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DETERMINING PRODUCTIVITY INDICES FROM AGE COMPOSITION OF MIGRANTS CAPTURED FOR BANDING: PROBLEMS AND POSSIBLE SOLUTIONS

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Abstract. Year, location, day, moon phase, and weather all influenced the daily proportion of young birds captured in nine species of passerines in fall migration at three stations on Long Point, Ontario, in 1961–1988. The proportion of young tended to be higher on days following nights when conditions for nocturnal migration were good. Annual proportions of young may be inconsistent indices of productivity, unless they are adjusted for the daily effects of confounding variables. For single species, correlations between annual proportions of young (adjusted and raw) and fall/spring population ratios were usually low and non-significant. In most species, the annual proportion of young did not explain significant amounts of variation in trend analyses of annual population indices. Nevertheless, adjusted proportions of young performed better than raw proportions in these analyses, suggesting that the proportion of young in populations of migrants does contain useful information about productivity. However, the assumption that proportions of young reflect productivity should not be accepted uncritically. More research is needed to determine how best to use information on ages of fall migrants to elucidate their demography.

Key Words: age proportions, fall migration, Long Point, Ontario, passerine migrants, productivity indices.

The age composition of migrants captured for banding is widely assumed to provide information on the productivity of the preceding breeding season (e.g., Ralph et al. 1993). However, it is not clear whether a direct relationship exists between productivity and the proportion of young birds captured in fall migration. The proportion of young captured over a single migration season at a single station could be influenced by many confounding factors, including differing vulnerability to capture, differing timing and speed of migration of age classes, habitat and coastal effects (e.g., Murray 1966; Ralph 1971, 1981; Hussell 1982, 1991; Dunn et al. *this volume* b), and perhaps by weather. Very little research has been done to determine what effects, if any, these factors have on the daily and annual proportions of young captured during migration and consequently upon annual measures of productivity.

Weather has profound effects on numbers of birds migrating and on the numbers occurring (and therefore available for capture) at a station (e.g., Richardson 1978). If the effects of weather differ among age classes, then even consistently collected data on the number of young and adult birds captured at a single station could be biased by year-to-year variations in weather. Given these potential biases, can we derive a consistent annual index of productivity from migrant age data and can we test that such an index does in fact reflect productivity?

I used regression analysis to examine the effects of weather, moon phase, date, and station on the daily proportion of young birds of nine species captured by personnel of the Long Point Bird Observatory at three stations on Long Point during the autumn migrations of 1961–1988. I calculated two annual indices of productivity: (1) the proportion of young birds (hatched in the preceding breeding season) captured over the entire migration at all stations; and (2) an adjusted proportion of young birds, derived from the regression analysis.

Indices of population size for spring and fall migrations at Long Point were also available (calculated by methods similar to those described by Hussell et al. 1992). If age proportions indicate productivity, and if the population size indices reflect population change, then the annual ratio of the fall to spring population index should be positively correlated with the annual proportion of young birds. This is the case because a high proportion of young birds in the fall population should usually be associated with a high fall population relative to that of the previous spring. The strength of this correlation should provide an independent means of evaluating the effectiveness of methods of calculating population and productivity indices.

If productivity fluctuates from year to year, and if age proportions reflect productivity, we might expect deviations of annual fall population size indices from their general trend to be positively correlated with the proportion of young birds captured in the fall.

Therefore, I tested whether the proportion of young explained additional variability in regression analyses of trends in fall population indices.

METHODS

STUDY LOCATION, SPECIES, AGING

I examined age proportions of nine species captured commonly in fall migration at Long Point, Ontario (approximately 42°33'N, 80°10'N): Swainson's Thrush (*Catharus ustulatus*), Red-eyed Vireo (*Vireo olivaceus*), Tennessee Warbler (*Vermivora peregrina*), Magnolia Warbler (*Dendroica magnolia*), Yellow-rumped Warbler (*D. coronata*), Blackpoll Warbler (*D. striata*), American Redstart (*Setophaga ruticilla*), White-throated Sparrow (*Zonotrichia albicollis*), and White-crowned Sparrow (*Z. leucophrys*).

Data were recorded at three stations: Station 1 at the eastern tip of Long Point; Station 2, 19 km west of Station 1; and Station 3, 9 km west of Station 2. Nearly all the data from Station 2 were collected after 1974 and nearly all from Station 3 after 1983. Nearly all birds were captured in mist nets or Heligoland traps (Woodford and Hussell 1961), but a few were taken in other types of baited ground traps. Trapping and netting effort (including numbers, types, and locations of traps and nets) varied both from year-to-year and day-to-day. I excluded birds captured or killed during nocturnal migration when they were attracted to the lighthouse at Station 1.

