

A SEARCH FOR STABILITY GRADIENTS IN NORTH AMERICAN BREEDING BIRD COMMUNITIES

BARRY R. NOON,¹ DEANNA K. DAWSON,² AND JOHN P. KELLY¹

¹*Department of Wildlife, Humboldt State University, Arcata, California 95521 USA, and*
²*U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, Maryland 20708 USA*

ABSTRACT.—To search for the existence of stability gradients in North American breeding land bird communities we operationally defined stability (after Järvinen 1979) as year-to-year persistence in species composition and distribution of species abundances. From the census data for 174 study plots we derived nine indices that estimate the annual variability of species composition, the species abundance distribution, diversity, and breeding density. The resulting matrix of study plot by stability indices was used to estimate the correlation structure of the stability indices. The correlation matrix was, in turn, subjected to a principal components analysis to derive synthetic gradients of variation. We then searched for patterns of variation in these stability gradients associated with either geographic location or habitat type. Three independent principal component axes reproduced most of the variation in the initial data and were interpreted as gradients of variation in species turnover, diversity, and breeding abundance. Thus, the annual stability of community structure apparently responds independently to species and abundance variation. Despite the clarity of the derived gradients, few patterns emerged when the plots were ordinated by either habitat or geographic location. In general, grasslands showed greater annual variation in diversity than forested habitats, and, for some habitats, northern communities were less stable than more southern communities. However, few of these patterns were very strong, and we interpret them cautiously. *Received 9 January 1984, accepted 2 August 1984.*

In this study we investigate annual patterns and variability in the structure of North American breeding bird communities. Specifically, we are interested in determining whether communities differ in their stability properties and whether observed differences can be associated with gross habitat type or geographic location. In general, we operationally consider a community stable if knowledge of its species composition and abundance distribution in year 1 enables us to accurately predict these same properties in year 2. The more accurate the prediction, the more stable the community is considered to be.

For a considerable period of time ecologists generally believed northern communities to be inherently less stable than more southern communities (e.g. MacArthur 1955, Slobodkin and Saunders 1969). This relationship between latitude and stability was believed to be indirect and partly a function of the underlying relationships between latitude and species diversity, and species diversity and stability (see review by Goodman 1975). The necessity of a causal relationship between diversity and stability has been largely refuted from a mathe-

matical perspective (May 1972), but the results from empirical studies have been equivocal or contradictory (McNaughton 1977, 1978). An additional factor believed to contribute to latitudinal differences in stability is a parallel gradient in seasonality. Northern communities should be composed of species populations that show larger annual fluctuations than their less seasonal, more southern counterparts. However, this contrast in seasonality between northern and southern latitudes also has been challenged (Leigh 1975), and apparently some low-latitude environments may be just as seasonal as high-latitude environments.

Despite a general consensus today that latitudinal gradients in stability and seasonality are weak at best, Järvinen (1979) recently has reported geographical gradients in stability of European breeding bird communities that are correlated with latitudinal differences in environmental predictability and seasonality. Employing data from study plots covering a latitudinal range of 19° (50°–69°N), Järvinen found north Scandinavian communities to be less stable than more southern communities. Järvinen's publication suggested to us that a similar

analysis of North American breeding bird communities would be of comparative interest and perhaps give some further insights into the apparent contradiction between empirical studies and mathematical theory.

In addition to a geographical analysis of North American breeding bird communities, we were interested in investigating the degree to which stability gradients are associated with habitat type. Recent reports from breeding bird community studies in structurally simple habitats suggest that these communities are highly unpredictable on an annual basis (Wiens and Rotenberry 1978, 1980, 1981; Rotenberry and Wiens 1980). This is in contrast to reports from forested habitats where the communities appear more stable on an annual basis (e.g. Ken-deigh 1946, Sanders 1970, Holmes and Sturges 1972, Winternitz 1976). Thus, our a priori expectation was that at least some habitat types could be discriminated on the basis of their stability properties, with stability positively related to increased complexity of the habitat structure, and possibly to species richness as well.

In our investigation the initial goal was to determine if it was possible to identify independent gradients of variation that would allow us to ordinate North American breeding bird communities on the basis of stability differences. Contingent upon identifying such gradients, our goals were (1) to give a biologically meaningful interpretation to the derived gradients, and (2) to determine if these gradients could be associated with either habitat type or geographic location. To derive these gradients of variation we used a variety of statistical models, primarily principal components analysis (PCA). Our data are derived from long-term bird censuses from 174 study areas in the United States and Canada. Our approach is empirical and exploratory—we are searching for any patterns that may be superimposed on the synthetic gradients of variation that we derive from a PCA of the annual census data.

MATERIALS AND METHODS

The data set.—The data set used in our analyses consists of breeding bird census reports from the United States and Canada. A large proportion of these censuses have been published in *American Birds* (formerly *Audubon Field Notes*), but we also extracted much census data from other literature sources and from unpublished accounts. (A complete listing of refer-

ences for the census data used in this study is available upon request.) Because of the great variability in methods used to study breeding bird populations, we established the following criteria for inclusion (cf. Järvinen 1979): 1) Only censuses of land bird communities were included. 2) The study period had to include at least 3 censuses within a 5-yr period, and at least 2 of these censuses had to have occurred in successive years. 3) The study plot had to be ≥ 9 ha in size. 4) The study plot should not have undergone any appreciable change in habitat during the course of the study. 5) Only censuses involving multiple visits and employing a method in which individual territories were mapped were included.

The data set consists of 174 study plots censused over 3–22 yr. The plots were distributed throughout the United States and Canada and covered a latitudinal range of 44° (27°–71°N) and a longitudinal range of 89° (68°–157°W; Fig. 1). The habitat of each study plot was classified into 1 of 10 general types on the basis of its dominant structural habitat characteristics. For the most part, these classifications follow habitat designations given in *American Birds* (see any recent issue listing Breeding Bird Census reports). Plot data derived from other sources were also classified into these categories. The types recognized were: (1) tundra; (2) desert, beach; (3) marsh, open bog, pond; (4) grassland, prairie, shrub-steppe (hereafter referred to as grassland); (5) mixed habitats (two or more distinct habitat types); (6) brush and scrub forest; (7) coniferous forest; (8) deciduous forest; (9) mixed deciduous-coniferous forest; and (10) urban, residential, cemetery. Additional data extracted for each plot were latitude, longitude, state or province, elevation, plot size, number of census years, and number of census hours (when available). Several of these variables acted as covariables in our analyses, and knowledge of them allowed us to statistically control for their influence on the stability indices and facilitated across-plot comparisons.

Stability indices.—In general we followed the operational definition of stability and the computational procedures for analysis of Järvinen (1979: 56). Starting with a census made in a bird community in a certain year, Järvinen considered "community X stabler than community Y if it is, on the basis of census results from X and Y, easier to predict the following properties of X next season than the same properties of Y": (1) total number of pairs on the plot (N), (2) species richness (number of breeding species = S), (3) species diversity (H'), (4) the evenness component of H' (J), (5) species composition, and (6) relative abundance of species present.

