCA summarizes those data with less distortion than any of the commonly used multivariate techniques (Gauch et al. 1981, Peet et al. 1988).

DCA has a number of characteristics that make it particularly useful in the analysis of phenological patterns (Gauch 1982, Pielou 1984). First, it provides a simultaneous ordination both of observations (censuses) and of individual bird species. These new ordination axes describe the joint distribution of censuses and bird species in a reduced-dimensional ordination space. As in PCA, DCA develops a set of scores for each observation on each axis. Here, the score of each census reflects its particular combination of species abundances; e.g. two censuses with very similar scores have very similar species composition and relative abundances, whereas two with very different scores have very different composition and abundances. Furthermore, because the ordination is reciprocal, species have scores on DCA axes as well. In general, a species' score represents the projected location of its peak or modal abundance along a particular DCA axis, and it is usually close to the sample(s) in which it is most abundant.

DCA axis scores are scaled such that one unit on an axis is equal to one standard deviation of the average distribution of all species on the axis (Hill and Gauch 1980, Wilson and Mohler 1983). Thus, on average, a species arises, reaches a peak, declines, and then disappears in the space of about four units (four standard deviations) along the axis. This implies that censuses four units apart on a correspondence axis likely have no species in common. The difference in DCA units between the two censuses at opposite end points of an axis is the axis "length," and it represents the total amount of compositional change (i.e. species turnover, or beta diversity) associated with that axis.

Second, DCA, like PCA, produces eigenvalues (denoted as $\lambda$); in this case, the eigenvalue of an ordination axis represents the correlation between species' scores and sample scores (maximum possible = 1.0). The relative magnitude of eigenvalues associated with DCA axes describes the relative strength of the pattern that each axis represents ("strength" meaning how well an axis distinguishes among a group of censuses based on their overall species composition).

Finally, DCA, unlike PCA and numerous other ordination techniques, is not affected by nonlinearity in species distributional patterns, which are an obvious attribute of migration data. Indeed, correspondence analysis (of which DCA is a modification) was developed specifically to capture quantitatively such nonlinear patterns (Hill 1974).

We performed DCA on raw absolute warbler abundances using PC-ORD (McCune and Mefford 1997). Use of raw rather than standardized abundances preserves any interannual variation that may be present. To assist in the interpretation of the output of DCA of migration data, we also provide several examples of DCA applied to simulated data of known, obvious structure. To assess the relationship of DCA scores with geographic locations, we first assigned rank scores to our categorizations of species' breeding (three ranks) and wintering (five ranks) localities, with northernmost regions ranked as 1. Recognizing the imprecision of our classification of these localities, we then used Spearman rank correlation to analyze the relationships statistically. All additional analyses were implemented in SAS (SAS Institute 1990).

## RESULTS

*General patterns.*—Of a total of 202 six-day censuses available for analysis, 42 fell within the spring sampling period and 52 fell within

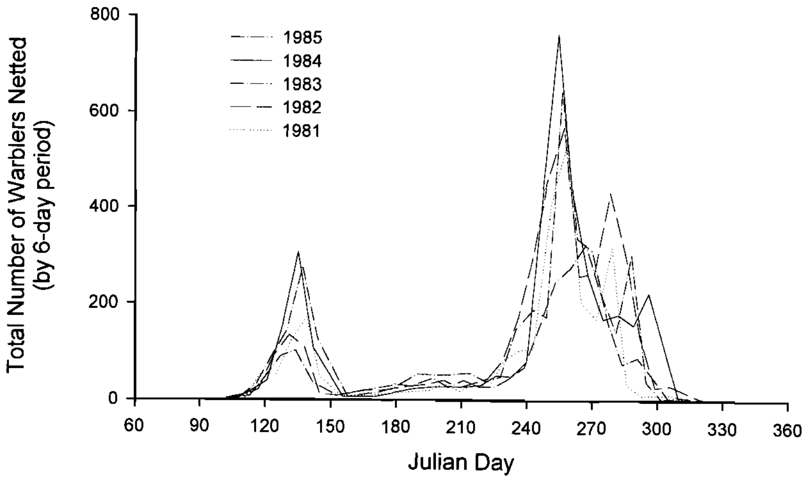

FIG. 1. Total number of warblers netted at Powdermill Nature Reserve, 1981 to 1985.

the fall; these are analyzed in detail below. A total of 14,660 individuals of 37 warbler species was netted during the 5-year sampling period. We omitted from analysis those species netted on fewer than 25 occasions, leaving a sample of 29 species and 14,595 individuals (Table 1). The total number of warblers netted varied considerably among years, with as much as a two-fold difference within the sampling period (Fig. 1). In addition to capturing about twice as many individuals, the fall censuses were also substantially more variable from year to year than the spring censuses.