Red-eyed Vireos and White-crowned Sparrows were aged as either young (hatched in the current year) or adult (hatched earlier) primarily by eye color and plumage differences, respectively, and I analyzed all data from 1961–1988. Other species were aged mainly by the degree of skull pneumatization (birds with incompletely pneumatized skulls were aged as young) or by obvious plumage characteristics (e.g., adult male American Redstarts and some young Swainson's Thrushes), and I used data only from 1966–1988, because skull examination was not used at Long Point prior to 1966.

For each species, a fall migration period ("migration window") was selected that was identical to that used previously for analysis of migration counts (Hussell et al. 1992). Individuals occurring outside the migration window were excluded from all analyses.

EFFECTS OF WEATHER, MOON, DAY, AND STATION ON AGE PROPORTION

Daily proportion of young was defined for each species, based on numbers of newly captured (unbanded) birds for each day that at least one bird was captured and aged, as: proportion of young = (number of young birds)/(number of young birds + number of adult birds).

I used multiple regression to examine effects of various potential predictor variables on daily proportion of young. The dependent variable was the arcsine (square root (daily proportion of young)). Proportions of 0 and 1 were counted as $1/4n$ and $(n - ¼)/n$, respectively, where n was the sample size (i.e., the number of young + adults), before transforming to the angular scale (Snedecor and Cochran 1967:327–328). Cases were weighted by $C \times n/N$, where C was the total number of cases (i.e., station-days), n was the sample size for that case (i.e., number of young + number of adults), and N was the sum of n over all cases. This weights in proportion to sample size, and makes the sum of the weights equal to the number of cases. The analysis was otherwise similar to that used for determining indices of abundance (Hussell et al. 1992).

Station-days with captures of aged birds varied from 373 in the White-crowned Sparrow to 942 in the Swainson's Thrush. However, captures and days with captures were not uniformly distributed among stations. If the sum of the case weights for a station was less than 90, it was judged that the coefficients of variables specific to that station could not be adequately estimated and data from that station were excluded from the multiple regression analyses. This criterion excluded Tennessee Warbler, Blackpoll Warbler, and White-crowned Sparrow at Station 3, and White-throated and White-crowned sparrows at Station 2.

I assumed that productivity effects, if they existed, would be associated with year, and would occur across all stations, days of the year (hereafter, "day"), and other conditions. Therefore I included dummy variables for year, as predictor variables in the regression model without interactions with station or any other variables. On the other hand, I assumed that day, weather, and moon effects might be station-specific. Therefore, I designed the regression model to accommodate this assumption by including predictor variables for day, weather, and moon only as interactions with each station.

Age proportion differences between two of the stations were already known to occur in warblers (Dunn and Nol 1980) and preliminary analyses indicated that age proportions change with day of the year, as expected from other research (e.g., Murray 1966, Hall 1981; Hussell 1982, 1991). Therefore, I included dummy variables for station and station-day interaction variables (1st, 2nd, and 3rd order terms in day, D, D^2, and D^3, respectively, where day D was the day of the year, set to zero on a day near the middle of each species' migration window) in the regression model. Inclusion of these predictor variables enables the regression analysis to detect both consistent station effects and different seasonal patterns of change in proportion of young at each station, if they exist in the data.

Moon phase variables were days from new moon (M, or "moonday") and the square of moonday (M^2). These variables enable the analysis to detect an unequal pattern of increase in proportion of young prior to new moon and decrease following full moon, or vice versa, with the possibility of a discontinuity in the proportion of young occurring at full moon. (The sky is moonless late in the night prior to full moon and early in the night following full moon, so the effects of moonlight are likely to by asymmetrical relative to full moon.)

Weather data were from Erie, Pennsylvania (about

50 km south of Long Point on the south shore of Lake Erie) and the variables were identical to those used by Hussell et al. (1992). I used eight variables representing east wind speed, south-east wind speed, south wind speed, south-west wind speed, temperature differences from normal, square root of horizontal visibility, cloud cover, and precipitation. All positive wind speeds indicated direction the wind was coming from, and negative values represented the opposite direction (e.g. a negative south wind speed was the speed of the wind from the north). I reduced the eight weather variables to six weather factors by principal components analysis, followed by varimax rotation. The six weather factors retained 86.2% of the variance of the original eight weather variables. Because the original four wind direction/speed variables were essentially uncorrelated, they loaded heavily on four factors (referred to as the E, SE, S, and SW wind factors for the wind directions involved). Visibility and temperature loaded heavily on the fifth factor (called "Visibility/Temperature"). Precipitation loaded heavily and cloud loaded moderately on the sixth factor (called "Rain/Cloud").

Predictor variables for weather were formed as interactions between station and the factor scores for the six rotated principal components, enabling the regression model to detect station-specific weather effects. By using factors instead of the original weather variables, the number of station-weather interaction variables was reduced from 24 to 18 at a cost of losing 13.8% of the variance in the original eight weather variables.