To estimate community stability, we calculated several indices for each study plot. The characteristics of several of these indices are discussed in detail by Järvinen (1979), and we will not elaborate on them here. We have added some additional indices, primarily to estimate the predictability of species com-

DISTRIBUTION OF CENSUS PLOTS BY STATE OR PROVINCE

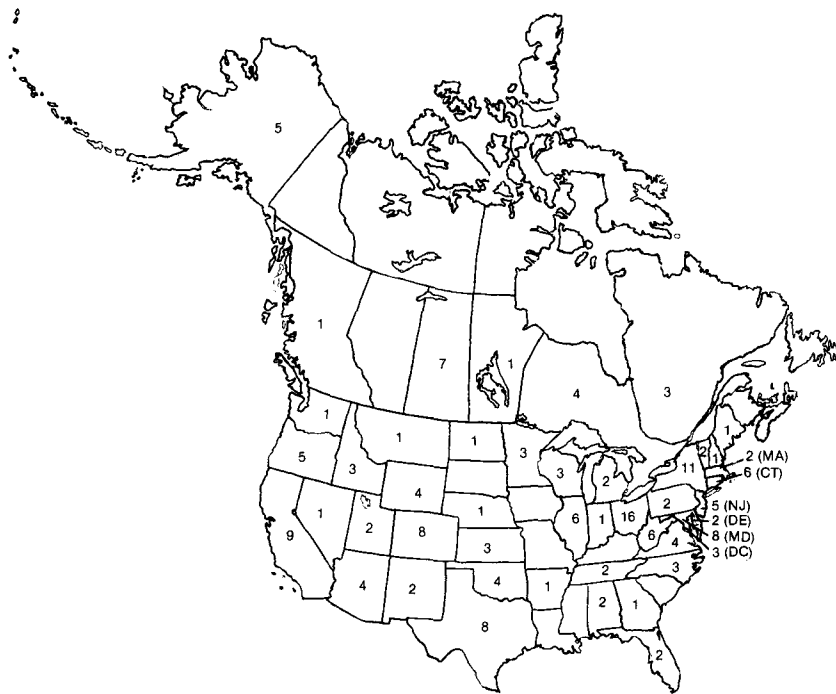


Fig. 1. Geographical distribution of the breeding bird census plots by state or province.

position and relative abundance patterns. The indices used in this study are indicated in Table 1.

Indices 5–9 (Table 1) are calculated only on census data from successive years because they vary as a function of census interval (see Järvinen and Väisänen 1976, Diamond and May 1977). This approach was necessary to assure comparability of across-plot comparisons. For index 3, $CV(H')$, we initially used the correction for H' as suggested by Hutcheson (1970). However, we found that H' -corrected values gave unrealistic diversity indices for study plots with few species, low overall diversity, and at least one very rare species.

Stability indices were calculated separately for each of the 174 plots, making the individual study plot the basic unit of the analysis. Indices were calculated using the actual number of territories reported for each study plot. Census results were not extrapolated to a constant area because of the problems inherent in this process (Verner 1981) and because we performed no direct between-plot comparisons based on the original data. If fractional territories were reported, we only considered species with ≥ 0.1 territory when calculating the indices T and $P(E)$. Analyses were run with larger cutoff values, but these had no effect on the final results. By including fractional territories, the number of colonizations and extinc-

tions may be overestimated. However, our purpose here is not to accurately estimate the true turnover values but rather to ordinate plots according to their relative turnover values.

All species included in the original censuses were retained for our analyses. We examined the effect of eliminating raptor and waterfowl species from the calculations, and these changes had no effect on the final results.

Many of the stability indices were not normally distributed, largely because of outlying points. However, in no case was the deviation from normality excessive. Rather than adjusting for outliers by transformation, we investigated their influence on the multivariate analyses directly. Outliers were identified by differences in the Mahalanobis distances between each plot and the grand centroid of all plots in factor space relative to observation space. The inclusion or exclusion of outliers identified by this method had little effect on the plot ordinations or on our final interpretations.

It is clear that few of the stability indices vary independently from any of the other indices (see Järvinen 1979 and further discussion below). However, prior to any formal analyses, the indices suggest a logical partitioning of the matrix X into subsets that are sensitive to different sources of variation in avian

TABLE I. Indices used in the stability analysis.

Index number and symbol	Description
(1) $CV(N)$	Coefficient of variation of breeding abundance, where $CV(N) = (\sigma/m)$, σ = standard deviation of N , and m = mean of N
(2) $CV(S)$	Coefficient of variation of species richness
(3) $CV(H')$	Coefficient of variation of species diversity, where $H' = -\sum p_i \ln p_i$, $p_i = n_i/N$, and n_i = the number of individuals in the i th species
(4) $CV(J)$	Coefficient of variation of the evenness component of H' , where $J = H'/\ln S$
(5) \bar{T}	Average species turnover, measured as the arithmetic average of the index (see Lynch and Whitcomb 1977): $T = (I + E)/(I + E + S_c)$, where I and E are the number of species that have immigrated and gone extinct, respectively, between two successive annual censuses and S_c is the number of species in common between two successive censuses
(6) \bar{CC}	Average coefficient of community, measured as the arithmetic average of the index (Sorensen 1948): $CC = 2S_c/(S_1 + S_2)$, where S_c is as defined above, S_1 = the estimated number of species in census 1, and S_2 = the estimated number of species in census 2
(7) \bar{rD}	Average change in community composition, measured as the arithmetic average of the index (Järvinen and Väisänen 1976): $rD = 100(\exp DIV_{diff} - 1)$, where $DIV_{diff} = H'_{1+2} - 0.5 \cdot (H'_1 + H'_2)$. H'_1 and H'_2 are the diversity indices for the bird community in census periods 1 and 2, and H'_{1+2} is the diversity index derived from pooling the census results across two successive years
(8) \bar{BC}	Average Bray-Curtis similarity coefficient (Bray and Curtis 1957) calculated as the arithmetic average between two successive censuses as: $BC = 1 - [\sum n_{i1}^* - n_{i2}^* / \sum (n_{i1}^* + n_{i2}^*)]$ where n_{i1} and n_{i2} are the number of territories of the i th species in censuses 1 and 2, respectively, and $n_{i1}^* = \ln(n_{i1} + 1)$ and $n_{i2}^* = \ln(n_{i2} + 1)$. (See Huhta 1979 for the rationale behind this transformation.)
(9) $\bar{P(E)}$	Average annual extinction probability, calculated as the arithmetic average between two censuses as: $P(E) = 1 - (S_2/S_1)$

community structure. The indices T , $P(E)$, and CC reflect changes in species composition between successive censuses and thus are indicative of species compositional stability. The indices $CV(S)$, $CV(J)$, and $CV(H')$ are sensitive to changes in the distribution of species abundances and species density, but, in theory, can be independent of changes in species composition. These indices thus reflect diversity variation. Indices rD and BC are sensitive to changes in both species composition and the abundance distribution. Unfortunately, the relative influence of these two sources of variation is confounded in these indices. In addition, rD and BC differ from each other in being sensitive to shifts in relative and absolute abundance, respectively. These indices can be interpreted as reflecting overall compositional stability in the breeding bird community. The final index, $CV(N)$, is sensitive to changes in overall breeding abundance and shifts in the abundance distribution and thus reflects annual variation in the number of breeding birds.

Univariate statistical analyses.—Means and standard deviations were calculated, by habitat, for each of the unadjusted stability indices and for \bar{S} , \bar{N} , and plot

size. The abundance of breeding birds is a direct function of area and was controlled by standardizing average abundances to 20 ha, the overall average plot size. The variable S is a function of plot size up to some asymptotic limit that probably varies by habitat type (James and Rathbun 1981). However, estimates of \bar{S} were not adjusted for differences in plot size because they did not covary (see Discussion).

