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THE USE OF MIGRATION COUNTS FOR MONITORING BIRD POPULATION LEVELS

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ABSTRACT.—Previous use of migration counts for monitoring bird population levels has been based largely on indices derived from a summation of counts over part or all of one or more migration seasons. A new method is described in which multivariate regression techniques are used to assign variability in counts at one or more sites to year, date, weather factors and other variables. Variability attributable to year provides a relatively reliable index of annual migration volume and allows statistical tests of differences between years. The method is illustrated by examples of indices calculated from spring counts of migrants at the Long Point Bird Observatory, Ontario, in the years 1962–79 and is validated as a population indicator by correlating migration indices with breeding bird survey indices for 1968–79. Pros and cons of migration indices as population indicators are discussed as well as the applicability to other groups of birds of the methods described here.

Although migration counts integrate information on bird populations over wide areas and often sample relatively large numbers of individuals at a single observation site, they have been little used to monitor changes in population levels. There are two main reasons for this: (a) it is often difficult to associate particular migrant populations with corresponding breeding and wintering populations, and (b) many factors other than population change contribute to variability in migration counts. The purposes of this paper are to present a method which attempts to overcome the second of these difficulties, to suggest how it can be applied elsewhere, and to discuss the pros and cons of migration indices.

Previous attempts to measure annual or longer-term changes in numbers of migrants include a variety of situations and objectives (e.g., Mueller and Berger 1967b; Hackman and Henny 1971; Busse 1973; Williamson 1975; Berthold and Schlenker 1975; Mueller et al. 1977; Nagy 1977; Langslow 1977, 1978; Hjort and Lindholm 1978; Berthold and Querner 1979). Svensson's (1978c) study is notable because he showed that migration indices for several species at Swedish bird observatories were correlated with independently-derived results from the Swedish Breeding Bird Census. He concluded, however, that the Breeding Bird Census was a more efficient method for detecting population changes because of high variability in the migration indices, which he attributed to the effects of weather factors.

Although the studies cited above differ in the level of standardization of field procedures and in the details of their methods, in essence all base their indices of migration volume on summation of counts over a period of days or weeks in one or more migration seasons. Because of the well-documented effects of weather on migration, such indices are often regarded as more or less unsatisfactory, except for demonstrating gross long-term changes in population level. Apart from the early attempt by Ulfstrand (1958) to compensate for the effects of wind on counts of migrating hawks, no methods have been described to correct migration indices for the effects of weather, nor have the statistical attributes of the data been examined carefully with a view to developing appropriate indexing procedures.

The relationships between weather and migration volume have been studied for decades and multivariate regression techniques have been used extensively to examine the effects of weather factors on migrating birds, particularly in radar studies (Richardson 1978). Here I extend these procedures to provide a method for detecting annual population change at one or more observation sites, while simultaneously compensating for the effects of date, weather factors and other variables. In its present form the method should be regarded as a preliminary attempt to correct migration indices for the effects of date of observation and weather factors; further study may lead to improvements and refinements. The method is presented first in the form of a general model which may be applicable to a variety of situations. As an example of its application, it is then used to determine migration indices from counts of nocturnal migrants at Long Point Bird Observatory, Canada, and the indices are validated as population indicators by comparison with independently-derived indices of breeding population size. In the Discussion section I examine the potential usefulness of migration indices derived from this procedure.

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THE MODEL

DESCRIPTION

The general model relating bird numbers to date, year, site, and environmental factors is

$$\ln(N_{ijk} + 1) = A_j + \sum_{m=0}^{M} c_{im}k^m + \sum_{v=0}^{V} b_{vi}X_{vijk} + e_{ijk} \quad (1)$$

where N_{ijk} is the number of birds at site i, in year j, on date k; A_j is a year factor specific to year j; $\sum_{m=0}^{M} c_{im}k^m$ is an M^{th} power polynomial in k (date), that is specific to site i and in which c_{im} are constants; X_{vijk} is the value of environmental variable v at site i, in year j, on date k, and b_{vi} are constants specific to environmental variable and site; and e_{ijk} is an error factor representing unexplained variation. Multiple regression techniques are used to estimate A_j, c_{im} and b_{vi} with c_{i0} for one of the sites arbitrarily set to zero. Certain characteristics of the model and the rationale for its use are discussed in the following paragraphs.

(1) The regression model assumes homoscedasticity (equal variances), normal distribution of residuals, and additive effects of variables. When (a) standard deviation of the residuals varies directly as the means, (b) the distribution of residuals is skewed (to high values), and (c) the effects on the original scale are multiplicative, a logarithmic transformation is appropriate in order to meet the assumptions of the regression (Snedecor and Cochran 1967:141–144, 329–330; for a good discussion of the assumptions of multiple regression in relation to analysis of migration data see Richardson 1974). Extensive examination of bird count data from Long Point shows skewed distributions and variances that increase with the means. This may prove to be a general rule with bird count data (cf. Alerstam 1978, Blokpoel and Richardson 1978, Prater 1979). Moreover, it is logical to assume that effects on the original scale are multiplicative. For example, if the population doubles between year j and year $(j + 1)$, we would expect the number of birds counted on day k in year $(j + 1)$ at site i to be twice that on day k in year j, if all other conditions remain constant. If the number of birds on day $(k + 5)$ in year j at site i is twice that on day k for the same year and site, however, we would expect four times as many birds at that site on day $(k + 5)$ in year $(j + 1)$ as on day k in year j, if all other factors remain the same. Logarithmic transformation converts these multiplicative effects to additive ones which can be analysed by multiple regression techniques. Note that one is added to N_{ijk} prior to taking logarithms because it is impossible to take a logarithm of zero. This introduces some distortion into the multiplicative-additive conversion, especially when there are many observations of zero or small numbers (less than 10) of birds.