In summary, the multiple regression contained up to 63 predictor variables, consisting of up to 28 dummy variables for year, two dummy variables for station, nine station–day interaction variables, six station–moon phase interaction variables, and 18 station–weather factor interaction variables.

PROPORTION OF YOUNG INDICES

I calculated an annual raw proportion of young index as (number of young birds)/(number of young birds + number of adult birds), where numbers were the sums of newly captured birds accumulated from all of the stations over each species' autumn migration window. In addition, I calculated an adjusted annual proportion of young index for each of the nine species from the results of the multiple regressions described above. The adjusted annual proportion of young index was the back-transformed adjusted mean for each year. It is an estimate of what the young proportion would have been in a given year, if the values of the regression variables representing weather, dates, and locations of capture had been the same in all years, and were equal to the average values of those variables recorded in the data.

SPRING AND FALL POPULATION INDICES

Spring and fall population indices for each species counted in migration at Long Point in 1961–1988 were calculated as back-transformed adjusted means for year, from a regression analysis in which the dependent variable was log (daily count + 1). The "daily count" was an estimated total of number of birds of each species occurring in or passing through a defined count area at each station. The estimate was based on a consistent procedure involving a count along a transect route, unstandardized trapping and netting (as described above), and incidental observations by all observers and banders present at the station (Hussell 1981, Hussell et al. 1992). Indices were calculated in the same way as described elsewhere (Hussell et al. 1992), except as indicated below. Three different sets of indices were calculated using the full data set. I had two reasons for using the full data set, instead of data reduced after an initial regression to remove cases with low predicted values (Hussell et al. 1992): (1) it enabled me to use exactly the same data sets for all three sets of indices, and (2) other analyses indicated that trends in annual indices calculated from the full data sets corresponded more closely to trends in Breeding Bird Survey counts in Ontario than trends based on indices calculated with reduced data sets (D. Hussell and L. Brown, unpublished). The three sets of annual population indices differed in the predictor variables used in the regression analyses. Dummy variables for year were included as predictor variables in all regressions, so that adjusted mean for year could be calculated. Index 1 was based on the full model with station, station–day, station–moon phase, and station–weather variables included as predictor variables (as in Hussell et al. 1992). Index 2 used a reduced model with station and station–day predictor variables. Index 3 was based on a model with dummy variables for station as the only predictor variables (in addition to the year dummy variables). I expected that index 1 would best reflect population size, because effects of variation in weather and moon phase are assigned to those variables. Index 3 would likely be the least satisfactory index of population size.

TESTS OF CONSISTENCY OF PROPORTION OF YOUNG AND POPULATION INDICES

The spring population consists of only adult birds, while the fall population has both young and adult birds. If we assume that the mortality rate of adult birds between spring and fall migrations does not vary importantly among years, then the population ratio = (fall population size index)/(spring population size index) should vary in parallel with fall proportion of young. Therefore, I calculated annual population ratios (population ratio 1, population ratio 2 and population ratio 3) based on each of the three population indices (index 1, index 2, and index 3 for spring and fall) for each of the nine species, and correlated them with annual raw and adjusted proportion of young. If adjustments of proportion of young and population indices were effective, we would expect the highest positive correlation to be between adjusted proportion of young and the population ratio for population index 1.

Rates of change in spring and fall migration indices of 42 species in the period 1967–1987 were positively correlated, as expected if spring and fall indices represent the same source population (Hussell et al. 1992). Fall indices, however, generally showed greater variability around the trend than did spring indices (D. Hussell, unpubl. analyses). This may reflect variability in proportion of young in fall populations. If so, proportion of young may explain additional variability in the trend analysis and allow more precise estimation of trends.

I tested for the effects of age proportion on trend in fall population index 1 of each species with the following model:

$$\text{Ln}I_j = a + bY_j + c\text{Ln}H_j + e_j \qquad \text{(Eq. 1)}$$

where I_j was index 1 in year j, Y_j was year j, H_j was either raw or adjusted proportion of young, and e_j was an error term, and a, b, and c were coefficients estimated by the regression analysis.

In addition, I tested the effect of age proportion on combined spring and fall trend in each species with the following model:

$$\text{Ln}I_{jk} = a + bY_j + cS_k\text{Ln}H_j + dS_k + e_{jk} \qquad \text{(Eq. 2)}$$

where I_{jk} was index 1 in year j and season k (spring or fall), Y_j was year j, S_k was a dummy variable for season ($S_k = 0$ for spring, $S_k = 1$ for fall), H_j was proportion of young in year j, $S_k\text{Ln}H_j$ was an interaction term (formed by multiplying S_k by $\text{Ln}H_j$), e_{jk} was an error term, and a, b, c, and d were coefficients estimated by the regression analysis. This model assumed a common trend b for spring and fall indices and tested whether fall proportion of young index H_j had a significant additional influence on the fall indices.