Tests of the null hypothesis of no difference in the means, by habitat, for each stability index and for \bar{S} and \bar{N} were conducted using Welch's ANOVA model (Brown and Forsythe 1974b), which does not assume homogeneity of group variances. Pairwise contrasts were based on Bonferroni confidence intervals and were calculated only after a significant overall ANOVA was found. Separate ANOVA's for each variable are not strictly valid because the variables are not all independent. We calculated them for heuristic purposes only and caution the reader that faulty inferences can be made from such comparisons. We employed correlation models frequently in our analyses. In all cases we computed Pearson product-moment correlation coefficients (Sokal and Rohlf 1981) on untransformed data. Correlation coefficients were

calculated only after examining bivariate scattergrams and assuring ourselves of the absence of nonlinear relationships.

Multivariate statistical analyses.—In practice the stability indices do not vary independently of each other. Therefore, we focused on synthetic gradients of variation in the stability matrix X by analyzing the correlation structure of X with principal components analysis (PCA). After initial extraction of the principal components, we rotate the eigenvectors (varimax rotation algorithm) to simplify the pattern of factor loadings and to facilitate interpretation. We are ultimately interested in giving these synthetic gradients a biological interpretation by incorporating our understanding of what the indices measure with their correlation to each component.

We considered the factor scores, partitioned by habitat, separately for each factor by ANOVA. In all cases we tested for equality of the variances by Levene's test (Brown and Forsythe 1974a) and found significant heterogeneity. As a result, we used the Welch ANOVA model to test for differences in the habitat-group means along each factor. When a significant overall ANOVA was found, we tested all possible pairwise combinations of means after adjusting for multiple comparisons by the Bonferroni method and maintaining an experimental error rate at $\alpha = 0.05$.

To clarify how individual habitat types were originated along these synthetic gradients, we computed factor scores for each of the plots, partitioned the scores by habitat, and examined them separately for each factor by ANOVA. We excluded three habitat types from further consideration because of small sample size.

Sample size and covariance problems with similarity indices.—Järvinen (1979) discussed some of the statistical difficulties encountered when similarity indices are applied to breeding bird data. In addition, there are unavoidable sampling correlations for several of our annually calculated indices. For example, successive calculations of the CC index both contain the value S_2 in the denominator. Thus, for both biological and statistical reasons some degree of correlation between these indices is inherent in our investigation. We are confident that any biases that are introduced are consistent across plots, and of small magnitude.

A more serious problem has been discussed by Wolda (1981), who showed that several similarity indices are affected by both sample size and diversity of the samples being compared. Wolda's results indicate that the BC index has higher expected maximum values for comparisons of large (greater S and N) than of small communities, and higher values for comparisons of communities of similar size. The CC index is similarly affected, but to a lesser degree.

To investigate how our stability indices were affected by sample size differences across study plots,

we examined the functional relationship between the mean value of each index and \bar{S} and \bar{N} with regression and correlation analyses. Untransformed models as well as transformations of the dependent variable and polynomial functions of the independent variable were employed to maximize fit to the data. For significant models, the effect of \bar{S} or \bar{N} was removed from the index by partial correlation analysis. In these cases only the residuals were retained for subsequent analyses.

The coefficient of variation indices were not adjusted for \bar{S} and \bar{N} because the CV statistic is already normalized for differences between the means of different samples (Lewontin 1966, Sokal and Braumann 1980, Sokal and Rohlf 1981). To illustrate, if we assume that random variables X and Y measure species richness in two habitat types and that the distribution of these two variables are identical except that Y is k times as large as X , then we have the following relationship among the coefficients of variation for these variables (see Lewontin 1966):

$$\text{if } Y = kX, \text{ then } \bar{Y} = k\bar{X} \text{ and} \\ S_y^2 = k^2 S_x^2, \text{ or } S_y = kS_x.$$

The coefficient of variation of Y is then:

$$CV(Y) = S_y/\bar{Y} = kS_x/k\bar{X} = CV(X).$$

Relationship of the stability indices to other covariables.—The relationships between the mean value of each index and the mean values of several covariables (latitude, longitude, elevation, plot size, number of census years) were examined by correlation analyses. Because we wished to focus on patterns of variation dependent as clearly as possible on differences in habitat or geographic location, we removed the linear effects of the covariables from the indices by partial correlation analysis before performing the multivariate analyses. The stability indices were adjusted for all covariables for the habitat analyses, and all covariables except latitude and longitude for the geographic analyses.

Some of the stability indices may be sensitive to differences in sampling effort. To investigate this effect we developed an index of sampling effort defined as the mean number of census hours/plot size (h/ha). We examined the correlation between this index and all of the stability indices.

Estimating the proportion of long-distance migrants.—We arbitrarily defined a long-distance migrant (LDM) as a species that travels $\geq 1,600$ km from its breeding ground to the northern extent of its wintering area. We assumed that mortality due to migration was linearly related to distance traveled and independent of point of departure. Minimum migration distances, computed as the distance from the study plot to the northern edge of the species winter range, were estimated by making reference to range maps in Peter-

TABLE 2. Correlation between each stability index and \bar{S} and \bar{N} .^a

Index	\bar{S}	\bar{N} ^b
CV(N)	-0.317**	-0.060
CV(S)	-0.486**	-0.128
CV(H')	-0.419**	-0.179*
CV(J)	-0.524**	-0.029
\bar{T}	-0.277**	-0.274**
\overline{CC}	0.256**	0.273**
\overline{rD}	-0.181*	-0.162*
\overline{BC}	0.191*	0.267**
$\overline{P(E)}$	-0.122	-0.221**

^a * $P \leq 0.05$; ** $P \leq 0.01$.

^b Standardized to an area of 20 ha.

son (1980) and Robbins et al. (1983). For each plot we determined the average proportion of LDM and investigated the relationship between this variable and each of the stability indices by correlation analysis. In addition, the null hypothesis of no difference in the mean proportion of LDM, by habitat, was tested with the Welch ANOVA model (see earlier discussion). In order to better meet the assumptions of the ANOVA model, the proportion LDM was transformed with the arcsine function prior to conducting the analysis.

RESULTS

Statistical aspects of the stability indices.—Wolda (1981) showed the indices BC and CC to be rather strongly dependent upon the sample size of the communities being compared over the range of 100–5,000 individuals. However, when calculating mean values within plots our estimates of these indices were insensitive to this problem. This occurs because the samples we compared for similarity were from the same plots in successive years and, consequently, did

not differ extensively in number of individuals or in diversity.

However, when examining across-plot comparisons, significant, but weak, relationships were found for both indices when regressed on \bar{S} and \bar{N} (Table 2). The maximum R^2 was <12% for any simple linear regression model. Transformations of the dependent variable to achieve a better model were judged less satisfactory than nontransformed models because of smaller R^2 values. Even a third-order polynomial of the independent variable for the BC index only increased the R^2 value from 12% to 16%. When the linear effects of \bar{S} and \bar{N} were removed from the indices BC and CC to correct for the effects of sample size difference, the residuals showed no linear trends when regressed back on \bar{S} and \bar{N} .

The remaining stability indices all had significant correlations with either \bar{S} , \bar{N} , or both (Table 2). The correlations were particularly strong for the coefficient of variation indices. We did not remove the linear effects of \bar{S} and \bar{N} from these indices because we had no evidence that these relationships were statistical artifacts as opposed to true biological relationships (see below).