(2) A_j is a year factor common to all sites, an assumption that is appropriate only for sites in the same local area or which for other reasons can be assumed to be sampling the same migrant bird populations. A_j is a measure of annual migration volume, which can be used to derive an annual migration index (see below).

(3) $\sum_{m=0}^{M} c_{im}k^m, i = 1, 2, \ldots, I,$ is a series of I polynomials in k, each of which represents the seasonal pattern of migration at site i (cf. Alerstam 1978). No assumptions are made concerning the similarity or otherwise of the patterns at different sites.

(4) $\sum_{v=0}^{V} b_{vi}X_{vijk}, i = 1, 2, \ldots, I,$ is a series of I sets of terms for different environmental variables v, whose coefficients b_{vi} are specific to each site i. Thus, no assumptions are made concerning the similarity or otherwise of the effects of environmental variables at different sites. In principle, the X variables need not be confined to environmental factors but can include any factor that is related to bird numbers. Thus, measures of sampling effort can be included here, provided that they meet the assumptions of the regression procedure (see Discussion section).

MIGRATION COUNT INDICES

The A_j values represent the effects of year on $\ln(N_{ijk} + 1)$. If $\ln(N_{ijk} + 1) = Y_{ijk}$, then the adjusted means for year, $\hat{\bar{Y}}_{.j.}$, provide a measure of migration volume in year j. The adjusted means are calculated as

$$\hat{\bar{Y}}_{.j.} = A_j + \sum_{i=1}^{I} \sum_{m=0}^{M} \left[\frac{n_i}{n} c_{im}(\overline{k^m})_{i..}\right] + \sum_{i=1}^{I} \sum_{v=1}^{V} \left[\frac{n_i}{n} b_{vi}\bar{X}_{vi..}\right] \quad (2)$$

Where n_i is the number of observations at site i (over all dates in all years), $n = \sum_{i=1}^{I} n_i$, and

$(\overline{k^m})_{i..}$ and $\bar{X}_{vi..}$ are the means of all values (over all dates in all years) at site i of k^m and X_{vijk}, respectively. An index of annual migration volume, expressed in terms of untransformed bird numbers is: $A_j' = e^{\hat{\bar{Y}}_{.j.}} - 1$.

MATERIALS AND METHODS

THE DATA

Bird Migration Counts

The migration counts were taken from the records of the Long Point Bird Observatory for 16 March–15 June, 1962–1979. No counts were available for 1965 and data for 1973 and 1974 were sparse. Migration counts were estimates of the number of each species occurring each day in specified areas at two sites on Long Point, a 32 km peninsula on the north shore of Lake Erie. Site 1 is at the eastern tip of the peninsula and consists mainly of dunes sparsely vegetated with cottonwoods (*Populus deltoides*). Site 2 is at the southwestern end of a wooded dune ridge 19 km west of site 1 (see Figure 1 in Hussell and Stamp 1965). Each morning that the Observatory stations were manned, a census of about 1 h duration was conducted over an approximately 2.0 km circuit covering a representative sample of the habitat at each site. On most days, Heligoland traps and/or mist nets were used to capture birds for banding (Hussell and Woodford 1961). At the end of the day, all observers present conferred and agreed on estimates of the totals of each species occurring within the specified area at the site. Estimates were based on the census, birds captured, and any other observations during the day. These estimates for six nocturnal migrant land birds were used as the migration counts in this analysis.

For most species, I used all available data spanning the period from the first observation to the last spring observation of that species in any of the years. For species with small summer resident populations in the sample areas, however, the data were inspected and an arbitrary cut-off date was selected for the end of the spring migration period. Sample sizes for each species are in Table 2.

Weather

Weather data were from weather stations at the Long Point lighthouse (within the site 1 area) and at Simcoe, Ontario, about 35 km N of site 2. I used the following weather factors measured at 07:00 Eastern Standard Time: (1) wind direction at Simcoe, recorded on a 16-point scale, N, NNE, NE, etc., and reduced to an eight-point scale by combining N and NNE to become 'N,' NE and ENE to become 'NE,' etc.; (2) wind speed at Simcoe in miles per hour; (3) dry bulb air temperature at Simcoe in °F; (4) cloud cover (total cover) at Long Point recorded as eighths of sky covered; (5) visibility at Long Point recorded on a nine-point scale and converted to km.

Weather data from Long Point were missing for 1976 (cloud cover only) and 1979 (cloud cover and visibility) and for scattered dates in other years. I preferred to use Long Point cloud and visibility data, however, because I suspect that these factors may directly influence the numbers of migrants terminating their flights on Long Point. Therefore, I estimated missing values of factors (4) and (5) from multiple regression equations obtained from regressing known values of each of these variables on 12 other weather variables and date. For cloud cover (4), $R^2 = 0.71$ ($n = 1169$, $P << 0.001$) and for visibility (5), $R^2 = 0.48$ ($n = 1266$, $P < 0.001$). As expected, the most important predictor of cloud cover at Long Point was opacity (opaque cloud cover) at Simcoe, while the most important predictor of visibility was the square of visibility at Simcoe.