Because there are too many data to show individual patterns for all species for each season and for all years (29 species × 2 seasons × 5 years = 290), we provide selected examples that demonstrate the components of variation in the total sample. Two of the most common species were Magnolia Warbler (*Dendroica magnolia*) and Common Yellowthroat (*Geothlypis trichas*; Table 1), and each had at least a two-fold variation in both peak and total abundances among years (Fig. 2). Magnolia Warblers were twice as abundant at their peak in spring 1984 than in all other springs, although all other springs were similar to each other. Yellowthroats were also relatively abundant in spring 1984, but even more so in spring 1983. In fall, Magnolia Warblers had relatively higher years in 1983 and 1984, whereas Common Yellowthroats had an obviously higher year in 1984 only. The shape of the Common Yellowthroat's curve was flatter in spring 1981 (to a lesser extent in spring 1985) than in the other springs, whereas the spring curve for Magnolia Warblers was sharper in 1984 than in other years. The time of peak abundance of yellowthroats also differed among years, occurring about 10 days later in 1985 than in the preceding year. Likewise, the time of peak abundance differed between the species, although to different degrees in different years (Fig. 2).

When even a subset of species is combined on a single temporal axis, the complexities inherent in interpreting community-level patterns become apparent (Fig. 3). For example, the 10 most abundant species netted during spring 1982 differed from the 10 most abundant in fall of the same year, although with some overlap. Likewise, within each season the degree of overlap between pairs of species differed substantially. For example, in spring 1982 American Redstarts (*Setophaga ruticilla*) overlapped relatively little with Magnolia and Tennessee (*Vermivora peregrina*) warblers, but substantially more so in fall. It is also apparent that species differ among themselves to greater or lesser degrees in the details of the shapes of their curves.

*Detrended correspondence analysis.*—We initially examined all years and seasons in a single DCA, which yielded an eigenvalue of 0.758 for the first axis, with a length of 4.08. However, an analysis of variance of census scores on DCA axis 1 using season (spring/fall) as a classification variable was highly significant ($P < 0.001$). Because of this, coupled with the obser-

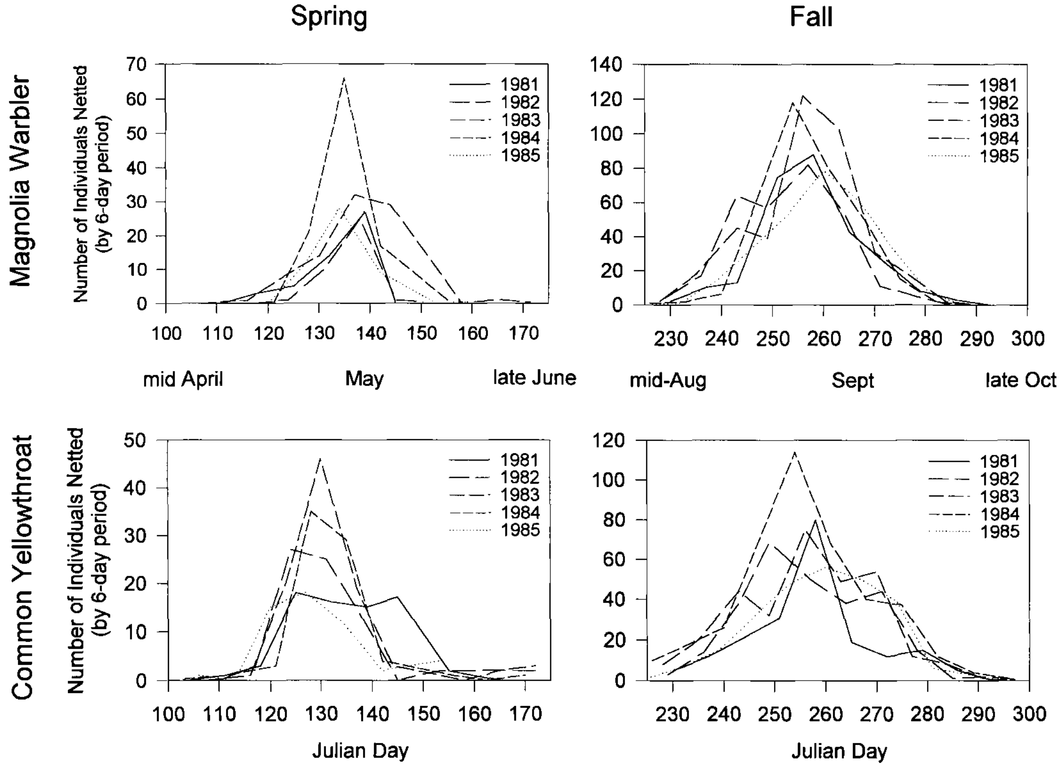

FIG. 2. Numbers of Magnolia Warblers and Common Yellowthroats netted during spring and fall sampling periods at Powdermill Nature Reserve, 1981 to 1985.

vation that community patterns appeared to differ between seasons (e.g. Fig. 3), we analyzed each season separately. The magnitudes of the eigenvalues showed that for each season only the first axis contained relevant information (spring, $\lambda_1 = 0.36$, all other $\lambda < 0.2$; fall, $\lambda_1 = 0.76$, all other $\lambda < 0.06$). Although the fall sample had a higher eigenvalue, the lengths of the first axes for each season were similar (spring = 3.6, fall = 3.4).