In both models, c was expected to be positive (i.e., the greater the proportion of young birds, the higher the annual fall population). In both analyses, cases were weighted by $C \times n_j / N$ where C was the total number of cases, n_j was the number of station-days of observations in year j used in calculating index I_j, and N was the sum of n_j for all cases. I tested for second and third order effects in year (with predictor variables Y_j^2 and Y_j^3) and, in the second model, for season-trend interactions (S_kY_j, $S_kY_j^2$ and $S_kY_j^3$) using a stepwise procedure. Because this involved many tests and the number of variables was large relative to the number of cases, these effects were considered important enough to be included in the model only if they were significant at the 0.01 level.

I used a sign test on the probabilities (P) associated with c in equations 1 and 2 to determine whether the adjusted proportion of young indices were more effective than raw proportion of young indices as predictors of fall population indices. Because low P values with positive estimates of c indicate good prediction and low P values with negative estimates of c indicate poor prediction, I scored P values associated with negative estimates of c as 2 - P for use in the sign test.

In all tests in this section, I used population ratios based on at least 25 station-days of observations in both spring and fall. Population ratios were excluded if either the spring or the fall index (or both) did not meet the criterion. Adjusted and raw proportion of young indices were used only if captures of aged individuals occurred on at least seven days and at least 50 individuals were aged in that year.

RESULTS

EFFECTS OF WEATHER, MOON, DAY, AND STATION ON AGE PROPORTIONS

Samples of aged birds ranged from 1,328 in the Red-eyed Vireo to 5,414 in the Yellow-rumped Warbler (Table 1). Overall proportion of young varied from 0.549 in the White-crowned Sparrow to 0.916 in the Yellow-rumped Warbler. Except for the Blackpoll Warbler, warblers had proportions of young near 0.90, as reported previously (Dunn and Nol 1980).

Predictor variables in multiple regression analyses accounted for a significant proportion of the variation in transformed proportion of young in all species, with R^2 varying from 0.290 in the White-

TABLE 1. SUMMARY OF AGE DATA AND REGRESSION RESULTS FOR NINE SPECIES CAPTURED AT LONG POINT, ONTARIO

Species	Number of first captures		Proportion of young[a]	Number of station-days[b]	R^2[c]
	Adult	Young			
Swainson's Thrush	937	3,245	0.776	942	0.300
Red-eyed Vireo	172	1,156	0.870	571	0.391
Tennessee Warbler	191	2,006	0.913	530	0.501
Magnolia Warbler	405	3,225	0.888	831	0.515
Yellow-rumped Warbler	453	4,961	0.916	683	0.393
Blackpoll Warbler	1,061	2,173	0.672	561	0.491
American Redstart	160	1,340	0.893	604	0.289
White-throated Sparrow	669	2,133	0.761	583	0.290
White-crowned Sparrow	1,037	1,260	0.549	372	0.484

[a] Proportion of young for the entire sample = (number of young)/(number of young + number of adults).

[b] Number of station-days for which aged birds were available during the species-specific migration window, over all years used in the analyses (1961–1988 for Red-eyed Vireo and White-crowned Sparrow, 1966–1988 for all other species).

[c] R^2 for the multiple regression of arcsine (square root (proportion of young)), on year, station, station-day, station-moonday, and station-weather predictor variables.

throated Sparrow to 0.515 in the Magnolia Warbler (Table 1). A high R^2 may reflect high year-to-year variability in the proportion of young (variance assigned to the year dummy variables), important effects of other variables, or both.

Interpretation of the effects of independent variables in multiple regressions presents some difficulties, both because some variables are correlated with each other and because effects of individual variables do not occur in isolation from those of other variables (especially where there are higher order terms in the same variable). Nevertheless major effects can be discerned. To summarise the effects of variables (other than dummy variables for station and year), I tabulated the number of times (called "cases" below) that a variable had a significant or near significant ($P \leq 0.1$) positive or negative effect on the proportion of young of a species at a station. In addition, I assessed the importance of positive and negative effects of each variable by summing scores (ordered in accordance with significance level) for each positive and negative effect (Table 2).

Station

The station dummy variables for Stations 2 and 3 always had significant or near significant ($P \leq 0.10$) positive effects on the proportion of young. For nine of the 13 dummy variables (in the regressions for nine species) the effect was significant at $P \leq 0.01$. This indicates a strong tendency for there to be a higher proportion of young birds at Stations 2 and 3 than at Station 1, as previously reported for warblers at Station 2 vs. 1 (Dunn and Nol 1980). In addition to warblers, the effect was also strong in Swainson's Thrush ($P < 0.01$ for both stations) and White-throated Sparrow ($P < 0.01$ for Station 3), but relatively weak in Red-eyed Vireo ($0.05 < P \leq 0.10$ at both sites).

