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SPATIAL AUTOCORRELATION AND LOCAL DISAPPEARANCES IN WINTERING NORTH AMERICAN BIRDS

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Abstract. I examined the degree to which population sizes of North American wintering birds exhibit spatial synchrony (autocorrelation) and local disappearances based on 30 yr of Christmas Bird Counts. The primary goal of these analyses was to determine whether processes expected in metapopulations, including low spatial synchrony, frequent local disappearances, and colonization leading to population rescue, play important roles in species that are not necessarily subdivided into discrete patches. In general, spatial autocorrelation was less than expected based on environmental factors, with only one-third of species significantly spatially autocorrelated between sites up to 100 km apart and only three (1%) spatially autocorrelated on a continental scale. Spatial autocorrelation was significantly lower for primarily aquatic compared to terrestrial species and tended to be higher among small, widely distributed, and relatively abundant species with more northern winter distributions and low relative population variability. Local disappearances (years when no individuals were detected) were also common and tended to last longer in aquatic, migratory species high in the food chain. When controlling for confounding factors, there was a significant positive relationship between spatial synchrony and the length of disappearances among resident species, as expected if population rescue contributes to interspecific variation in these parameters. These results support the hypothesis that processes expected in metapopulations may be important in many resident bird species. They also provide insight as to which species are more vulnerable to global extinction as well as those for which monitoring efforts aimed at detecting large-scale population declines may be performed efficiently by extrapolating from data acquired at relatively few sites.

Key words: extinction; metapopulations; North American wintering bird populations; population rescue; population synchrony; spatial autocorrelation.

INTRODUCTION

Two key characteristics of classical metapopulations are that the density of individuals should not fluctuate highly synchronously over large geographic areas and that there should be a reasonable probability of extinction at sites (Harrison and Quinn 1989, Hanski and Gilpin 1991, Hanski 1997). These phenomena are theoretically related through the phenomenon of population "rescue" (Brown and Kodric-Brown 1977, Stacey and Taper 1992, Martin et al. 1997). Specifically, populations that are declining are more likely to be rescued from extinction or recolonized if already extinct by immigrants from other populations that are doing well, the existence of which is directly related to the degree of geographic asynchrony exhibited across the metapopulation. It follows that recolonization of local populations that have gone extinct should occur sooner when species exist as a metapopulation complex.

Unfortunately, because little is known about local extinction probabilities and patterns of spatial autocorrelation have only recently started to be investigated in many natural populations, we currently do not know the prevalence of these characteristics in most taxa. Such information is important if we are to understand the generality of metapopulation theory. In particular, does the theory apply only to the relatively few taxa that are distributed in clearly defined habitat patches? Or, can species that do not apparently live in such habitats still exhibit metapopulation-like population dynamics?

A more practical application of spatial autocorrelation data is in providing information critical to interpreting population monitoring efforts. Local population declines in species exhibiting low spatial autocorrelation may not reflect trends even a short distance away, whereas declines in species exhibiting extensive spatial autocorrelation should be examined more seriously, since they may reflect large-scale population declines covering much or all of a species' range. The ecological correlates of spatial autocorrelation are also important because they may indicate species whose populations tend to be geographically synchronous and thus whose overall population trends can be inferred from changes observed on a local scale.

Here I extend prior work on California land birds (Koenig 1998) to an analysis of spatial autocorrelation and the length of local disappearance events in wintering North American birds. As in the earlier study, I used 30 yr of data acquired in conjunction with the

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National Audubon Society's Christmas Bird Counts (CBC). The CBC data are subject to a variety of biases, such as the desire to count as many species as possible, and potentially strongly affected by weather conditions during particular counts (Bock and Root 1981). Nonetheless, this survey effort, covering the United States and Canada, is one of the most extensive databases available on the distribution and abundance of a taxon over such a large geographic area (nearly 2×10^7 km^2). Counts are standardized to a specific circle 24 km in diameter and take place each year on some day within a 2-wk period around Christmas. However, counts vary widely in the number of people and the amount of time devoted to them. These parameters are reported and thus counts can be standardized to yield relative densities by dividing the number of individuals reported by the total number of hours spent counting by the groups of people in separate parties within a site (Raynor 1975, Bock and Root 1981).