*Within-year patterns.*—Patterns of migration variation within years are revealed by plotting census scores on DCA axis 1 versus census date, which describes the temporal trajectory of assemblage composition. To illustrate a range of potential outcomes, we first provide an analysis of specifically structured simulated data. If, for example, turnover in bird species abundance is relatively smooth throughout the season (i.e. migration curves are regularly spaced; Fig. 4A), and we take a series of "censuses" from such a community, then the axis 1 scores of these censuses resulting from a DCA ordination will yield a relatively straight line when plotted against date (Fig. 4B). If instead species pass through in distinct "suites" (i.e. migration curves are clumped; Fig. 4C), an analogous ordination will produce a stair-step pattern (Fig. 4D), with periods of relative stasis in migrant assemblage composition (identified by the flat parts of the ordination curve in Fig. 4D) followed by periods of more rapid turnover (the steep parts of the curve).

Fall censuses showed a distinct stair-step pattern, with a period of relatively uniform species turnover through about day 250 (slope = 0.038 DCA units/day) followed by a period of relative stasis (ca. days 250 to 263; slope = 0.019), then a longer period of turnover (days 264 to 284, slope = 0.091; Fig. 5). The community then changed little through the end of the fall sampling period at day 300 (slope = 0.012). The second period of turnover was more rapid than the first, as indicated by its steeper slope. The correlation between census DCA score and date was quite high ($r = 0.95$, df = 52, $P <$

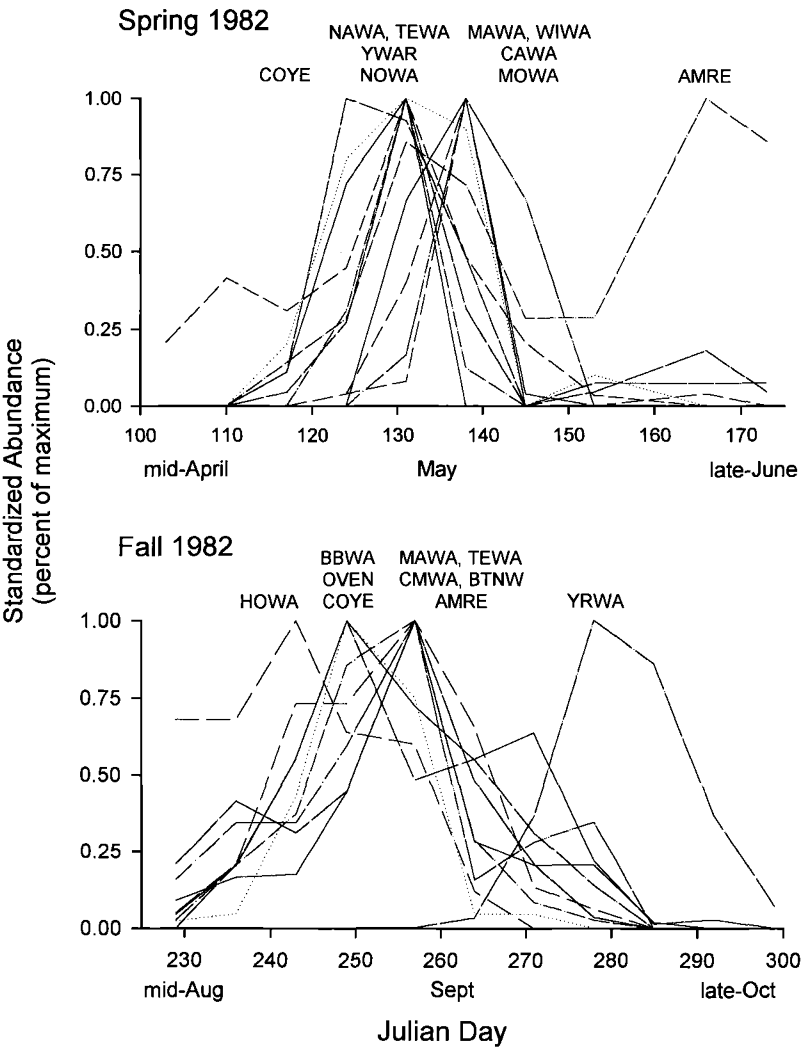

FIG. 3. Standardized numbers of the 10 most abundant species of warblers netted during spring and fall 1982 at Powdermill Nature Reserve. Data are the proportion of the maximum number of that species netted during the sampling period. See Table 1 for species codes.