Relationship of the stability indices with other covariables.—We were unable to adjust the indices for differences in sampling effort because these data were not available for all plots. However, we were able to compute sampling effort for 131 of the plots, and the maximum correlation between this variable and any of the indices was <0.150 (Table 3). Thus, there is no evidence that differences in sampling intensity biased any of our results. Of the 45 possible bivariate correlations between the re-

TABLE 3. Correlations between the stability indices and the covariables.^a

Covari- able	Stability index								
	CV(N)	CV(S)	CV(H')	CV(J)	\bar{T}	\overline{CC}	\overline{rD}	\overline{BC}	$\overline{P(E)}$
Latitude	0.058	0.128	0.055	0.003	0.210*	-0.205*	0.098	-0.160*	0.195*
Longitude	0.008	0.179*	0.113	0.177*	0.125	-0.122	-0.002	0.025	0.025
Elevation	0.071	0.235*	0.180*	0.117	0.170*	-0.177*	0.146	-0.079	0.053
Plot size	0.042	0.034	0.057	-0.012	-0.013	0.017	-0.169*	0.086	-0.072
Number of years	0.059	0.025	-0.086	-0.105	-0.132	0.138	-0.169*	0.170*	-0.083
Sampling effort ^b	-0.117	0.072	0.126	-0.019	0.146	-0.148	0.052	-0.065	0.126

^a * $P \leq 0.05$; ** $P \leq 0.01$.

^b Based on a sample size of $n = 131$.

TABLE 4. Means (SD) for each stability index and for \bar{S} , \bar{N} , plot size, and the proportion of long-distance migrants (LDM) by habitat type.

Index	Habitat type						
	Tundra (n = 5)	Grassland (n = 30)	Mixed (n = 9)	Scrub (n = 15)	Conifer (n = 24)	Mixed D-C (n = 22)	Deciduous (n = 65)
CV(N)	0.232 (0.074)	0.262 (0.184)	0.170 (0.105)	0.154 (0.068)	0.216 (0.118)	0.139 (0.082)	0.163 (0.103)
CV(S)	0.175 (0.048)	0.184 (0.109)	0.118 (0.054)	0.185 (0.137)	0.162 (0.106)	0.121 (0.077)	0.104 (0.062)
CV(H')	0.062 (0.022)	0.112 (0.088)	0.031 (0.020)	0.121 (0.193)	0.075 (0.067)	0.049 (0.033)	0.042 (0.026)
CV(J)	0.044 (0.027)	0.079 (0.051)	0.026 (0.009)	0.070 (0.066)	0.033 (0.028)	0.029 (0.023)	0.032 (0.020)
\bar{T}	0.332 (0.055)	0.269 (0.144)	0.233 (0.056)	0.322 (0.103)	0.293 (0.092)	0.268 (0.074)	0.263 (0.091)
\bar{CC}	0.795 (0.039)	0.831 (0.102)	0.864 (0.038)	0.797 (0.076)	0.822 (0.067)	0.842 (0.049)	0.844 (0.064)
\bar{rD}	7.69 (3.72)	6.59 (5.13)	5.78 (1.76)	7.47 (4.81)	9.04 (3.95)	6.97 (3.34)	6.21 (3.82)
\bar{BC}	0.788 (0.040)	0.820 (0.084)	0.833 (0.030)	0.809 (0.062)	0.792 (0.057)	0.811 (0.059)	0.822 (0.056)
$\bar{P(E)}$	0.189 (0.058)	0.156 (0.100)	0.145 (0.060)	0.170 (0.105)	0.140 (0.062)	0.154 (0.050)	0.153 (0.068)
\bar{S}	14.9 (2.0)	7.3 (5.2)	40.1 (9.0)	14.4 (8.5)	18.3 (8.4)	25.3 (6.0)	27.1 (8.7)
\bar{N}^a	27.0 (8.9)	117.0 (217.0)	159.9 (65.9)	96.8 (100.9)	125.0 (102.9)	112.0 (57.8)	155.5 (144.6)
Plot size	60.8 (40.7)	17.3 (9.2)	21.0 (10.5)	18.7 (10.9)	14.9 (6.3)	13.4 (4.4)	17.0 (9.7)
LDM	0.823 (0.069)	0.179 (0.182)	0.361 (0.147)	0.167 (0.151)	0.259 (0.151)	0.396 (0.119)	0.409 (0.136)

^a Standardized to a plot size of 20 ha.

maintaining covariables and the 9 stability indices, 13 were significant at $P < 0.05$. Only one stability index (rD) was significantly correlated with area ($r = -0.169$, $P < 0.05$).

Geographic and habitat trends in plot size.—Inferences drawn from the multivariate analyses may be influenced by geographic or habitat trends in plot size. The correlations between plot size and latitude and longitude were 0.413 ($P < 0.01$) and 0.301 ($P < 0.01$). However, when tundra plots were removed from the analysis, the correlations became nonsignificant ($r_{\text{lat., plot size}} = -0.022$ and $r_{\text{long., plot size}} = 0.002$). This dramatic change is a result of the large plot size and extreme geographic location of the tundra study areas. They acted as outliers in the analysis and had a disproportionate effect on the magnitude of the correlation coefficient. Tundra plots were not considered in our geographical analyses (see below).

When the data were partitioned by habitat

there was only one significant relationship between geographic position and plot size (scrub forest plots are significantly correlated with longitude, $r = 0.545$). However, the linear effects of both plot size and geographic position were removed from all indices prior to performing the habitat PCA. We thus conclude that our results were not confounded by either geographic or habitat trends in plot size.

Univariate analyses of the stability indices by habitat.—Means and standard deviations, by habitat, for each of the stability indices and for \bar{S} , \bar{N} , and plot size are reported in Table 4. We report plot size in this table because of the possible bias this may give to comparisons of stability variables and \bar{S} across plots (see Discussion).

The results of significant pairwise comparisons of habitat means for each stability index and \bar{S} and \bar{N} are shown in Table 5. A significant ANOVA was detected for \bar{CC} , but there

TABLE 5. ANOVA results from all possible pairwise comparisons of habitat means for each stability index, \bar{S} , \bar{N} , and the proportion of long-distance migrant species (LDM). Tests are based on Bonferroni confidence intervals and separate variances. Only variables with both significant ANOVA's and a posteriori comparisons are tabulated.^a

Groups compared	CV(N)	CV(S)	CV(H')	CV(J)	\bar{S}	\bar{N}^b	LDM
Tundra vs. grassland					+		+
Tundra vs. mixed					-	-	+
Tundra vs. scrub							+
Tundra vs. conifer						-	+
Tundra vs. mixed D-C					-	-	+
Tundra vs. deciduous					-	-	+
Grassland vs. mixed			+	+	-		
Grassland vs. scrub							
Grassland vs. conifer				+	-		
Grassland vs. mixed D-C	+		+	+	-		-
Grassland vs. deciduous		+	+	+	-		-
Mixed vs. scrub					+		
Mixed vs. conifer					+		
Mixed vs. mixed D-C					+		
Mixed vs. deciduous					+		
Scrub vs. conifer							
Scrub vs. mixed D-C					-		-
Scrub vs. deciduous					-		-
Conifer vs. mixed D-C							-
Conifer vs. deciduous					-		-
Mixed D-C vs. deciduous							

^a "+" indicates that the first group listed had a significantly larger mean value; "-" indicates that the second group had a larger mean value.

^b Standardized to an area of 20 ha.

were no significant a posteriori comparisons. The most striking result to arise from these multiple contrasts was that of 189 pairwise comparisons of the indices only 8 were significant. The significant differences suggest that grasslands differ from other habitat types by showing greater annual variation in species diversity, richness, and evenness. Tundra habitats differ from all the others, except grassland and scrub forest habitats, by having significantly lower breeding densities. The most extensive differences between habitats occurred

in their average species-richness values. Grassland habitats have significantly lower \bar{S} values than all other habitat types, and mixed habitats significantly higher values. In addition, deciduous forest habitats have significantly larger \bar{S} values than either scrub or coniferous forest habitats.