In order to determine the average degree of geographic synchrony exhibited by species, I subjected the CBC data to spatial autocorrelation analyses (Koenig and Knops 1998*a*, Koenig 1999), measuring the extent to which population densities, as measured by CBC data, fluctuate in synchrony over different geographic scales. Mean spatial synchrony was then examined for ecological correlates and compared to comparable values of spatial autocorrelation in annual rainfall and mean summer temperature. The frequency and length of local disappearances, defined as years when a species was not recorded at a site, was also derived from the CBC data. These data allow for a test of the potential applicability of metapopulation processes to a large and diverse taxon distributed over a wide geographic area.

Methods

The CBC data spanning 30 yr between the winters of 1959–1960 and 1988–1989 were downloaded from the CBC database maintained by the National Biological Service (Patuxent Wildlife Research Center, Laurel, Maryland, USA). Counts that did not overlap in time and that were within 3′ of both latitude and longitude were assumed to be continuations of the same site and were combined. Only sites from continental North America were included, and four taxa that have been variably split during the time period covered by the counts (Eastern and Western Screech Owl, Yellow-bellied, Red-breasted, and Red-naped Sapsucker, Yellow and Red-shafted Flicker, Boat-tailed and Great-tailed Grackle) were combined for analysis. A total of 1139 sites with an average of 16.4 yr per site were used. Species detected at fewer than 40 sites were excluded, leaving 323 species for analysis.

I assembled various characters for each species tested to examine both the ecological correlates and potential confounding factors associated with the tests performed for spatial autocorrelation and disappearance frequency. Variables associated with the CBC data included the relative distribution of the species as indexed by the number of sites at which the species was recorded (''NSITES''; values from Root 1988), mean density (MEANDEN; calculated by averaging the birds counted per party-hour per year across all sites at which a species was recorded), and population variability (POPCV), estimated by calculating the coefficient of variation (CV) of birds counted per party-hour within a site and then averaging CV values across all sites. Mean latitude was estimated by averaging the latitude of all sites at which a particular species was recorded, weighting each site by the overall mean density of individuals recorded at the site. I also estimated the maximum intrinsic growth rate (MAXGROWTH) by calculating the maximum value of $\log(N_{t+1}/N_t)$ averaged across all sites for each time series with no zeros and no missing years (Hanski and Woiwod 1993), where N_t is the number of birds per party hour counted in year t. Ecological variables and their sources included body mass (Dunning 1984), diet (omnivorous, primarily herbivorous, primarily insectivorous, or primarily eats vertebrates), whether the species is primarily aquatic or terrestrial (Ehrlich et al. 1988), and whether the species is primarily migratory, partially migratory, or resident (National Geographic Society 1983). Analyses were conducted using multiple regressions and ANCOVAs controlling for the significant effects of the number of sites at which species were recorded. Body mass and mean density were log transformed prior to analysis.

Spatial autocorrelation was measured as follows. Birds per party-hour were calculated for each year. Values (x) were then normalized by log transformation ($\log(x + 1)$). Next, for each species $\times$ site combination, I eliminated long-term trends in population numbers counted by replacing the log-transformed x values with the residuals obtained from a regression of year on x. This avoids significant autocorrelations between sites attributable to common long-term trends rather than synchronous population densities on a year-to-year basis (Hanski and Woiwod 1993). Pearson correlation coefficients (r) and great-circle distances between all pairwise combinations of sites that were censused concurrently for at least 5 yr were then calculated. I then computed the slope of the regression of the pairwise r values on distance in order to determine whether there was an overall decline in spatial synchrony with increasing distance between sites. Next I analyzed the data using the modified correlogram technique described by Koenig and Knops (1998*a*). This involves performing randomization trials on sets of correlation coefficients from combinations of sites located a given distance apart. Because of the large number of taxa involved, randomization trials were limited to 100 per species.

Pairwise combinations of sites were divided into six distance categories depending on whether sites were $<$100 km, 100–$<$250 km, 250–$<$500 km, 500–$<$1000

TABLE 1. Spearman rank correlations of mean spatial autocorrelation across species at different distance categories (in kilometers).