0.001). That the length of this axis was somewhat lower than 4 implies that species turnover was not complete throughout the fall (i.e. the earliest fall census was not completely dissimilar to the latest one).

Within-year patterns in spring were qualitatively different from those in fall. Here, species turnover was relatively constant through about day 140 (slope = 0.080), but then census scores reversed and declined from that point through the end of the period (Fig. 6). This decline had a slightly shallower slope than the initial increase (slope = −0.070). Both slopes were roughly comparable in magnitude to the second period of turnover in the fall. The correlation between census score and date was not significant ($r = 0.28$, df = 40, $P > 0.05$). As for fall, compositional turnover was not complete between the most different censuses (i.e. early and middle ones).

Again, the interpretation of patterns in real data was enhanced by analysis of structured simulated data (Fig. 7). In this case, it appeared that spring contained species with some disparity in passage times; although many species migrated through the site relatively rapidly,

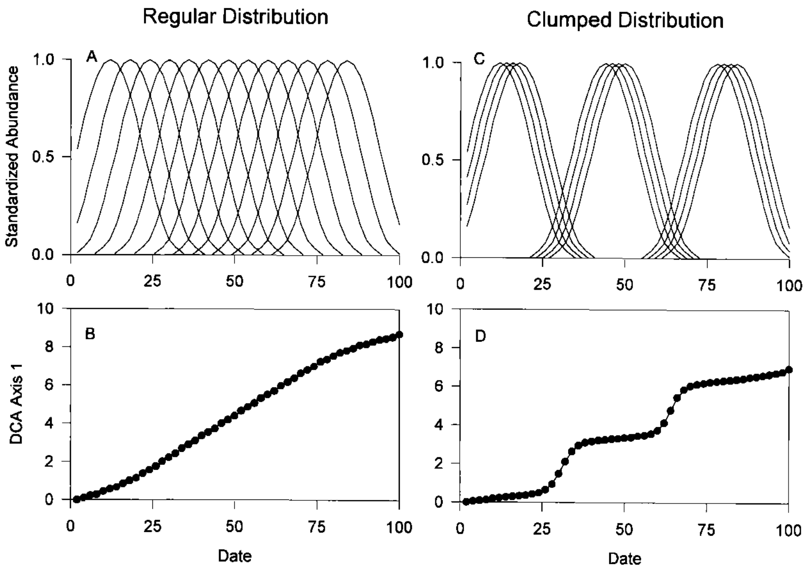

FIG. 4. Expected patterns of detrended correspondence analysis (DCA) of simulated migration data. Top figures represent simulated migration curves of 12 species with (A) regularly or uniformly spaced passage times, and (C) clumped or aggregated passage times. Bottom figures show results of DCA applied to 50 "censuses" taken at uniform intervals from each set of simulated curves; points represent scores of censuses on DCA axis 1 plotted against "date" census was taken. (B) censuses taken from (A); (D) censuses taken from (C).

passage for several took place over an extended period of time, with a few even remaining to breed. This community-level pattern produced a distinct peak in DCA scores plotted against date of census. To a considerable degree, the community composition at the end of the period came to resemble (i.e. have similar DCA scores) that nearer the beginning. This accounts for the lack of significant correlation between DCA score and data of census.

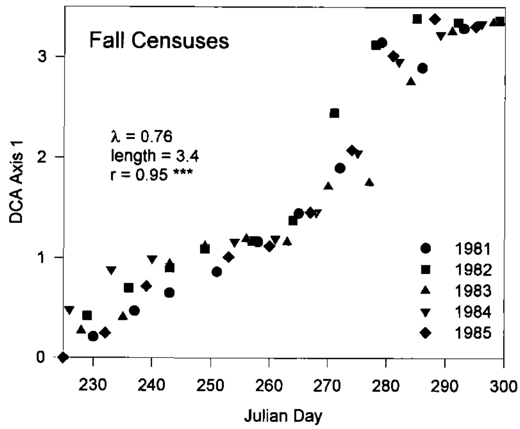

FIG. 5. Scores of censuses on axis 1 of detrended correspondence analysis (DCA) performed on fall sampling periods at Powdermill Nature Reserve, 1981 to 1985, plotted against date census was taken. λ denotes eigenvalue, length is the difference in DCA units between the highest and lowest scores, and $r$ is the correlation between DCA score and date (***, $P < 0.001$).

Because several species continued to linger in the spring, their distributions were not symmetrical, but instead had tails extended somewhat to the right. Extending the tails of the distributions in the simulated data (Fig. 7A) produced slightly more conformance to the observed pattern (Fig. 6), mainly by elevating the right-hand tail of the simulated output (Fig. 7B).