A search for habitat gradients (PCA I).—The correlation matrix of residuals used as input to the PCA for habitat effects is presented in Table 6. This matrix can be partitioned into three subsets of highly correlated variables: (1) T^* , CC^* ,

TABLE 6. Correlations of residual stability indices—habitat analysis.^a

	CV(S)*	CV(N)*	CV(H')*	CV(J)*	\bar{T}^*	\overline{CC}^*	\overline{rD}^*	\overline{BC}^*
CV(N)*	0.259							
CV(H')*	0.743	0.275						
CV(J)*	0.467	0.256	0.658					
\bar{T}^*	0.432	0.019	0.255	0.139				
\overline{CC}^*	-0.425	-0.054	-0.251	-0.166	-0.960			
\overline{rD}^*	0.329	0.350	0.269	0.002	0.658	-0.660		
\overline{BC}^*	-0.299	-0.375	-0.189	-0.022	-0.700	0.746	-0.900	
$\overline{P(E)}^*$	-0.220	0.024	0.105	0.010	0.836	-0.814	0.580	-0.603

^a * = residual stability indices with the linear effects of all covariables removed.

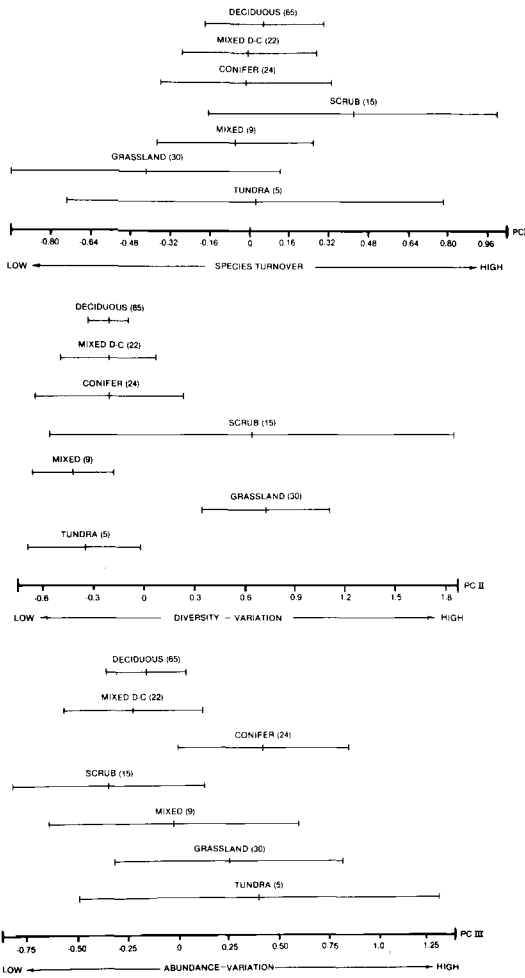


Fig. 2. Ordination of the breeding bird census plots along the first three principal components, partitioned by habitat type. For each habitat type the sample size is given in parentheses, and the mean and 95% confidence interval are illustrated. Axis PC I represents a gradient in species turnover, axis PC II represents a gradient in diversity variation, and axis PC III represents a gradient in abundance variation.

rD^* , BC^* , and $P(E)^*$; (2) $CV(S)^*$, $CV(H)^*$, and $CV(J)^*$; and (3) $CV(N)^*$. These subsets are largely those that one might expect a priori to measure similar aspects of stability.

The percent total variation in the system accounted for by the three factors is >84% (Table 7). Because of the clarity of the factor loadings, we feel we can give meaningful interpretations to the gradients. We interpret factor I (accounting for 43% of the variation) as a species- and

TABLE 7. Rotated factor loadings—habitat analysis. Dominant factor loadings are in boldface.

Index ^a	Factor		
	I	II	III
T^*	0.949	0.205	-0.045
\overline{CC}^*	-0.943	-0.207	0.001
$\overline{P(E)}^*$	0.895	0.017	-0.053
\overline{BC}^*	-0.789	-0.013	-0.529
rD^*	0.749	0.046	0.537
$CV(H)^*$	0.112	0.901	0.154
$CV(J)^*$	-0.047	0.846	0.036
$CV(S)^*$	0.298	0.798	0.124
$CV(N)^*$	-0.034	0.224	0.901
% variance	43.0	25.6	15.8
Cumulative variance	43.0	68.6	84.4

^a * = residual stability indices with the linear effects of all covariables removed.

individual-turnover gradient, factor II (25.6%) as a diversity-variation gradient, and factor III (15.8%) as an abundance-variation gradient. Factor I is subsequently referred to as a species-turnover gradient, reflecting its dominant factor loadings. Factor III is dominated by $CV(N)$ but also has high loadings for indices \overline{BC} and rD , which are both influenced by changes in the distribution of abundance across species. In fact, Järvinen (1979) referred to rD as an index of "average individual turnover."

Graphical display of the mean and variance of each factor by habitat type gives a visual impression of the dispersion of plots along each gradient (Fig. 2). Testing the differences among habitat types separately for each factor by ANOVA is premised on the statistical independence of the factors. However, independence is assured only across the entire sample and may not hold across factors within a given habitat type. We examined this effect and found no significant correlations. As a consequence of an almost complete independence across factors, we proceed with a separate ANOVA for each.

The ordination of plots by habitat type along the species-turnover gradient (factor I; Fig. 2, top) shows no clear pattern. Each habitat type seems to be characterized by extensive variability rather than a strong central tendency. Grassland plots on the average showed the lowest species turnover, scrub forest the highest, with the remaining groups being inter-

TABLE 8. Rotated factor loadings—geographic analysis. Dominant factor loadings are in boldface.

Index ^a	Factor		
	I	II	III
\bar{T}^*	0.945	0.214	-0.045
$\bar{C}\bar{C}^*$	-0.941	-0.184	0.013
$\bar{P}(E)^*$	0.897	0.028	-0.047
$\bar{B}\bar{C}^*$	-0.794	0.009	-0.512
$\bar{r}\bar{D}^*$	0.764	0.048	0.517
CV(H') [*]	0.114	0.897	0.160
CV(J) [*]	-0.063	0.848	0.028
CV(S) [*]	0.315	0.795	0.121
CV(N) [*]	-0.015	0.220	0.908
% variance	43.5	25.4	15.5
Cumulative variance	43.5	68.9	84.4

^a * = residual stability indices with the linear effects of all covariables, except latitude and longitude, removed.

mediate and almost coincident. There were no significant differences among group means on factor I ($F_{6,34} = 0.86, P = 0.546$). The relative positions of some habitat groups along this gradient were substantially affected by partialling out the effects of \bar{S} and \bar{N} from the indices $\bar{B}\bar{C}$ and $\bar{C}\bar{C}$. For example, the grassland group shifted towards lower turnover and the deciduous group towards higher turnover when residuals were used.

A clearer pattern of ordination occurred along factor II (Fig. 2, middle), where an overall significant difference is evident in the position of habitat means ($F_{6,34} = 5.07, P = 0.0008$). Pairwise, a posteriori tests of the equality of habitat means indicated that grassland plots showed significantly higher ($P < 0.005$) diversity variation than tundra, mixed, coniferous, mixed deciduous-coniferous, and deciduous plots. No other comparisons of habitat types showed significant differences.