REGRESSION PROCEDURE

A_j, c_{im} and b_{vi} in equation (1) were estimated using a backward stepwise regression procedure with Biomedical Computer Program P-series BMDP2R (Dixon and Brown 1979). The dependent variable was the natural logarithm of (migration count + 1), named LN(N + 1) in the computer program. Sixty-one independent variables were used in the regression analysis: these were made up of 1 dummy variable for site, 16 dummy variables for year, 14 site-date interaction variables, and 30 site-weather interaction variables (Table 1).

One year (1970) was designated the reference year and its variable was excluded from the regression. The other 16 year variables were forced into the regression at the start and retained throughout, since determination of all values of A_j is the objective of the analysis. Likewise, site 1 was made the reference site and the dummy variable for site 2 was forced into and retained in the regression to provide a unique intercept for site 2.

The only environmental variables used in this study were weather variables and the data were the same for both sites, since only one suitable set of data was available. In some situations it might be preferable to use weather data specific to site, for at least some of the weather variables. Second and third order terms were used in the temperature and wind variables because experience showed that bird count numbers were often nonlinearly related to these variables. Date variables and weather variables used in the regressions were always in the form of interactions with the dummy variable for site and they were made available for entry and removal by the stepwise procedure.

A backward stepping procedure was used in order to detect the effects of interactions between polynomial terms. I used the stepwise procedure 'F' in BMDP2R (Dixon and Brown 1979:405–406). By setting F-to-remove and F-to-enter at very low values (0.10 and 0.11, respectively) all or nearly all available variables were entered. The F-to-remove and F-to-enter values were then reset to higher values and backward stepping began. By setting F-to-enter at 2.71 and 2.72, respectively, only those variables with $P < 0.10$ in a standard F-test were retained in the regression. Significance of variables selected in a stepwise procedure should be treated with caution, however, as their true probability levels may be substantially higher by an unknown amount (Freund and Minton 1979:129, 149; Hall 1979:7–8).

Plots of residuals (observed-predicted) showed that their dispersion was not uniform over the range of values of the dependent variable predicted by the regression. For example, in a residual plot for the Ruby-crowned Kinglet (*Regulus calendula*) (Fig. 1a)

TABLE 1
INDEPENDENT VARIABLES USED IN REGRESSION ANALYSIS

Factor or variable	Variable names[a]	Explanation[b]
Year	Y62, Y63, Y64, Y66, Y67, Y68, Y69, *Y70*, Y71, Y72, Y73, Y74, Y75, Y76, Y77, Y78, Y79.	Dummy variables. Example: Y62 = 1 if j = 1962, otherwise Y62 = 0.
Site	*A1*, A2.	Dummy variables. Example: *A1* = 1 if i = 1, otherwise *A1* = 0.
Date[c]	*DRT*, *D1*, *D2*, *D3*, *D6*, *D7*, *D10*, *D11*.	$DRT = \sqrt{\lvert k/50 \rvert}$, $D1 = k/50$, $D2 = (k/50)^2$, etc.
Site-date interaction[d]	A1DRT, A1D1, A1D2, A1D3, A1D6, A1D7, A1D10, A1D11, A2DRT, A2D1, A2D2, A2D3, A2D6, A2D7.	For each case A1DRT = *A1* × *DRT*, A1D1 = *A1* × *D1*, etc.
Temperature[e]	*TP*, *TP2*, *TP3*	*TP* = (dry bulb air temperature − 45), $TP2 = (TP)^2$, $TP3 = (TP)^3$.
Cloud	*CL*	*CL* = cloud cover.
Visibility[f]	*VSRT*	*VSRT* = square root of visibility.
Wind[g]	*E*, *SE*, *S*, *SW*	*E* = 1 if wind direction is E, *E* = −1 if wind direction is W, otherwise *E* = 0; etc.
	EV, *SEV*, *SV*, *SWV*	*EV* = *E* × (wind speed/10), *SEV* = *SE* × (wind speed/10), etc.
	EV2, *EV3*, *SEV2*, *SEV3*, *SV2*, *SV3*, *SWV2*, *SWV3*	$EV2 = (EV)^2$, $EV3 = (EV)^3$, etc.
Site-temperature interaction	A1TP, A1TP2, A1TP3, A2TP, A2TP2, A2TP3.	A1TP = *A1* × *TP*, A1TP2 = *A1* × *TP2*, etc.
Site-cloud interaction	A1CL, A2CL	A1CL = *A1* × *CL*, etc.
Site-visibility interaction	A1VSRT, A2VSRT	A1VSRT = *A1* × *VSRT*, etc.
Site-wind interaction[d]	A1EV, A1EV2, A1EV3, A1SEV, A1SEV2, A1SEV3, A1SV, A1SV2, A1SV3, A1SWV, A1SWV2, A1SWV3, A2EV, A2EV2, A2SEV, A2SEV2, A2SV, A2SV2, A2SWV, A2SWV2.	A1EV = *A1* × *EV*, A1EV2 = *A1* × *EV2*, etc.