*Between-year patterns.*—Average census scores on DCA axis 1 did not differ among years for spring ($F = 0.39$, df = 4 and 37, $P = 0.81$) or fall ($F = 0.16$, df = 4 and 47, $P = 0.96$) samples. An analysis of covariance (Dunn and Hussell 1995; following Zar 1984), treating day of year as the covariate, also was not significant for spring ($P = 0.83$) or fall ($P = 0.37$). The early fall stair-step pattern was not apparent in 1981 and 1982, although the second period of stasis following rapid turnover was present in both years. The other three years showed both steps. All five spring samples showed a sharp peak.

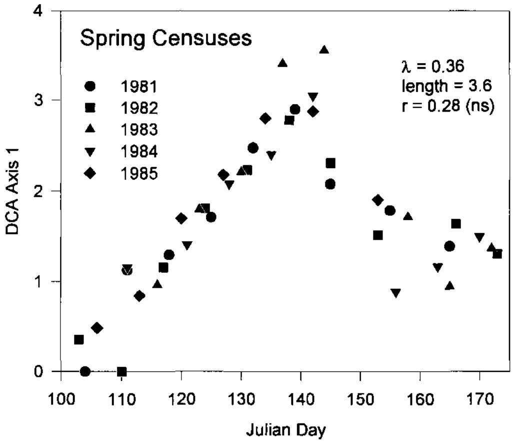

FIG. 6. Scores of censuses on axis 1 of detrended correspondence analysis (DCA) performed on spring sampling periods at Powdermill Nature Reserve, 1981 to 1985, plotted against date census was taken. λ denotes eigenvalue, length is the difference in DCA units between the highest and lowest scores, and $r$ is the correlation between DCA score and date (ns, $P > 0.05$).

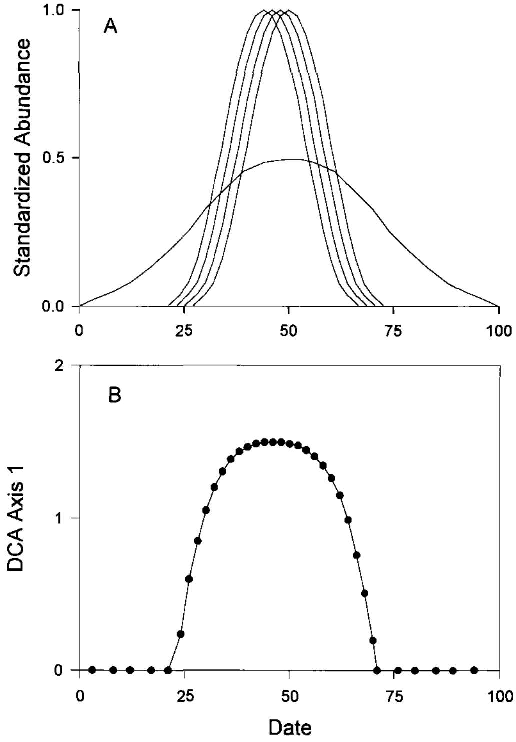

FIG. 7. Expected patterns of detrended correspondence analysis (DCA) of simulated migration data. (A) Simulated migration curves of five species, four with relatively rapid passage times and one with extended passage time. (B) Results of DCA applied to 35 "censuses" taken at uniform intervals from each set of simulated curves; points represent scores of censuses on DCA axis 1 plotted against "date" census was taken.

*Species ordinations.*—The relations of individual species to community-level patterns were identified by examining their scores on DCA axes (Fig. 8). For example, species with lower scores on fall DCA axis 1 occurred earlier in the season than those with higher scores (Fig. 8B). The earliest species were those with the lowest set of scores in the ordination, namely Louisiana Waterthrush (*Seiurus motacilla*) through Golden-winged Warbler (*Vermivora chrysoptera*; Fig. 8B), which were already declining in numbers by the start of the fall period. The first period of turnover (Fig. 5) was characterized by species ranging from Chestnut-sided Warbler (*Dendroica pensylvanica*) through Wilson's Warbler (*Wilsonia pusilla*). The first period of stasis, between days 250 to 263, with DCA 1 scores of about 1.0 to 1.25, consisted of Cape May Warbler (*Dendroica tigrina*), Magnolia Warbler, Mourning Warbler (*Oporornis philadelphia*), Connecticut Warbler (*O. agilis*), Northern Waterthrush (*Seiurus noveboracensis*), and Ovenbird (*S. aurocapillus*). The second period of turnover was associated with species ranging between Black-throated Blue Warbler (*Dendroica caerulescens*) and Blackpoll Warbler (*D. striata*), whereas the second period of stasis (the last two weeks of sampling; Fig. 5) was dominated by the late-arriving Palm Warbler (*D. palmarum*) and Yellow-rumped Warbler (*D. coronata*; Fig. 8B).