Factor III suggests some pattern to the relationship between habitat type and abundance stability (Fig. 2, bottom), but no overall significant differences among means were found ($F_{6,32} = 1.91, P = 0.11$). Very slight overlap of the 95% confidence intervals of the coniferous and deciduous forest plots suggests a significant difference, but this difference was obviated by holding the experimental error at $\alpha = 0.05$ ($t = -2.56, P = 0.015$; critical Bonferroni $P = 0.0024$). A slightly larger sample size may have shown that coniferous forests experience

TABLE 9. The linear correlation of each factor with latitude and longitude, overall and by habitat.^a

Habitat	Factor	Correlated with:	
		Latitude	Longitude
Overall (n = 174)	I	0.217**	-0.002
	II	0.051	0.094
	III	0.026	-0.073
Grassland (n = 30)	I	0.150	-0.170
	II	-0.108	-0.093
	III	-0.198	-0.483**
Mixed (n = 9)	I	-0.005	0.287
	II	0.383	-0.208
	III	-0.124	0.104
Scrub (n = 15)	I	0.548*	0.033
	II	-0.003	0.228
	III	-0.266	-0.265
Conifer (n = 24)	I	0.440*	-0.360
	II	0.470*	-0.314
	III	0.061	-0.259
Mixed D-C (n = 22)	I	0.458*	-0.376
	II	-0.356	-0.235
	III	-0.268	-0.281
Deciduous (n = 65)	I	0.013	0.191
	II	0.204	-0.002
	III	0.073	-0.112

^a * $P \leq 0.05$; ** $P \leq 0.01$.

greater abundance variation among years than other forest types.

A search for geographical gradients (PCA II).—The rotated factor loadings resulting from the analysis of the residual correlation matrix controlling for all covariables except latitude and longitude are shown in Table 8. More than 84% of the total variation in the original data is explained by the first three factors. Even though 6 of the 18 correlations between latitude and longitude and the 9 stability indices were significant (Table 3), none were large (maximum $r = 0.210$). As a result, the residual correlation matrix, the derived factor loadings, and our overall interpretation of the factors as gradients in species turnover, diversity variation, and abundance variation are basically unchanged from the previous analysis.

We calculated the linear correlation of each factor with latitude and longitude (Table 9). Over all plots the only significant correlation observed was between factor I and latitude ($r = 0.217, P < 0.01$), suggesting that species and individual turnover generally increased from south to north. None of the other correlations suggested even a slight relationship between community stability and geographical location.

TABLE 10. The linear correlation of \bar{S} and \bar{N} ^a with latitude and longitude, overall and by habitat.^b

Habitat	Variable	Correlated with:	
		Latitude	Longitude
Overall (n = 174)	\bar{S}	-0.155*	-0.275**
	\bar{N}	-0.262**	-0.016
Grassland (n = 30)	\bar{S}	0.078	0.044
	\bar{N}	-0.299	0.030
Mixed (n = 9)	\bar{S}	0.237	-0.312
	\bar{N}	0.518	-0.132
Scrub (n = 15)	\bar{S}	-0.057	-0.180
	\bar{N}	-0.021	-0.058
Conifer (n = 24)	\bar{S}	-0.375	0.234
	\bar{N}	-0.418*	0.346
Mixed D-C (n = 22)	\bar{S}	0.270	0.266
	\bar{N}	-0.287	0.398
Deciduous (n = 65)	\bar{S}	-0.122	-0.218
	\bar{N}	-0.316*	0.179

^a Standardized to a plot size of 20 ha.

^b * $P \leq 0.05$; ** $P \leq 0.01$.

Because significant relationships between community stability gradients and habitat type may be masked by considering only the entire sample, we partitioned the analysis by habitat type (Table 9). (Tundra study plots were omitted because of little variation in geographic location.) The significant results are as follows: (1) grasslands: density variation decreases from east to west; (2) scrub forests: species turnover increases from south to north; (3) coniferous forests: species turnover and diversity variation increase from south to north; and (4) mixed deciduous-coniferous forests: species turnover increases from south to north. Overall, even the statistically significant results offer little support for any strong relationship between geographical position and community stability.

Geographical gradients in species richness and abundance.—We examined our data set for geographic gradients in species richness and breeding abundance by computing the correlation between \bar{S} and \bar{N} and latitude and longitude. Over all plots there were three significant correlations (Table 10). The strongest correlation was the negative relationship between \bar{S} and longitude suggesting that mean species richness decreased from east to west. In addition, \bar{S} and \bar{N} generally decreased from south to north. These results generally support the longitudinal relationships reported by Short (1979) but contrast somewhat with his latitu-

TABLE 11. The linear correlation (and partial correlations) of the average proportion of long-distance migrants with each of the stability indices.^a

	CV(N)	CV(S)	CV(H')	CV(J)	\bar{T}	CC	rD	BC	P(E)
Proportion of long-distance migrants	-0.120 (-0.070)	-0.221** (-0.010)	-0.274** (-0.114)	-0.195* (0.012)	-0.062 (0.049)	0.086 (0.063)	-0.065 (-0.086)	0.018 (-0.133)	-0.023 (0.010)

^a * $P \leq 0.05$; ** $P \leq 0.01$.

dinal patterns. However, all of these associations are weak, and we are reluctant to make further inferences from these statistics.

We also partitioned the data by habitat type and recomputed the correlations between \bar{S} and \bar{N} and latitude and longitude (Table 10). Only two significant correlations resulted: mean breeding density in coniferous forests and in deciduous forests decreased from south to north. None of the habitat correlations was particularly strong, possibly because \bar{S} and \bar{N} are not monotonically related to either latitude or longitude for most habitat types.

Long-distance migrants as a stabilizing influence.—The habitat types differed extensively in their average proportion of LDM (Table 5; $F_{6,34} = 43.73$, $P < 0.0001$). A posteriori comparisons showed tundra habitats to have a significantly greater proportion than other habitat types, and grassland, scrub, and coniferous forests significantly smaller proportions than mixed deciduous-coniferous and deciduous forests.

The correlations between the proportion of LDM and the stability indices were significant for 3 of the 4 coefficient of variation indices (Table 11). However, for all of the indices the sign of the correlation coefficient suggested that the greater the proportion of LDM among breeding species, the more stable the communities are from year to year. Separate tests of significance of the correlations are not valid because of a high degree of covariation among some of the indices. To address this problem we computed partial correlations, controlling in each case for the linear effects of all the other indices (Table 11). No significant partial correlations were found suggesting a complex relationship among the proportion of LDM and the stability indices. A PCA including the proportion of LDM along with the nine indices showed this variable to load most heavily on the diversity-variation gradient. The sign on the loading suggested that species that are seasonal residents, and migrate long distances to their wintering grounds, may buffer these communities somewhat from extensive annual diversity variation.

DISCUSSION

The overriding impression from our analyses was that few patterns of breeding bird community stability are associated with either habitat or geographical location. We did not expect such an absence of pattern. Published accounts

of relationships between geographic location and community stability strongly suggest that northern communities should be less stable than more southern communities (e.g. Fischer 1960; Pianka 1966; Järvinen 1979, 1980). We also were surprised by the lack of correlation between our derived stability gradients and habitat type. From our own experiences with breeding bird communities, primarily in eastern deciduous and coniferous forests, we expected sharp contrasts at least between these habitat types and grassland plots. Overall, our analyses from both habitat and geographical perspectives are most noteworthy for the lack of pattern observed. Our geographical analysis suggested a positive but weak relationship between species turnover rate and latitude. We are uncertain why our results are not in greater accord with those of Järvinen (1979).