Distance category (km)	Distance category 100–250	250–500	500–1000	1000–2500	>2500
<100	0.82**	0.79**	0.64**	0.41**	−0.03
100–<250	···	0.80**	0.68**	0.51**	0.10
250–<500	···	···	0.69**	0.50**	0.05
500–<1000	···	···	···	0.55**	0.16*
1000–<2500	···	···	···	···	0.25**

Notes: Except for comparisons involving the 1000–2500 km distance category (N = 322) and the >2500 km distance category (N = 299), N = 323 species.
* $P < 0.01$; ** $P < 0.001$.

km, 1000–<2500 km or ≥2500 km apart; the maximum distance between sites used in the analysis was 6578 km (the distance between Nome, Alaska, and the Florida Keys). Analyses yield mean autocorrelation coefficients for pairwise sites located a given distance apart and the statistical significance of each value based on randomization trials. Although correlations can vary from −1 to 1, they cannot be significantly negative; thus, P values are one-tailed and test the null hypothesis that the mean spatial autocorrelation between sites a given distance apart is not significantly different from zero.

Spatial autocorrelation across species was significantly correlated between all distance categories except for the largest (Table 1). In order to minimize the number of statistical tests performed, I therefore compared ecological and life-history characters with mean spatial autocorrelation calculated from the above procedure only at SHORT (<100 km) and LONG (1000–<2500 km) distance categories. The largest distance category (≥2500 km) was also tested but yielded no significant relationships with life history characters and was not considered further. Statistical tests were first done with univariate analyses and then by ANOVAs controlling for confounding effects.

I calculated two measures to quantify local disappearances at individual CBC sites, the mean length of disappearances and the probability that a given year in which a species was observed would be followed by a disappearance. To calculate these values, I recorded the number of ''runs'' of zeros for each species × site combination, where a run consisted of a series of years in which no individual of the species was counted at the site. Only complete runs of years not broken by missing data were used and only runs of zero both preceded and followed by the species being recorded at the site were counted, thereby eliminating species only observed once at a site. The probability of a disappearance was the number of runs in a site divided by the number of years in which birds were observed at the site, while the mean length of disappearances was the average length of runs of zeros. These two indices are highly correlated ($r_s = 0.71$, $N = 323$ species, $P < 0.001$). Consequently, I only present results using the mean length of disappearances, chosen because of its more intuitive relationship to the potential incidence of population rescue: more frequent population rescue should decrease the length of local disappearances.

It is unlikely that asynchrony at very large distances would contribute to population rescue in most species. Consequently, I analyzed for a relationship between demographic rescue (estimated by the mean length of local disappearances) and mean spatial autocorrelation using only the latter measured at the SHORT (<100 km) distance category. The prediction of metapopulation theory is that, controlling for other factors, lower spatial autocorrelation should result in more frequent population rescue and thus there should be a positive relationship between spatial autocorrelation and the mean length of disappearances.

Comparisons of spatial autocorrelation values were made with annual rainfall measured from October through September of each year, as recorded at 2697 sites throughout North America north of Mexico, and mean spring/early summer temperature measured from 1 April through 31 July, as recorded at 2301 North American sites. Raw data were downloaded from the National Oceanic and Atmospheric Administration web site[1] and analyzed identically to the CBC data.

In order to compensate for the large number of species involved as well as some of the statistical problems associated with spatial analyses (Koenig 1999), I set the alpha level for rejection of the null hypothesis at $P \leq 0.01$.