[a] Names of variables used in the computer program. Variables not used as independent variables in the stepwise regression analysis are italicised.
[b] i = site, j = year, k = date. For a discussion of the use of dummy variables and interaction variables, see Nie et al. (1975:373–383). See text for further explanation.
[c] Because of the tolerance limitations of BMDP2R, it was necessary to reduce correlations among date variables by setting k = 0 to a date near the midpoint of the season for each species and by omitting some terms from the polynomial series. $k/50$ was used to avoid large values and small coefficients in the polynomial terms.
[d] Tenth and eleventh order site-date interaction variables and third order site-wind interaction variables for site 2 were omitted to reduce the possibility of overfitting of the site 2 data, which make up only about one third of the observations. Overfitting tends to occur if the number of cases does not greatly exceed the number of variables.
[e] Temperature difference from normal is preferable (Richardson 1974, 1978) but was not used in this study.
[f] Square root of visibility was used, following Richardson (1974).
[g] Wind speed/10 was used to avoid large values and small coefficients in the polynomial terms.

the distribution of residuals becomes increasingly distorted at predicted values below 1.5 because observations of zero place a lower limit on the value of the residual (cf. Blokpoel and Richardson 1978:357). The lowest diagonal band of points in Figure 1a represents observations of zero birds. When the predicted value is less than zero, the residuals and their means are necessarily positive, a condition which is a serious violation of the assumptions of the regression. This problem is most pronounced in species that occur in small numbers and have many observations of zero.

To mitigate this situation, I removed cases with predicted values of zero or lower and recalculated the regressions from the reduced data set. Indices and other results quoted in this paper are always from this second calculation. A plot of residuals for the second

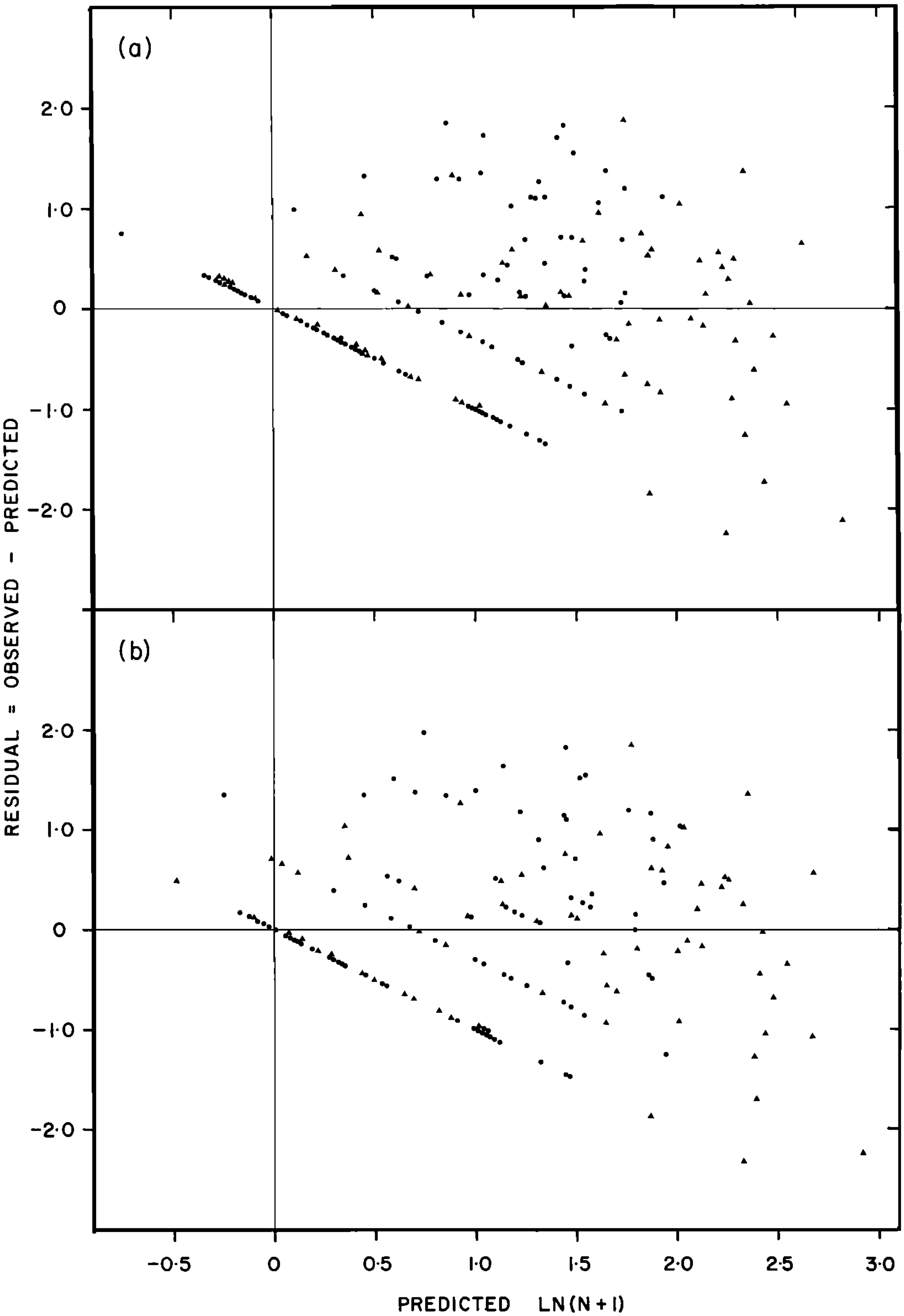

FIGURE 1. Plot of residuals against predicted values of LN(N + 1) for the Ruby-crowned Kinglet. (a) First calculation using all data. (b) Second calculation with reduced data set (see text). Only data for 1976 and 1977 are shown (computer plots of all data show a similar dispersion). Circles = site 1; triangles = site 2.

calculation in the Ruby-crowned Kinglet is shown in Figure 1b. The case removal procedure does not entirely eliminate predicted values of less than zero in the second calculation, because it often results in lower predicted values for the remaining cases; but it does provide an objective method for removing many observations which contribute to distortion in the distribution of the residuals. In most instances the excluded observations are from extremely early or late in the migration season or represent conditions that are otherwise relatively unfavorable for occurrence of the species in question.