Because the spring DCA axis was not linearly correlated with date (Fig. 6), the interpretation of species' scores was less direct (Fig. 8A). Community composition of censuses early in the season was not repeated, in contrast to that of middle censuses, and turnover was uniform (Fig. 6). Species that occurred during this period (DCA axis 1 score ca. <1.0; Fig. 8A) included Palm Warbler through Yellow-rumped Warbler and Hooded Warbler (*Wilsonia citrina*). Species with relatively longer passage times, or that stayed to breed, were those with scores of about 2.0, particularly Yellow Warbler (*Dendroica petechia*), Common Yellowthroat, and American Redstart, which commonly bred in the area. Those species that occurred in the sec-

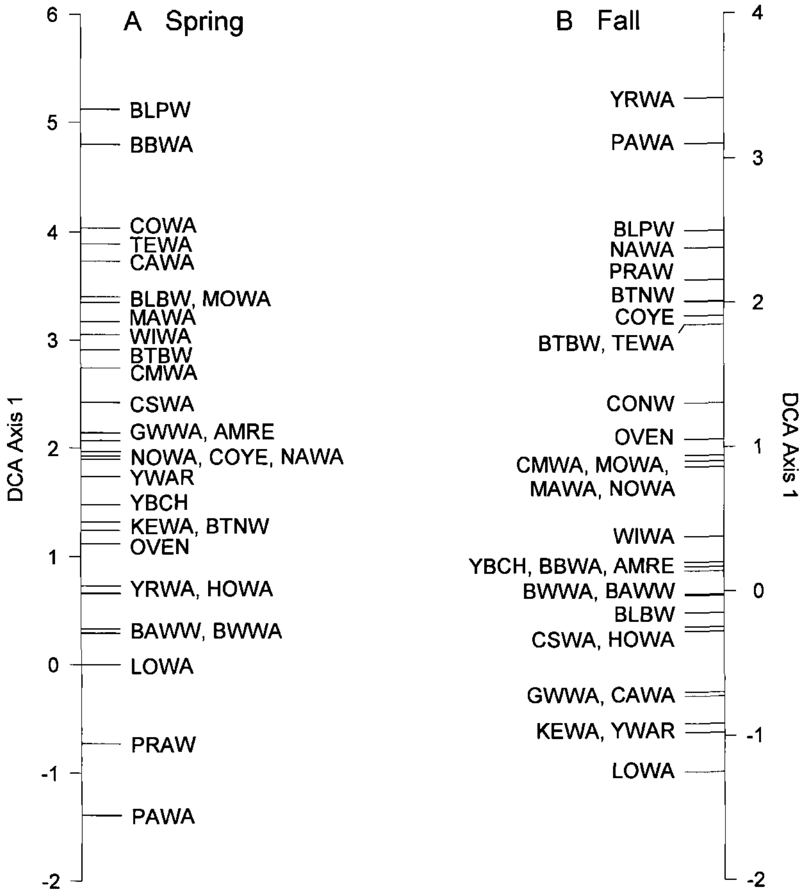

FIG. 8. Scores of warbler species on axis 1 of detrended correspondence analysis (DCA) performed on (A) spring and (B) fall sampling periods at Powdermill Nature Reserve, 1981 to 1985. See Table 1 for species codes.

ond part of the spring, but passed through the area relatively quickly, were those with scores of about 3.0, such as Magnolia Warbler (Fig. 8A).

*Geographic correlates.*—Statistically significant rank correlations occurred between species' scores on spring axis 1 and their general breeding ($r_s = -0.495$, $P = 0.006$) and wintering ($r_s = 0.661$, $P < 0.001$) ranges. Likewise, there was a significant correlation between scores on fall axis 1 and species' breeding localities ($r_s = -0.510$, $P = 0.005$). However, there was little relationship between fall scores and wintering regions ($r_s = -0.284$, $P = 0.136$; $n = 29$ for all tests).

## DISCUSSION

Detrended correspondence analysis provides a powerful tool for extracting community-level patterns from phenological data (Rotenberry 1990). Substantial complexity is inherent in variation in abundances of 29 species sampled in 94 censuses distributed over two 75-day seasons and five years. This variation includes differences in (1) peak and total numbers, both within and among species; (2) timing of peak years among species; (3) shapes of curves among years within species; and (4) timing of peak abundances (Figs. 2 and 3). Despite this complexity, however, clear patterns emerged (Figs. 5 and 6).