Habitat analysis.—In addition to our own research experiences that lead us to suspect differences in stability across habitat types, we cite the obvious contrast between experimental studies of stability following perturbation in eastern forests (Hensley and Cope 1951, Stewart and Aldrich 1951, Noon and Robbins 1983) and recent reports of high annual variability in breeding bird community structure in grassland and shrub-steppe habitats influenced only by climatic variability (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981). Admittedly, the former studies largely document within-season stability. However, in the eastern deciduous forest, stability to a direct perturbation of species populations was apparent both within and across years (Noon and Robbins 1983). This contrast in pattern suggests that the bird communities of these habitat types may actually differ in their stability properties. However, on the basis of a much larger sample, the only significant difference observed between grassland and forested habitats was in relation to annual diversity variation. The relative position of the habitat types along a gradient of diversity variation (factor II; Fig. 2, middle) showed grasslands to be more variable in this dimension.

The only other pattern that we observed was the difference in degree of annual abundance variation among forested habitats. Though not significant, the data suggest that coniferous forests show greater abundance variation than other forest types. Järvinen (1980) reports a similar pattern for northern European bird communities.

What most characterized the ordination of plots by habitat type along the three stability gradients was the extensive variability that occurred within a habitat type. Indeed, with a nonrandom selection of study areas across habitat types, it would be possible to reject almost any hypothesis of no difference in stability. However, with large sample sizes any such conclusions that may arise from smaller-scale analyses quickly disappear. Our results suggest that it is impossible to make general statements such as "grassland breeding bird communities are inherently less stable than those of eastern deciduous forests." Järvinen (1980) also observed that geographic location was of greater importance in determining community stability patterns than habitat.

Given this conclusion, we can suggest explanations for the lack of pattern in community stability across habitat types. One possibility is that much of the variability within a plot is a result of regional changes in land use that affect local populations. This effect may be particularly pronounced in the eastern deciduous forest biome where habitat fragmentation has been severe and apparently has greatly increased avian turnover rates (Lynch and Whitcomb 1977, Whitcomb et al. 1981; but see McCoy 1982). We attempted to minimize such effects by only including plots that have not undergone appreciable habitat change during the period of study. However, it was impossible to control for changes that may have occurred beyond plot boundaries.

Another possibility is that our habitat classifications were too broad, and the heterogeneity that this introduced masked any true habitat differences. However, a compromise was essential when allocating plots to habitat types. Too fine a partitioning would have reduced group sizes, decreased the power of statistical tests, and lowered the precision of estimated mean stability metrics.

The problem of the scale at which stability and its variation have been estimated may contribute to the lack of pattern. Locally derived point estimates of annual stability in community structure may show high variability when compared across plots within a habitat category. This sampling problem arises because we may be attempting to make inferences about community properties based on sampling units too small to reflect the scale at which the pro-

cesses are occurring (see Wiens 1981, Connell and Sousa 1983).

Total diversity, and its variation, may also be increased by including plots from different geographic regions in a common habitat group. If patterns of variation were generally clouded by collapsing geographically distinct study plots into common habitat groupings, we would expect some of these patterns to reveal themselves in our geographic analyses. However, we found few distinct patterns of geographic variation even when the data were analyzed separately by habitat.

It is perhaps important at this point to recall that the individual plot was the basic unit of our study; each plot carried equal weight in all analyses. As a result, many problems of scale introduced by comparing plots across habitats or biogeographic regions have been avoided. We simply tested whether any patterns emerged as a result of grouping plots on the basis of gross habitat similarity. Our results suggest that individual plots, but not habitat groups, may have distinct patterns of annual variation.

An additional factor contributing to both the observed within-habitat heterogeneity and the few between-habitat differences may be that plots differed in their overall degree of habitat saturation by breeding birds. If certain habitats (or plots) consisted of species populations generally below their carrying capacities, then successive annual censuses from small plots may show extensive variation simply because plot sizes were not large enough to reflect the scale at which population processes acted. To illustrate this line of reasoning we refer to the "checkerboard" model of Wiens (1981). For example, consider a comparison of grassland and deciduous forest plots represented by two checkerboards (habitats) of equal size. We assume that the deciduous forest habitat is considerably more saturated (i.e. has a greater density of territories) than the grassland habitat. Random redistribution of the checkers (territories) on the respective checkerboards would give the appearance of substantially greater density and species variation, relative to plot boundaries, on the grassland plot. This contrast would arise even if the grassland habitat experienced no variation in density or species richness at a regional level. Although this is a very simple model, with several strict assumptions (Wiens 1981), we feel it may accurately

portray a difference between those habitat types, or plots, that differ in their degree of saturation by breeding birds.

If Wiens's model is accurate, it suggests that plot size may need to be a function of the degree of saturation in order to make valid between-plot comparisons. However, we feel there is nothing inherently misleading in estimating population processes, and their variability, relative to similar plot sizes. Even if some patterns can be explained by recourse to a simple model of differences in saturation, this does not preclude a role for differences in species or habitat properties. Characteristic undersaturation of some habitats actually may be indicative of underlying biotic and abiotic properties that distinguish them from saturated habitats. Some of these properties may be generalizable across major habitat groupings.

Geographic analysis.—In contrast to much ecological dogma, we did not find strong support for the prediction that northern animal communities are less stable than more southern communities. Factor I, a gradient in species and individual turnover, was significantly correlated with latitude and suggested a positive relationship between latitude and species turnover. Although the overall association between these variables was weak ($r = 0.217$, $P < 0.01$), the relationship between latitude and species turnover became stronger when the data were partitioned by habitat type. Scrub, coniferous, and mixed deciduous-coniferous forests showed particularly strong evidence of decreasing stability with increasing latitude (Table 9), as was found by Järvinen (1979) for Scandinavian forests. Interestingly, deciduous forest plots, our largest sample ($n = 65$), showed no relationship among these variables.

Grassland plots showed a significant decrease in annual abundance variation moving from east to west. This pattern may simply result from the fact that many of the eastern grassland plots were of recent origin and rather small in spatial extent. As a result they were subject to biogeographic influences characteristic of small islands of recent origin (see Whitmore 1980).

Of the five significant latitudinal correlations with the stability gradients, all showed decreasing stability from south to north. Järvinen (1979) examined three hypotheses that attempt to explain similar latitudinal relation-

ships. These hypotheses propose that northern communities are less stable than southern ones because (1) northern communities have lower species richness, (2) northern communities experience greater environmental unpredictability, or (3) environmental productivity decreases northward. Järvinen favored the environmental unpredictability hypothesis.

Our data show a trend of decreasing species richness with increasing latitude, but this pattern is not consistent across habitat types (Table 10). The eastern deciduous forest plots would be particularly confounding in this regard because of the reversed latitudinal gradient in species richness in this biome (Rabenold 1979). To look at the possible influence of species richness on stability we examined the correlation structure between each of the stability gradients and \bar{S} . A significant association occurred between the diversity-variation gradient and \bar{S} ($r = -0.528$, $P < 0.001$), suggesting that areas with high \bar{S} values have low diversity variation.

Our study plots could be ordinated along an environmental predictability gradient (separately for variables such as temperature and rainfall), but we doubt if this gradient would clearly parallel a gradient in either latitude or longitude. In general, we expect northern bird communities to be exposed to greater environmental variability at a given longitude, but when considering longitude and latitude together such patterns are easily obscured (see Rotenberry 1978). Length of the breeding season, probability that the breeding season will be disrupted by climatic events, and the probability that such climatic events would surpass a bird's physiological thresholds all increase with increasing latitude. However, we do not believe that any of these factors would increase monotonically with latitude for the study areas in our data set.