Day

Day of the year (D) had significant effects ($P \leq 0.01$) on proportion of young in 17 of 22 station-species cases (Table 2), including one or more stations in all species. The direction of significant effects was always consistent among stations within species, but was not consistent among species. In most species the effect was negative, indicating that proportion of young tended to decline as the season progressed, but Red-eyed Vireo and Yellow-rumped Warbler showed strong and Swainson's Thrush and White-crowned Sparrow showed weak tendencies in the opposite direction. These effects indicate that the timing of peak migration differs among age classes.

The second order term in day (D^2) had significant effects in 13 of 22 cases (Table 2), but the direction of the effect varied. Negative effects predominated. Because day zero was set near the middle of the species' migration window, a negative second-order effect indicates a tendency for the proportion of young to be higher at the middle of the season than at the

TABLE 2. EFFECTS OF DAY, MOONDAY, AND SIX WEATHER FACTORS FROM PRINCIPAL COMPONENTS ANALYSIS ON PROPORTION OF YOUNG CAPTURED

	Significant and near-significant effects ($P \leq 0.10$)			
	No. of species-stations with significant effects [a]		Score total of strength of effects [b]	
Predictor variable	Positive	Negative	Positive	Negative
Day	7	10	15	26
Day^2	4	9	10	23
Day^3	10	0	25	0
Moonday	3	4	5	8
Moonday^2	5	1	12	2
Visibility/Temperature	5	2	12	4
Rain/Cloud	1	6	3	14
E Wind	2	1	3	2
SE Wind	1	4	3	7
S Wind	3	3	5	7
SW Wind	0	3	0	7

[a] Number of species-station combinations (out of 22) that show positive or negative significant effects of the indicated variable.

[b] Score total indicates the strength of positive and negative effects of variables. Score total = sum of scores assigned to each species-station combination according to the significance level of the effect of the variable. Scores were as follows: score = 1 if $0.05 < P \leq 0.10$, score = 2 if $0.01 < P \leq 0.05$, score = 3 if $P \leq 0.01$. Maximum possible score total is 66.

beginning and end, although this may be modified or reversed (at one end of the season) by the direction and magnitude of the first- and third-order effects. Swainso's Thrush showed a strong tendency for the mid-season proportion of young to be high ($P < 0.01$ at all three stations). Tennessee Warbler at Station 2, and White-throated and White-crowned sparrows at Station 1, showed strong ($P < 0.01$) tendencies in the opposite direction: proportion of young tended to be lowest in the middle of the season. These results may indicate that adult Swainson's Thrushes have a long migration period relative to young birds, whereas the opposite is true for Tennessee Warblers, White-throated and White-crowned sparrows.

When present, the effects of the third order term in day (D^3) were consistently positive (Table 2). This indicates that the proportion of young tended to be relatively low near the start of the season and high near the end of the season. However, these effects usually occurred in combination with negative first-order effects, indicating that proportion of young started at a high plateau, declined during the course of the season, then levelled off again near the end of the migration. Such a pattern would be expected if there was a substantial average difference, but much overlap, in the timing of migration of the two age classes. Species showing this pattern strongly at all stations were Tennessee Warbler and Magnolia Warbler.

Moon

First order effects of the number of days from new moon (M) occurred in seven of 22 cases and the results were somewhat equivocal (Table 2). Negative effects in four species all occurred at Station 2, indicating a tendency for the proportion of young to be lower in the days before full moon, when the sky is moonless late in the night, than in the days following full moon, when the moon is above the horizon late in the night. In one of those species (Blackpoll Warbler) a strong opposite effect ($P < 0.01$) occurred at Station 1.

The important result with respect to moon phase was the strong tendency for second-order effects to be positive (Table 2). In four of five cases, these effects occurred at Station 1, where the presence of a lighthouse may magnify the effect (Dunn and Nol 1980). This result indicates that the proportion of young tends to be lower near new moon than near full moon, when both the size of the illuminated lunar disk and the number of nocturnal hours that it is above the horizon are near their maximum values. Species showing this pattern strongly at Station 1 were Swainson's Thrush, Blackpoll Warbler, White-crowned Sparrow (all $P < 0.01$), and American Redstart ($P < 0.05$). Red-eyed Vireo showed a tendency to have a higher proportion of young near full moon at Station 2 ($P < 0.10$) and a lower proportion of young near full moon at Station 3 ($P < 0.05$).

Weather

Only 23% (31/132) of weather-station interactions had significant ($P \leq 0.10$) effects on the proportion of young. Nevertheless some patterns could be detected. High horizontal visibility and warm temperatures usually had positive effects on the proportion of young (Table 2). In the Red-eyed Vireo, however, the effect was strongly positive at Station 1 but strongly negative at Station 3 ($P < 0.01$ in both cases). Rain and cloud tended to have negative effects on the proportion of young (Table 2). The single exception was Swainson's Thrush at Station 3, where the effect was positive ($P < 0.01$).