Migration Count Indices (MCI)

The adjusted mean for each year was calculated by replacing each variable (except the year variables) in the regression equation by its mean value for all cases, and adding the coefficient of the dummy variable for that year. This gives the same result as equation (2) since the means of site interaction variables are weighted means of observations at each site with weights equal to n_i/n. The indices A_i' were calculated from the adjusted means, as described previously, then rescaled so that the MCIs have an average value of 100 for the years 1975–79.

The significance of differences between indices for different years is determined by testing the differences between adjusted means for year. The significance of the difference between the adjusted mean for any year and the adjusted mean for the reference year in the regression can be determined from the F-to-remove value for the dummy variable for that year with 1 and $(n - v - 1)$ degrees of freedom, where n is the number of cases and v is the number of independent variables in the regression. To determine the significance of differences between all successive years 1962–79, I used Program BMDPIR (Dixon and Brown 1979) to recalculate the regression with different reference years (i.e., omitting another year variable instead of Y70).

Validation

To determine whether migration indices reflect population trends, the MCIs were correlated with indices from an independent method for monitoring population change, the Breeding Bird Survey (BBS). The BBS indices were for two regions generally to the north of Long Point, designated as "central Ontario and Quebec" and "southern Ontario and Quebec" (Erskine 1978, Freemark et al. 1979, Finney et al. 1980). These regions presumably contain the summer ranges of many of the spring migrants that pass through Long Point. The six species considered here are common migrants at Long Point that are well represented in the central region; they are Common Flicker (*Colaptes auratus*), Winter Wren (*Troglodytes troglodytes*), Hermit Thrush (*Catharus guttatus*), Ruby-crowned Kinglet, Yellow-rumped Warbler (*Dendroica coronata*), and White-throated Sparrow (*Zonotrichia albicollis*). BBS indices are available for these species for the central region for the years 1969–79 and for the Common Flicker and White-throated Sparrow for the southern region for 1968–79. (Populations of the other four species in the southern region are too small to give useful BBS indices.) Unfortunately, the BBS indices are believed to be subject to inaccuracies except for relatively short-term comparisons (G. H. Finney, pers. commun.), but these indices are the best indicators of breeding bird population levels that are currently available to me.

If either the BBS index or the MCI for any species does not reflect population change or if the two indices are measuring uncorrelated changes in different populations, the expected correlation coefficient between the two indices is zero. If the two indices measure changes in the same or overlapping populations or correlated changes in different populations of a species, then r should be positive. Considering several species, average r should be positive or zero, respectively, if the indices do or do not track the same or correlated population changes. Demonstration of positive r provides evidence that MCIs (and BBS indices) measure population change; lack of such a demonstration provides contrary evidence only if there are independent reasons to indicate that the two indices are sampling the same, overlapping or correlated populations.

RESULTS

Regression Results

Using 1970 as the reference year, the regression equation for the White-throated Sparrow is given below (see Table 1 for definitions of variables). One and two asterisks indicate variables whose coefficients have F-to-remove values greater than 3.85 and 6.67, respectively ($P < 0.05$ and $P < 0.01$, respectively, in a standard F-test). Regression coefficients of all other date and weather variables have F-to-remove greater than 2.71 (P between 0.10 and 0.05).

LN(N + 1) = 3.55 − 0.13 A2 + 0.82 Y62** + 0.86 Y63** + 0.05 Y64 + 0.78 Y66** + 0.78 Y67 + 0.03 Y68 + 0.24 Y69 + 0.62 Y71** + 0.40 Y72** + 0.12 Y73 + 0.16 Y74 + 1.02 Y75** + 0.54 Y76** + 0.38 Y77* + 0.26 Y78 + 0.04 Y79 − 1.82 A1D1* − 24.0 A1D2** − 30.5 A1D3* + 476 A1D6** + 1340 A1D7* − 5550 A1D10* − 15300 A1D11* − 2.81 A2D1** − 1.86 A2DRT − 11.7 A2D2** + 0.071 A1TP** − 0.0038 A1TP2** − 0.0008 A1TP3 + 0.029 A1CL − 0.089 A1VSRT** + 0.340 A1EV* − 0.157 A1EV3* + 0.093 A2TP** − 0.0018 A2TP3** − 0.442 A2EV2** + 0.488 A2SEV** − 0.308 A2SWV*

R^2 for the regression is 0.537, which is highly significant ($P << 0.01$). For site 1, seven date variables and seven weather variables had large enough effects for inclusion in the regression whereas for site 2 three date variables and five weather variables were included. The date variables alone accounted for 37.3% of the variation, weather variables alone for 8.9% and year variables alone for 3.2%. When entered in sequence after the date variables, however, the weather and year variables explained an additional 13.1% and 3.3% of the variation, respectively. In a similar analysis for the Ruby-crowned Kinglet, date variables alone accounted for 25.8% of the vari-