The magnitude of seasonal fluctuations in resource productivity also varies positively with latitude (Ricklefs 1980). However, it is difficult to imagine distinct monotonic gradients in productivity paralleling latitude for the same reasons that confound the geographic relations of climatic predictability. In general, extensive seasonal variation in productivity would decrease species diversity (MacArthur 1972), and presumably stability, by increasing the probability of extinction among small populations.

However, we feel we cannot easily relate trends we observed to productivity differences because of the suspected importance of annual variability at the local level. Local-level effects could easily be of different magnitude, or sign, from regional trends in productivity.

The weakness of the relationship between latitude and stability may have been a consequence of the length of our latitudinal gradient. Although our sample plots covered more than 40° in latitude, we had no samples from subtropical or tropical communities. It may well be that the functional relationship between latitude and stability does not show a smooth decline with decreasing latitude, but rather changes abruptly when one moves from temperate to tropical regions.

In summary, we are reluctant to draw conclusions about geographical gradients in stability because the relationships that we observe are not very strong and are not consistent across habitat types, and because it is difficult to infer any causal mechanism for the patterns that we do observe. Patterns are confounded by covariation in latitudinal and longitudinal influences, as well as possible local effects. The reader is referred to Järvinen (1979) for a discussion of the way in which similar correlational results have been interpreted.

Long-distance migrants as a stabilizing influence.—If we assume that breeding abundance is positively related to saturation, our data suggest a weak association between this variable and the proportion of LDM ($r = 0.147$, $0.05 < P < 0.10$). However, this relationship is confounded by geographic effects ($r_{\text{LDM, lat.}} = 0.442$, $P < 0.001$). Controlling for the linear effects of latitude and longitude by partial correlation analysis showed the correlation between the proportion of LDM and \bar{N} to be even stronger ($r = 0.313$, $P < 0.001$). That is, there is a tendency for communities with higher abundances to have a larger proportion of LDM, with this relationship dependent on geographic location.

The possible stabilizing influence of a large proportion of LDM (Table 11) may be a function of its correlation with \bar{N} . If excess birds are excluded from breeding in saturated communities, they may act as a buffer to within-season perturbations. As a result, these communities would give the appearance of a more stable annual pattern. As a corollary, communities close to saturation may be more likely to

produce an excess of individuals and thereby maintain stability by increased recruitment. Collectively, these correlations suggest that northern communities may be characterized by even greater instability were it not for the stabilizing influence of a large, annual influx of LDM.

Patterns of variation in community stability.—Despite the lack of pattern in our derived gradients, our analyses did reveal three apparently independent sources of variation in community predictability. Breeding bird communities can independently show annual variation in species composition, species richness and equitability, and breeding abundance. Individual communities may be subject to one or any combination of these three sources of variation. We have illustrated that there is little tendency for any of these sources of variation to be closely associated with either gross habitat structure or geographic location. However, we are struck by the clarity of these synthetic gradients and believe that they have increased our understanding of the manner in which avian communities may vary from year to year.

Our results also suggest a positive relationship between community stability and both average species richness and breeding density. Järvinen (1980) reported a similar pattern for Scandinavian bird communities. Communities with higher values for \bar{S} and \bar{N} tended to be more stable, a pattern that was reflected in all nine of our indices (Table 2). Admittedly, \bar{S} is a function of plot size up to some asymptotic limit that may vary by habitat type (James and Rathbun 1981). However, to a large extent we controlled for this source of variation by excluding from our analyses plots <9 ha in size. Across-habitat comparisons may still have been confounded by a possible residual relationship between area and \bar{S} .

To rigorously test for differences in \bar{S} by habitat, differences in plot size, or abundance, could be normalized by the method of rarefaction (see Simberloff 1978, James and Rathbun 1981). This is a separate question that we are considering elsewhere (Noon and Kelly in prep.). However, we believe that our current estimates accurately reflect the true rankings of habitats by species-richness values. We have little evidence that plot size affected our estimates of \bar{S} , as the correlation between these two variables over all the data was nonsignificant ($r = 0.049$, $P \gg 0.05$). Even when the data were parti-

tioned by habitat only two significant correlations resulted, and these were small and of opposite sign.

There is a strong inverse relationship between \bar{S} and the coefficient of variation indices. However, speculation about the significance of the relationship to the diversity-stability controversy seems injudicious at this time. Our findings do suggest that diverse, high-density communities are more stable than less diverse, low-density systems (Table 2). The relative contributions of species richness and breeding abundance to stability is unclear; in addition, these variables are highly correlated ($r = 0.449$). The coefficients of variation indices showed stronger linear relationships with \bar{S} , and the remaining indices were more strongly associated with \bar{N} (Table 2). Partial correlation analysis, controlling for the confounding effects of either \bar{S} or \bar{N} , verified these patterns. Thus, the relative influence of species richness or abundance is dependent upon which indices are used to measure stability.

McNaughton (1978) observed similar species-richness differences in plant communities of African grasslands and attributed much of the enhanced stability of diverse systems to the arrangement of these communities into guilds (see King and Pimm 1983 for an alternative explanation). As communities become more species-rich, guild structure becomes more pronounced, and the average overall interaction strength among species declines (McNaughton 1978, Colwell 1979). There are extensive biotic interactions within a guild and very little interaction across guilds. The decreased average connectance among the species composing the community could enhance the stability properties of the system (May 1972).

Guild structure was excluded from our analyses, but many avian guild studies suggest that bird communities are organized in this manner (e.g. Cody 1974, Willson 1974, Holmes et al. 1979, Landres and MacMahon 1980, Short and Burnham 1982, Verner 1984). A direct relationship is expected between the number of guilds (defined at a given similarity level) and the bird species richness of the community. If a guild substructure in a species-rich community produces stability through a lowering of average species connectance, it provides a partial explanation for the results we observed.

Future efforts to understand patterns in community stability.—There are several additional

sources of information on avian populations that, if more generally available, would give insight into the causes of variability in community stability. For example, many of the contrasts in stability patterns that we observed are explained by a simple model of differences in saturation of the available habitat by breeding birds. Related to this possible influence is the observation that there are few studies that document the number and sex ratio of nonbreeding individuals (= floaters) in these habitats. Clearly, a supply of nonbreeding but physiologically capable and motivated individuals could act as a buffer to within-season perturbation to the breeding component and add to the observed stability of a community.

Community stability, at least as estimated by many of the metrics used in this study, would be enhanced if populations experienced compensating fluctuations in abundance. Compensatory shifts would suggest nonindependence of the species populations. A method of detecting and testing for significant covariation patterns has recently been proposed by Schluter (1984), and we are in the early stages of examining this data set for the prevalence of such patterns using his method.

Within any one habitat type we generally observed extensive variation in stability properties. It would be of interest to contrast, in more detail, those communities that are either particularly stable or unstable, while controlling for the confounding effects of gross differences in habitat structure. Such contrasts may go a long way toward revealing the processes underlying different patterns of annual variation.

As a final recommendation, several recent studies (Grossman 1982, Grossman et al. 1982, Connell and Sousa 1983) have indicated that the accuracy of stability estimates are improved if the study period covers at least one complete turnover (2–3 average lifespans) of all individuals in the community. Many of our shorter time-series studies did not meet this standard. In this regard, it would be of interest to recalculate our stability estimates in 5–10 yr when more long-term census data are available and determine if our current conclusions need to be amended.

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