Effects of wind variables were more erratic. Easterly and westerly winds had little effect. Winds with a southerly component tended to have a negative effect on the proportion of young, scoring 21 negative points versus eight positive points (Table 2).

ANNUAL PROPORTIONS OF YOUNG AND FALL/SPRING POPULATION RATIOS

Annual raw and adjusted proportions of young for each species are shown in Figure 1 (left side). In some species (e.g., Swainson's Thrush, Yellow-rumped Warbler) differences between raw and adjusted proportions were small; in others (e.g., Tennessee Warbler, Magnolia Warbler), there were large discrepancies in some years between adjusted and raw proportions of young. Proportions of young showed substantial year to year fluctuations. There were no very obvious trends, although the proportion of young in White-throated Sparrows was generally higher from 1975 to 1988 than between 1966 and 1972, and there was a tendency for Tennessee Warbler proportions of young to decline between 1975 and 1987.

Fall/spring population ratios also fluctuated (Fig. 1, right side). Again there were few obvious trends. Red-eyed Vireo population ratios tended to decline from 1966 to 1988. Population ratios of Tennessee, Magnolia, and Yellow-rumped warblers were high in the 1975–1980 period, corresponding with a spruce budworm (*Choristoneura fumiferana*) outbreak that peaked in Ontario in 1980 (Hussell et al. 1992).