RESULTS

Spatial autocorrelation

Values for spatial autocorrelation ranged as high as 0.44 (for Pine Grosbeaks at sites <100 km apart; scientific names of species are listed in the Appendix). In all, 114 (35.3%) of the 323 species were significantly autocorrelated at sites <100 km apart, the shortest distance that was feasible to test, and 3 (1.0% of the 299 with data in this category) were significantly autocorrelated at sites ≥2500 km apart (Fig. 1, Appendix). These values are generally much lower than those of the two environmental factors considered, with be-

[1] ⟨ftp://ftp.ncdc.noaa.gov/pub/data/ghcn⟩

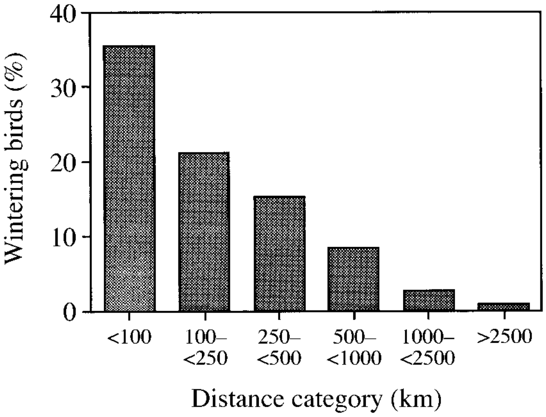

FIG. 1. Percentage of North American wintering bird species significantly ($P < 0.01$) spatially autocorrelated at different distances apart, as determined by randomization tests. $N = 323$ species (≤1000 km distance categories), 322 species (1000–<2500 km category), or 299 species (≥2500 km category).

tween 90.7% and 100% of species exhibiting lower spatial autocorrelation at all distance categories up to 2500 km than either annual rainfall or mean summer temperature (Fig. 2).

Spatial autocorrelation declined with distance in 312 (96.6%) of the species as indicated by a negative slope of the regression of the pairwise correlation coefficients on distance. In all but one case, species significantly autocorrelated at distance category *x* were significantly autocorrelated at all distance categories $<x$, as expected if these results reflect real spatial patterns rather than statistical artifacts. The single exception was Say's Phoebe, which was significantly autocorrelated at the <100, 100–<250 km, and 500–<1000 km categories but not at the 250–<500 km category. This counterexample represented only 0.6% of the 156 possible cases of such anomalies and thus is reasonably attributable to chance.

Although not specifically dealt with further here, spatial autocorrelation values generated using the residuals were strongly correlated with those obtained from the raw, untransformed data, with r_s values between the two sets of values ranging from 0.86 for the <100 km and 100–<250 km distance categories to 0.53 for the ≥2500 km distance category ($N \geq 299$, all $P < 0.001$). Thus, the detrending performed on the data analyzed here are not likely to seriously affect the conclusions.

Using all species, LONG spatial synchrony was uncorrelated with any of the tested variables. SHORT spatial synchrony was positively correlated with NSITES and mean latitude and negatively correlated with body mass and POPCV. Thus, larger species with greater population variability from year to year generally exhibited lower synchrony between populations relatively close together while more widespread species with more northern distributions exhibited higher population synchrony. SHORT spatial synchrony was also significantly greater in terrestrial than aquatic species. Relationships with population density, MAXGROWTH, migratory status, and diet were not significant at the $P < 0.01$ level.

Because of the strong difference between aquatic and terrestrial species, I also analyzed these two groups separately. For the aquatic species, no variable was significant at the 0.01 level in any of the tests. In contrast, spatial autocorrelation for terrestrial species, besides exhibiting the same relationships with NSITES, mean latitude, and POPCV as the complete data set, was positively related to MEANDEN and varied significantly depending on diet at both SHORT and LONG distances (Table 2). With respect to diet, primarily herbivorous species exhibited the greatest spatial synchrony (Fig. 3). Differences between aquatic/terrestrial species and dietary differences remained similar in ANCOVAs in which the NSITES, body mass, mean latitude, MEANDEN, and POPCV were held constant.

Local disappearances

Disappearances were common in the data set, occurring with a probability averaged across species of 0.22 ± 0.12 (mean ± 1 SD; $N = 323$). No species failed to suffer a disappearance event somewhere throughout its range and 47.4% of species × site combinations ($N = 110\,912$) experienced at least one such event. The mean length of disappearances was 3.00 ± 0.89 yr (Fig. 4).