TABLE 2
REGRESSION RESULTS FOR SIX SPECIES

Species	Sample size[a] (n)	Mean birds/day[b]	R^2	No. of variables in regression[c]			
				Site 1		Site 2	
				Date	Weather	Date	Weather
Common Flicker	971 (1016)	5.25	0.630	6	4	6	6 (1)
Winter Wren	828 (972)	0.66	0.266	2	7	3	1
Hermit Thrush	892 (1080)	0.83	0.410	6	8	3	9 (1)
Ruby-crowned Kinglet	957 (1090)	2.06	0.469	3	5	4	8 (2)
Yellow-rumped Warbler	967 (1177)	0.96	0.391	7	3	5	6
White-throated Sparrow	955 (1002)	8.36	0.537	7	7 (2)	3 (1)	5

[a] Figures in parentheses are original sample sizes used in the initial regression calculation, prior to exclusion of cases with predicted values less than or equal to zero (see text).
[b] Geometric mean of $(N + 1)$, minus 1.
[c] Figures in parentheses are number of variables of marginal significance (with $0.10 > P > 0.05$ in a standard F-test) included in the total. In addition to variables shown, site variable A2 was included in all regressions but was not significant ($P > 0.10$) in Yellow-rumped Warbler or White-throated Sparrow. A2 was significant with $P < 0.05$ in the other 4 species.

ation, weather variables alone for 10.4% and year variables alone for 5.1%, but year variables explained more variation when entered second than did weather variables. Year variables and weather variables explained an additional 9.8% and 11.3% of the variation when entered in that sequence to give a total of 46.9% of the variation explained by all variables in the regression. The greater percentage of variability explained by year variables in the Ruby-crowned Kinglet compared with the White-throated Sparrow is presumably a reflection of greater year-to-year variability in populations of the former species. In both species year variables explained a highly significant amount of the variation ($P << 0.01$) when entered last. This provides evidence that in these migratory populations there are measurable annual fluctuations that are unrelated to the other variables in the regressions.

Significance levels of year variables in the regression equation for the White-throated Sparrow indicated that in 1962, 1963, 1966, 1967, 1971, 1972, 1975, 1976, and 1977 the level of migration was significantly greater than in the reference year (1970). All of the coefficients of year variables are positive because the reference year had the lowest migration level of any year; negative coefficients would indicate years with lower migration levels than the reference year.

Regression results for 6 species during spring migration are summarized in Table 2. R^2 varied from 0.268 in the Winter Wren to 0.630 in the Common Flicker. Mean birds/day gives a rough indication of the relative abundance of each species and in general the more abundant species had higher R^2 values. Two to seven date variables (mean 4.6) and one to nine weather variables (mean 5.8) for each site were included in the regressions. Every date and weather variable except A1SEV2 and A1SEV3 was included in a regression for at least one of the six species. The most frequently included variables for date were A1D2 (6 species), A2D1 (6), A1D1 (5), and A2D6 (5); and for weather were A1TP (6), A2TP (6), A1TP2 (5), and A2SWV (5). Interpretation of the significance of individual date and weather variables in relation to migratory behavior is often difficult because of correlations between variables, and is outside the scope of this paper.

MIGRATION COUNT INDICES

The Migration Count Indices shown in Figure 2 indicate that migration levels at Long Point fluctuate substantially: in the period 1962–79, 28 significant differences were detected among 77 possible comparisons between successive years in six species. The Winter Wren and Ruby-crowned Kinglet, two species believed to be subject to high mortality in cold winters, showed wide fluctuations in numbers with coefficients of variation (CV) of 63.7% and 66.8%, respectively (n = 14 and 16, respectively, using only indices based on 20 or more cases). Both species had low numbers in 1963–64 and 1977–79, and relatively low numbers in 1970. The Hermit Thrush and White-throated Sparrow also occurred in low numbers in 1970, but over the long-term the indices for these species have been relatively stable with CVs of 42.1% and 38.6%, respectively. The Yellow-rumped Warbler indices also fluctuate in a relatively narrow range (CV = 36.0%), but in this species there are indications of a decline in numbers, especially in the last five years. In the Common Flicker the overall variation is greater (CV = 61.4%) and indices have averaged substantially lower in the last five years than in the period 1962–74.