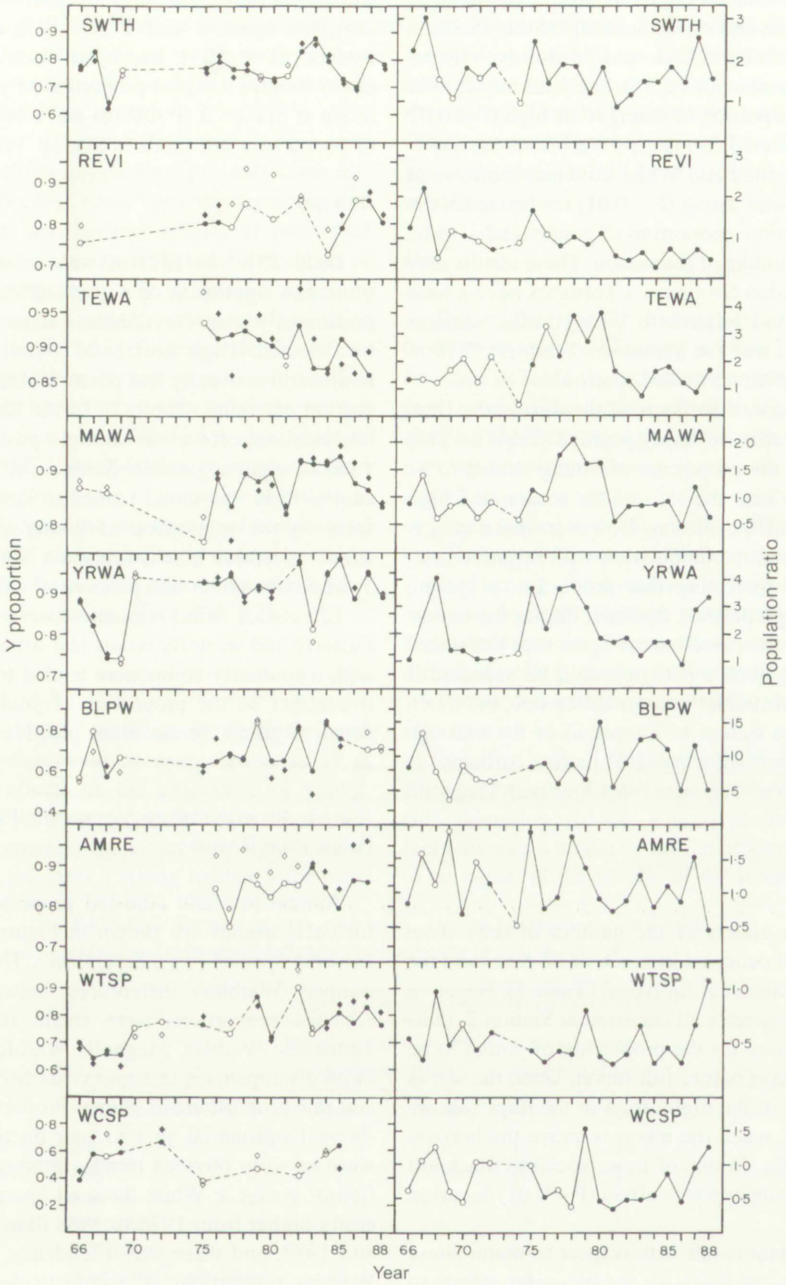

FIGURE 1. Proportion of young (Y proportion, left panels) and fall:spring ratios for population index 1 (right panels) for nine species. Left panels: circles = adjusted proportion of young, diamonds = raw proportion of young; open and closed symbols indicate proportions based on 50–99 and 100+ aged birds, respectively; lines join annual adjusted proportion of young; broken lines span years with missing data. Right panels: closed circles indicate population ratios derived from indices both of which were based on 50+ station-days of observations; open circles indicate ratios calculated from indices at least one of which was based on <50 (25–49) station-days; lines join annual ratios; broken lines span years with missing data. Species Codes: SWTH = Swainson's Thrush, REVI = Red-eyed Vireo, TEWA = Tennessee Warbler, MAWA = Magnolia Warbler, YRWA = Yellow-rumped Warbler, BLPW = Blackpoll Warbler, AMRE = American Redstart, WTSP = White-throated Sparrow, WCSP = White-crowned Sparrow.

For individual species, the only significant correlations between proportions of young and population ratios were those between raw proportion of young and all three population ratios in the White-crowned Sparrow ($r_S = 0.536$ for population ratio 1, $r_S = 0.573$ for population ratio 2, $r_S = 0.664$ for population ratio 3; $N = 11$, $P \leq 0.05$). If proportions of young and population ratios are positively related, however, then the mean correlation coefficient for the nine species should be positive. Mean correlation coefficient between adjusted proportion of young and population ratio 1 was 0.161, which was significantly greater than zero (Table 3). Means of correlations between all other combinations of methods of determining proportion of young and population ratio were non-significant and close to zero. Ranges and standard deviations of the correlation coefficients were lowest when population ratio 1 was used.

The effect of adjusted proportion of young in the trend analyses was positive (in accordance with expectation) in six of nine species for both the fall trend alone and for the combined spring and fall trend (Table 4). Significant or near-significant effects occurred in three and four species for the fall and spring/fall analyses, respectively (Table 4). Raw proportions of young had positive effects in four of nine species in the fall and three of nine species in the spring/fall analyses, with none of the effects significant or near significant. A sign test on the probabilities associated with the effect of proportion of young showed that adjusted proportion of young index was a marginally non-significantly better predictor of fall population indices than raw proportion of young index in the fall trend analyses (seven positive, two negative differences, one-tailed $P = 0.090$). In the spring/fall trend analyses, adjusted proportion of young was a significantly better predictor of the fall population index than the raw proportion of young (eight positive, one negative differences, one-tailed $P = 0.020$).

DISCUSSION

Daily proportion of young was influenced by year, station, date, moon phase, and weather (Table 2). As far as I am aware, this is the first demonstration of effects of weather on the proportion of young captured during fall migration. Although there was considerable variation among species and stations, it appears that there was a general tendency for the proportion of young to be higher when conditions were good for migration than when they were poor. The proportion of young tended to be higher near full moon than near new moon, higher when horizontal visibility was good than when it was poor, higher when there was no rain than when it was raining, and higher when there were tail-winds (northerly component) than when there were head-winds. This indicates that a greater proportion of adult birds land on Long Point when conditions for migration are poor than when they are good. This, perhaps, reflects the relative inexperience of young birds, which are less likely to overfly Long Point when conditions are good.

These effects were detectable despite the fact that capture methods at Long Point were not standardized and varied from day to day and year to year. We do not know to what extent consistent use of the same methods would have improved the precision of the productivity estimates. If the proportion of young captured is influenced by types and siting of traps and nets, then it is likely that the effects of environmental variables, such as station, moon phase and weather, would have been detected even more readily had the data collection been more standardized.

The proportion of young birds varied among the three Long Point stations, with more young recorded at Stations 2 and 3 than at Station 1. Therefore my annual raw proportion of young index (based on numbers of adults and young accumulated over all three stations) is certain to be biased by annual

TABLE 3. SPEARMAN CORRELATION COEFFICIENTS (R_S) BETWEEN PROPORTION OF YOUNG AND POPULATION RATIO FOR NINE SPECIES

		Population ratio model		
Proportion of young		Full	Station + station-day	Site only
Raw	mean	0.072	0.012	-0.020
	min, max	-0.056, 0.434	-0.302, 0.462	-0.496, 0.531
	SD	(0.164)	(0.222)	(0.296)
Adjusted	mean	0.161*	0.070	0.065
	min, max	-0.212, 0.467	-0.212, 0.420	-0.441, 0.420
	SD	(0.202)	(0.242)	(0.314)

* denotes $P \leq 0.05$ for one-tailed t-test for H_0: mean $r_s = 0$.

variations in the proportion of the total captures at each station. This problem exists only if there are significant differences in the proportions of young birds captured among different stations used to calculate a combined raw proportion of young index. If this is so, then the combined proportion of young index should be standardized such that each station is represented in the same proportion in the total index each year.