Patterns of warbler community dynamics qualitatively differed between spring and fall, the former being bi-directional and the latter unidirectional. In fall, turnover in the passage of species was more or less continuous, punctuated by periods of relative stasis that lasted for about two weeks each (Fig. 5). In contrast, whereas spring began with a period of continuous turnover in species composition, slightly more than halfway through the sample period the turnover reversed, and censuses later in the season came to resemble those that occurred earlier (Fig. 6). The high eigenvalue associated with analysis of fall data implies that those data are a good fit to the correspondence analysis model, and that censuses at either end of the temporal gradient can be distinguished from one another readily. The reduced fit (i.e. smaller eigenvalue) of the spring data to the statistical model arose from the substantial variation in breadth of the occurrence of species through time. Because the composition of later censuses was similar to that of earlier ones, some censuses separated by up to 50 days could not be readily distinguished from one another. Both spring and fall DCA axes had a length of somewhat less than 4, which implies that compositional turnover between the most different censuses within each period was not complete, although overall similarity was low.

Although we used a standardized sampling period of 75 days to facilitate direct comparison of spring and fall, it is apparent that passage during spring, at least in some years, may wind down sooner than that (Fig. 1). To assess if this affected our conclusions, we reanalyzed the spring migration data after truncating the ending date to day 160. The results were virtually unchanged; the first eigenvalue was 0.35 (vs. 0.36), the length of the first axis was 3.7 (vs. 3.6), and species were ranked in almost exactly the same order as in Figure 8. When DCA scores were plotted against time, we observed the same pattern as in Figure 6, only with the last seven points now missing. This had the effect, however, of raising the correlation between DCA scores and date to statistical significance.

Patterns in assemblage dynamics at least in part were associated with breeding and wintering areas of migrant warblers. For example, in spring, species that had less distance to cover from their wintering grounds arrived first. This is reflected in the positive rank correlation between species' wintering localities (lower ranks associated with more northerly regions) and scores on spring axis 1 (lower scores associated with early arrivals; Fig. 6). A significant but negative association also occurred between species' breeding latitudes and scores on spring axis 1; middle and later species generally bred in the northern half of the continent. Similarly, there was a negative association between breeding latitudes and scores on fall axis 1; species moving through earlier in the fall tended to breed at more southerly latitudes. There was, however, no significant rank relationship between fall migration patterns and wintering region.

In an analysis of spring migration patterns at Manomet Bird Observatory in coastal Massachusetts (which shared 12 species with our study), Hagen et al. (1991) also noted that species that wintered in southern North America migrated through significantly earlier than those that wintered farther south (i.e. Central or South America). However, they found that timing of spring migration was unrelated to breeding latitude. Taken together with our results, we conclude that there is a significant geographic component to the pattern of migration observed at a point; the sequence of passage of species in the spring can reflect either the distance from the breeding ground for which each species is bound, or that to the wintering ground from which each has departed. Likewise, the sequence in the fall is related to the distance from the breeding ground from which species have departed.

Other processes associated with individual species that could lead to the observed seasonal community patterns are not known. One alternative is that patterns of species co-occurrence reflect avoidance of potential competitors, as has been suggested for phenological patterns in other taxa (e.g. Kochmer and Handel 1986). However, elucidating such relationships requires a much more rigorous assessment of the dynamics of resource availability than we can provide here. We also suggest that a similar analysis that contains and is restricted to all members of a specific foraging guild would be more appropriate for investigating resource-driven processes.

Neither spring nor fall demonstrated statistically significant among-year variation in the temporal trajectories described by DCA. This was visually apparent in Figures 5 and 6, where points from different years seemed to deviate little from a line fitted through the data. The annual variation in late fall numbers that appeared in the raw data also appeared as increased variation in points late in the period

(Fig. 5), but this was insufficient to generate statistical significance. Although analysis of variance revealed no differences among average scores for censuses using year as a main effect, this test probably was weak, because all five years of censuses were pooled in a single DCA. More powerful is the analysis treating date as a covariate, which is equivalent to asking whether scores that occur on the same day of the year differ among years. If the trajectory of community composition differs among years (i.e. one year is particularly "early" or "late" compared with the others), then this analysis should detect it relatively efficiently. However, during the period covered by these data, temporal variation among years was insufficient to produce statistical significance in analysis of covariance. Note that this annual consistency in assemblage-level pattern does not preclude between-year differences for some species, as was observed by Woodrey and Chandler (1997).

Although we have employed methods developed for the analysis of species' distributions along spatial environmental gradients, we do not wish to take the analogy between a temporal gradient and a spatial gradient too far; a literal interpretation of time as an environmental gradient may not be warranted. Nonetheless, the issue of what sorts of environmental conditions or other attributes are associated with the distributional changes that we observed through time is relevant. This will be difficult to assess, however, because the number of individuals of a warbler species captured in one week at Powdermill is a function not only of local environmental conditions (e.g. local weather and food abundance), but also of conditions expressed over larger spatial scales (e.g. weather fronts moving through eastern North America) and at sites at some considerable geographic distance (local conditions on wintering or breeding grounds that may be thousands of kilometers away). This latter factor introduces an additional temporal complication in that the number of warblers at Powdermill may be controlled by an event that occurred several weeks earlier several thousand kilometers distant.