Using all species, length of disappearances was inversely correlated with NSITES, MEANDEN, and in-

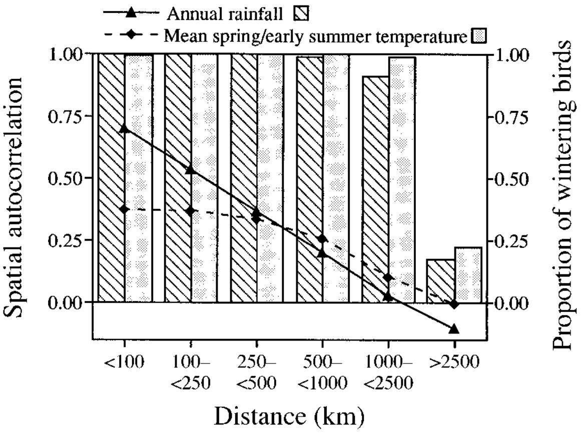

FIG. 2. Mean spatial autocorrelation (lines; left vertical axis) in annual rainfall (October–September; solid line marked with triangles) and in mean spring/early summer temperature (April–July; dashed line marked with diamonds) for North America north of Mexico between sites different distances apart (categories listed on the *x*-axis). Sample sizes are 2697 sites (for rainfall data) and 2301 sites (for temperature data). Superimposed on these values are bars representing the proportion of species (right vertical axis) exhibiting spatial autocorrelation less than the mean values for annual rainfall (hatched bars) and mean temperature (shaded bars). Number of species tested = 323.

TABLE 2. Statistical tests for relationships between mean spatial autocorrelation at SHORT (<100 km) and LONG (1000–2500 km) distances and the number of sites at which species were recorded, mean latitude, body mass, mean density, mean population variability (coefficient of variation, CV), and life history characters.

Variable	All species SHORT	All species LONG	Terrestrial species SHORT	Terrestrial species LONG
N sites (r_s)	0.21	0.07	0.24**	0.15
Mean latitude	0.25**	0.12	0.27**	0.23**
Body mass (r_s)	−0.28**	−0.12	−0.12	−0.08
Mean density (r_s)	0.14	0.13	0.32**	0.22**
Population CV (r_s)	−0.26**	−0.09	−0.22**	−0.10
Intrinsic growth rate (r_s)	−0.03	0.09	0.17	0.14
Aquatic/terrestrial (*z* value)	5.74**	1.06	···	···
Migratory status (χ^2)	6.93	2.00	1.89	1.59
Diet (χ^2)	10.0	5.7	17.9**	15.8**

Notes: Values are derived from Spearman rank correlations (r_s), Mann-Whitney *U* tests (*z* value), and Kruskal-Wallis one-way ANOVAs (χ^2). Analyses are for all species ($N = 323$) and terrestial species only ($N = 214$); no tests were significant for aquatic species only. For categories, see *Methods*. Degrees of freedom are 1 for the aquatic/terrestrial comparison, 2 for the comparison of migratory status, and 3 for diet.
* $P < 0.01$; ** $P < 0.001$.

creasing spatial autocorrelation, while it was positively correlated with POPCV (Table 3). There were also significant differences in two of the three categorical life history characters, with aquatic, migratory species being most prone to lengthy local disappearance events.

Because of the highly significant effects of whether species were primarily aquatic or terrestrial and the migratory status of the species, I performed analyses separately on aquatic, terrestrial, resident, and migratory species (Table 3). The variable POPCV was the only one that was significantly related to the length of disappearance events in all categories of species: the greater the population variability, the longer disappearance events lasted. Beyond this, aquatic species exhibited no significant relationships with the length of disappearance events, restricting the significant effects of the NSITES, POPDEN, spatial autocorrelation, migratory status, and diet to terrestrial species. There were also significant effects of diet among residents, but not among migrants, whereas relationships with NSITES and spatial autocorrelation are apparently due to differences among migrant rather than resident species (Table 3). Residents, but not migrants, with more northern wintering distributions experienced longer local disappearances than those with more southern distributions.