Overall, the results presented here imply that we should not assume that raw annual age proportions are reliable and consistent indices of productivity (see also Dunn et al. *this volume* b). It may be necessary to make adjustments for the confounding effects of station, day, moon phase, and weather. This conclusion was supported to a limited extent by my tests of consistency of proportion of young indices and population indices.

The annual proportion of young indices that were adjusted for the confounding effects of station, day, moon phase, and weather sometimes differed substantially from raw proportion of young (Fig. 1). The only significant correlation between proportion of young and population ratio was the one that matched adjusted proportion of young with population ratio 1, which was also fully adjusted for effects of day, moon, and weather (Table 3). Adjusted proportion of young was also more effective than raw proportion of young in accounting for variability in trend analyses (Table 4). All of these results suggest that adjusted proportions of young perform better as indices of productivity than do raw proportions of young.

My attempts to validate proportions of young as productivity indices were disappointing, however, in that most of the single-species correlations between proportion of young and population ratios were low and non-significant (Table 3) and, in most species, the effects of proportion of young in the trend analyses were also not significant (Table 4). My analysis is consistent with the view that both age proportions and population ratios contain information about productivity, but one or both of these measures lack precision. Given small sample sizes of aged birds in some years (particularly adults), and variability in migratory populations, it is likely that both age proportions and population ratios lack precision. Nevertheless, my results indicated that adjusted proportions of young performed better than raw proportions of young. Moreover, fully adjusted population indices outperformed other population indices, as is expected because the adjustments are designed to reduce variability that is not attributable to population size.

Inclusion of proportion of young as a predictor variable in trend analyses may enhance precision of estimates of trends in fall populations of some migrants. In several species proportion of young was not significant and it had little effect on the estimate of trend. In other species proportion of young was significant and its inclusion resulted in a relatively large reduction in residual variance, which would allow earlier detection of a trend, if it exists. For example, explained variation (R^2) in fall abundance indices increased by 18.6% in the Tennessee Warbler and 25.4% in the Magnolia Warbler when proportion of young was included as a predictor variable.

These results indicate that either proportions of young or population ratios or both may be useful for

TABLE 4. EFFECT OF PROPORTION OF YOUNG IN TREND ANALYSES OF ANNUAL POPULATION INDICES [a]

			Direction and significance of effect of proportion of young [b]			
	Sample sizes		Adjusted proportion of young		Raw proportion of young	
Species	Spring	Fall	Fall	Spring/fall	Fall	Spring/fall
Swainson's Thrush	22	18	+	+	–	–
Red-eyed Vireo [c]	22	12	+*	+**	+	+
Tennessee Warbler	22	13	+(*)	+**	–	–
Magnolia Warbler	22	16	+*	+**	+	+
Yellow-rumped Warbler	22	18	–	–	–	–
Blackpoll Warbler	22	17	–	–	–	–
American Redstart	22	12	–	–	–	–
White-throated Sparrow	22	18	+	+	+	–
White-crowned Sparrow	25	13	+	+*	+	+

[a] Except as indicated in footnote c, trends were linear as in equations 1 and 2; that is, there were no higher order or season interaction terms.

[b] (*) = $P \leq 0.10$, * = $P \leq 0.05$, ** = $P \leq 0.1$ in one-tailed test of significance of coefficient c in equation (1) for fall and equation (2) for spring and fall (see METHODS).

[c] Spring and fall linear trends of Red-eyed Vireo differed significantly ($P < 0.01$). Therefore a season interaction term was included in the spring/fall regression model.

detecting productivity changes in songbird populations, but appropriate adjustments may be necessary to account for effects of confounding variables. Small sample sizes and sampling errors are likely to result in imprecise annual estimates, but long-term trends in productivity should be detectable.

It was notable that in the nine common species selected for analysis here, annual samples of aged birds were often fewer than the 50 that I judged was the minimum acceptable for inclusion in the analyses. Most banding stations probably do not capture large enough samples of more than a few species to be useful for estimating age proportions, unless the data are combined with those from other stations (with appropriate adjustments for station effects). Possibly, much larger samples than this will be needed to obtain precise indices of productivity. Alternatively or additionally, inland stations where higher proportions of adult birds are captured than at Long Point may give more precise estimates and may be less affected by confounding variables.

Validation of productivity indices for small landbird migrants is a difficult problem because reliable benchmark measures of productivity are generally not available. More research is needed to determine the reliability of indices and required sample sizes and to examine the effects of confounding variables at different stations (inland versus coastal). We need more information on whether different capture methods have an important influence on the proportion of young birds captured. Alternative methods of analysis should also be explored.

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