In conclusion, detrended correspondence analysis provided a means of answering several questions about assemblage dynamics that we posed at the outset. Our foremost finding was that patterns of temporal change differed qualitatively between spring and fall, the latter being unidirectional, with species replacing each other in sequence, and the former being bidirectional, where community composition in late spring returned toward that occurring a few weeks earlier. Furthermore, the unidirectional pattern of the fall was not uniform, but instead showed distinctly varying rates of species compositional turnover. The fall pattern was clearly the stronger of the two, although both represented approximately the same amount of total compositional turnover between the most disparate censuses, and each season's pattern was consistent across the five years we analyzed. The next step is to inquire about processes involving individual species that may be responsible for the community patterns detected, particularly the difference between spring and fall in what we call "directionality." It will also be informative to apply this analysis to a more ecologically relevant group of species, such as a foraging guild, rather than to a taxonomic group that was chosen somewhat arbitrarily. Regardless of the outcome of these steps, we believe that the conceptual and analytical models presented here will prove valuable in organizing thoughts about the structure of bird assemblages during migration.

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## LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1998. Check-list of North American birds, 7th ed. American Ornithologists' Union, Washington, D.C.

AUSTIN, M. P. 1985. Continuum concept, ordination methods, and niche theory. Annual Review of Ecology and Systematics 16:39–61.

DUNN, E. H., AND D. J. T. HUSSELL. 1995. Using migration counts to monitor landbird populations: Review and evaluation of current status. Current Ornithology 12:43–88.

GAUCH, H. G. 1982. Multivariate methods in community ecology. Cambridge University Press, Cambridge, United Kingdom.

GAUCH, H. G., R. H. WHITTAKER, AND S. B. SINGER. 1981. A comparative study of nonmetric ordinations. Journal of Ecology 69:35–152.

HAGEN, J. M., T. L. LLOYD-EVANS, AND J. L. ATWOOD. 1991. The relationship between latitude and the timing of spring migration in North American landbirds. Ornis Scandinavica 22:129–136.

HILL, M. O. 1974. Correspondence analysis: A neglected multivariate method. Applied Statistics 23:340–354.

HILL, M. O., AND H. G. GAUCH. 1980. Detrended correspondence analysis: An improved ordination technique. Vegetatio 42:47–58.

HUSSELL, D. J. T. 1981. The use of migration counts for monitoring bird population levels. Studies in Avian Biology 6:92–102.

KOCHMER, J. P., AND S. N. HANDEL. 1986. Constraints and competition in the evolution of flowering phenology. Ecological Monographs 56:303–325.

LEBERMAN, R. C., AND D. S. WOOD. 1983. Bird-banding at Powdermill: Twenty years reviewed. Powdermill Nature Reserve Research Report No. 42. Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

MCCUNE, B., AND M. J. MEFFORD. 1997. Multivariate analysis of ecological data, version 3.0. MjM Software, Gleneden Beach, Oregon.

PEET, R. K., R. G. KNOX, S. J. CASE, AND R. B. ALLEN. 1988. Putting things in order: The advantages of detrended correspondence analysis. American Naturalist 131:924–934.

PIELOU, E. C. 1984. The interpretation of ecological data: A primer on classification and ordination. John Wiley and Sons, New York.

RICHARDSON, W. J. 1978. Timing and amount of bird migration in relation to weather: A review. Oikos 30:224–272.

ROTENBERRY, J. T. 1990. Variable floral phenology: Temporal resource variation and its implications for flower visitors. Holarctic Ecology 13:1–10.

SAS INSTITUTE. 1990. SAS/STAT user's guide, vol. 2, version 6.1, 4th ed. SAS Institute, Inc., Cary, North Carolina.

TER BRAAK, C. J. F. 1985. Correspondence analysis of incidence and abundance data: Properties in terms of a unimodal response model. Biometrics 41:859–873.

TER BRAAK, C. J. F., AND I. C. PRENTICE. 1988. A theory of gradient analysis. Advances in Ecological Research 18:271–317.

WARTENBERG, D., S. FERSON, AND F. J. ROHLF. 1987. Putting things in order: A critique of detrended correspondence analysis. American Naturalist 129:434–448.

WHITTAKER, R. H. 1967. Gradient analysis of vegetation. Biological Reviews of the Cambridge Philosophical Society 42:207–264.

WILSON, M. V., AND C. L. MOHLER. 1983. Measuring compositional change along gradients. Vegetatio 54:129–141.

WOODREY, M. S., AND C. R. CHANDLER. 1997. Age-related timing of migration: Geographic and interspecific patterns. Wilson Bulletin 109:52–67.

ZAR, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall, Englewood Cliffs, New Jersey.

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