Indices for 1962–70 were compared with those

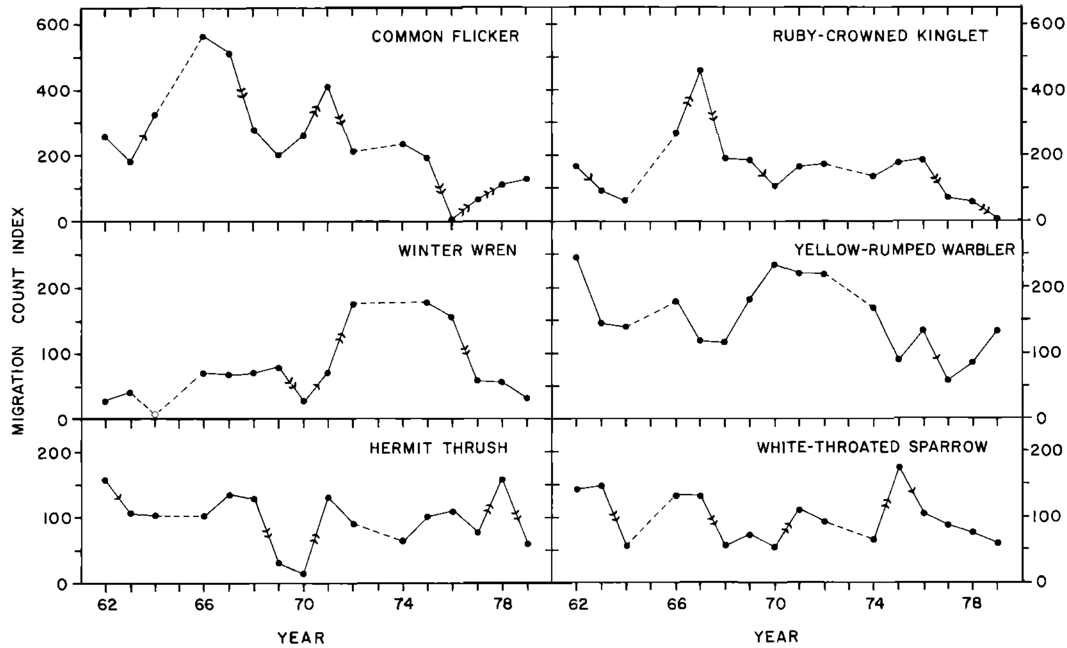

FIGURE 2. Migration Count Indices (MCIs) for six species during spring migration at Long Point, 1962–79. Solid circles = MCIs based on 20 or more cases; open circle = MCI based on 10–19 cases. Indices based on fewer than 10 cases were excluded, and those years are spanned by broken lines. Single and double arrows indicate significant differences between successive years at the 5% and 1% level, respectively.

for 1971–79 for each of the six species in Figure 2 (Wilcoxon 2-sample Rank Test). The only significant difference was in the Common Flicker in which indices for 1971–79 averaged lower than for 1962–70 ($P < 0.05$).

Validation of MCIs as Population Indicators

Correlation between MCI and BBS indices is shown in Table 3. Seven of the eight simple correlation coefficients (r) are positive and two are significant. The mean r is 0.429 and is significantly greater than zero ($P < 0.01$, one tailed t-test), providing evidence that the two indices vary in parallel. It might be argued that correlation coefficients for the central and southern regions in the same species are not independent and both should not be included in the tests. If the two southern region coefficients are excluded, the mean r becomes 0.396 and remains significantly greater than zero with $P < 0.05$.

In two species it was possible to calculate multiple correlation coefficients (R) between the MCI and BBS indices for two regions. In the Common Flicker R differed little from r for the central region for the same years, but in the White-throated Sparrow two BBS indices together explained about 24% more of the variation than either one alone.

DISCUSSION

This paper describes a method for measuring year-to-year changes in numbers of migrants at one or a series of sites on the migration route of a species. The index of migration level (MCI) is corrected for effects of date, site, and weather factors and allows tests of significance of differences between indices in different years. The method is illustrated here for counts of small nocturnal landbird migrants, but the general model is probably applicable to a wide range of situations that involve counts or other samples of migrants.

Although the computations are quite complex, the indexing method is designed to use data that are derived from field procedures that are simple and straightforward and that are already available at many migration stations. Several years of data will be necessary from any site to properly assign variability to various factors. Although this is a disadvantage for new migration stations, it is an advantage for established ones such as many European bird observatories and North American hawk migration lookouts. Once

TABLE 3
CORRELATION BETWEEN MIGRATION COUNT INDICES AND BREEDING BIRD SURVEY INDICES

Species	BBS region[a]	Sample size[b]	Correlation coefficient[c]
Common Flicker	C	9	0.641
	S	11	0.415
	CS	9	0.642
Winter Wren	C	8	0.168
Hermit Thrush	C	9	0.464
Ruby-crowned Kinglet	C	9	0.864**
Yellow-rumped Warbler	C	9	−0.331
White-throated Sparrow	C	9	0.572
	S	11	0.636*
	CS	9	0.786*

[a] Breeding Bird Survey region: C = central Ontario and Quebec; S = southern Ontario and Quebec (Erskine 1978).
[b] Years in which MCIs were based on fewer than 20 cases or BBS indices were based on fewer than 20 routes were excluded.
[c] When one region is given (C or S) the coefficient is the simple correlation coefficient between MCI or BBS index. When two regions are given (CS) the coefficient is the multiple correlation coefficient between MCI and the two BBS indices. One and two asterisks indicate coefficients that are significant at the 5% and 1% levels, respectively.

the necessary computer programs and data handling procedures have been set up, entering new data and calculating indices each year should prove to be a relatively simple process.

The MCI is a measure of the migration level at the observation site(s) in a particular year, corrected for some of the confounding effects of environmental factors, but it is not necessarily an index of population level. The Long Point MCIs reflect trends in another presumed population index, the Breeding Bird Survey Index, thus providing evidence that these MCIs do track population changes at least to some degree. Nevertheless it must be borne in mind that factors other than population change may influence MCIs, and that it may be difficult or impossible to assign variation to them. Such factors may include year-to-year changes in the site (including changes in characteristics, vegetation or food supply), changes in the migratory behavior of the species sampled (e.g., change in speed or route of migration), changes in sampling procedures and other consistent errors between years, and effects of environmental factors not used in the regression analysis. Sampling the same population at several sites will help to reduce the effects of random year-to-year changes at individual sites and strict standardization of counting or other sampling procedures over long periods of time is clearly desirable. Because consistent errors in sampling between years will introduce biases into the indices, field procedures should avoid practices that might lead to such errors or should include methods for correcting them. An example of a possible source of consistent errors is the use of counts made by different observers in different years. Use of data from many observers at several sites is likely to reduce such effects, even if some individual sites are subject to such errors.

In the examples given here, 27–63% of variability in counts was explained by year, date, site, and weather variables (Table 2). Better standardization of field procedures or skillful choice of additional or alternative weather variables for inclusion in the regressions might lead to higher values of R^2 (explained variation) and lower standard errors. In turn this would give improved resolution of differences between years. In lieu of standardization of field methods it may be possible to explain additional variation by including one or more variables for sampling effort, e.g., number of observers, hours of observation, net-hours. To meet the assumptions of the regression, however, the values of sampling variables must be independent of bird numbers, i.e., sampling effort must not be influenced by bird numbers. Except for sampling effort variables that are clearly independent of bird numbers, a safer approach is to measure correction factors in some way and apply them to the data before starting the regression analysis. Whenever possible, however, it is preferable to standardize procedures so that such correlations are unnecessary.

Because factors other than population change may influence MCIs, it is prudent to be cautious in drawing conclusions about apparently significant year-to-year and short-term changes in migration levels, at least until we have had more experience with MCIs. Examination of the behavior of MCIs in relation to other population indices and to short-term changes in avian environments will allow us to develop a better understanding of the relationships between population dynamics and migration levels. There is less reason to believe that nonpopulation factors would consistently influence MCIs over longer periods of time, however, especially if the indices are based on data from more than one site. In this paper, I was able to show that indices for 1962–70 were significantly higher than for 1971–79 in the Common Flicker, but not in five other species. Based on Breeding Bird Survey results, Finney et al. (1980) also noted the recent decline of the Common Flicker in central Canada. Ability to corroborate such long-term trends is one of the objectives of migration indexing.

In the data used in the central region correlations in Table 3 there were 17 statistically significant changes in the MCI between successive years compared with seven in the BBS index, from a possible total of 41. For the two species with southern region populations the corresponding figures were eight and three, respectively, from a possible total of 18. That the MCI shows more significant differences than the BBS index is probably due to relatively large fluctuations in migration levels at Long Point and does not necessarily indicate greater sensitivity to population change. The coefficients of variation of the MCIs averages 53.0% (range 39.7–67.0%) whereas for the central region BBS indices in the same years they averaged 26.4% (range 9.3–42.9%). Svensson (1978) argued that such differences between coefficients of variation indicate that migration indices are less effective at detecting changes in population levels than are breeding bird indices. In the present state of the art, I regard this as an untenable argument since we do not know enough about the characteristics of either type of index in relation to true population changes to state what the coefficients of variation mean. A plausible hypothesis, for example, is that breeding bird indices vary less than do bird populations because of the inability of observers to detect very high or very low breeding densities and/or because populations of territorial birds vary less than the total population. More analysis of data from as many sources as possible is needed to elucidate the behavior of populations.

This brings me to a discussion of the potential value of migration indices as measures of population change. As far as I can determine wide-scale population censusing or indexing is usually undertaken for one or both of two purposes: (a) to monitor the condition of the birds' environment and (b) to study population dynamics.

To monitor environmental quality there must be a clear association between the bird species and the habitat or geographic area we wish to monitor. At first sight it would appear that breeding bird indices have a distinct advantage over migration indices in this respect, but we must remember that most species only spend a small proportion of the year on their breeding grounds, especially at high latitudes. An extreme example is the Least Flycatcher (*Empidonax minimus*) which is estimated to spend an average of no more than 64 days or 17.5% of the year on the breeding range (Hussell 1981b). If we are to use such species to monitor breeding habitat quality we must also have knowledge of conditions in the wintering areas and along the migration route. Thus, breeding bird indices alone are inadequate for monitoring habitat quality except for purely sedentary species.

Although migration indices can be associated with a particular migratory population (e.g., the population that migrates through Long Point), we are often uncertain which breeding and wintering areas are represented in those populations. From band encounters, we know that some of the White-throated Sparrows that migrate through Long Point winter in Alabama (unpubl. data), but we have almost no precise information about where they spend the summer. More detailed analyses of band encounters, perhaps supplemented by other approaches (e.g., Kelsall and Calaprice 1972, Taylor 1980), are needed to determine breeding areas, migration routes and wintering areas of subpopulations if information from migration indices, and indeed from breeding and wintering censuses, is to be fully utilized. Once distinct wintering and breeding ranges are known for migrant populations, migration indices will provide a way to examine the structure of and fluctuations in populations at a time during the annual cycle for which such information was not previously available.

Migration indices may prove to be most useful for those species whose populations are not easily monitored in other ways, because of low density, inaccessibility or difficulty in detecting them in the breeding or wintering areas. In Canada many song birds such as the Gray-cheeked Thrush (*Catharus minimus*), Cape May Warbler (*Dendroica tigrina*), Blackpoll Warbler (*Dendroica striata*), and White-crowned Sparrow (*Zonotrichia leucophrys*) are undersampled by the Breeding Bird Survey because their ranges are relatively inaccessible or their songs difficult to detect or both. Moreover many of the same species winter south of the United States where their populations are difficult to monitor. Most raptors are also undersampled because of low densities and/or low detectability. The method described here should be suitable not only for small nocturnal migrants, however, but also for diurnal migrants such as hawks, that concentrate along leading lines in response to weather conditions. It may also be applicable to coastal waterbird migrants such as loons, eiders and scoters.

Finally, it should be noted that all of our methods for monitoring bird populations are relatively primitive and uncertain when compared, for example, to those for determining human population changes. When preservation of bird species, populations or habitats is involved, we need to marshall all the evidence we can from as many independent sources as possible to make a strong case. None of the present methods has been validated against an absolute measure of population. Under these circumstances two independent methods that show the same trends will always be more than twice as convincing and useful as one, even if one of the methods alone seems more "efficient" than the other.

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