Is the relationship between spatial autocorrelation

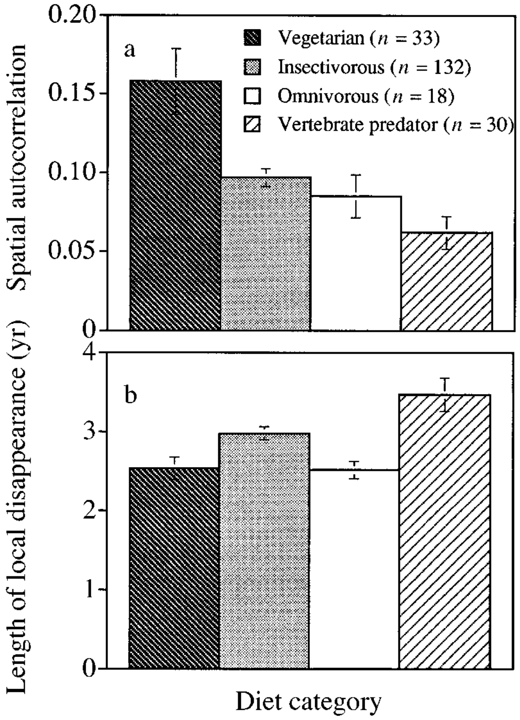

FIG. 3. (a) Spatial autocorrelation at SHORT distances and (b) length of local disappearances as a function of diet for terrestrial species only (means ± 1 SE). Differences are significant ($P \leq 0.001$) by Kruskal-Wallis one-way ANOVAs (Tables 2 and 3).

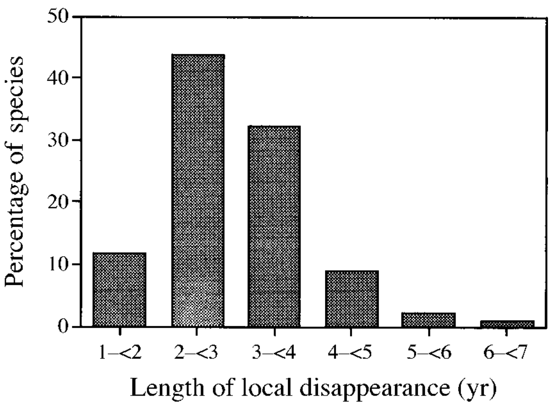

FIG. 4. The distribution of the mean length of local disappearances across all species ($N = 323$).

TABLE 3. Statistical tests for relationships between the mean length of disappearance events and the number of sites at which species were recorded, mean latitude, body mass, mean density, mean population variability (coefficient of variation, CV), spatial autocorrelation at the SHORT (<100 km) distance category, and life history characters.

Variable	All species	Aquatic	Terrestrial	Resident	Migratory
N sites (r_s)	−0.28**	−0.10	−0.36**	−0.05	−0.32**
Mean latitude	−0.08	0.09	−0.13	0.28*	−0.02
Body mass (r_s)	0.13	0.14	−0.03	0.19	0.05
Mean density (r_s)	−0.29**	−0.02	−0.51**	−0.37**	−0.25*
Population CV (r_s)	0.79**	0.60**	0.81**	0.69**	0.74**
Spatial autocorrelation (r_s)	−0.21**	−0.02	−0.20*	0.17	−0.25*
Intrinsic growth rate (r_s)	0.10	0.07	−0.01	0.07	0.04
Aquatic/terrestrial (*z* value)	3.12**	···	···	1.11	1.35
Migratory status (χ^2)	46.1**	4.2	36.8**	···	···
Diet (χ^2)	11.0	4.6	17.4**	13.5*	1.19
N (species)	323	109	214	85	122

Notes: Statistics are as in Table 2. Analyses are for all species, primarily aquatic species, primarily terrestrial species, resident species, and migratory species. Degrees of freedom are 1 for the aquatic/terrestrial comparison, 2 for the comparison of migratory status, and 3 for diet.

*$P < 0.01$; **$P < 0.001$.

and the length of disappearance events consistent with population rescue? In general, the results reported in Table 3 indicate an inverse, or positive but nonsignificant, relationship between these variables. However, in multiple regressions of spatial autocorrelation at the SHORT distance category on the mean length of local disappearance events controlling for NSITES and mean latitude, the significance of the negative correlations in Table 3 disappeared, and a significant positive relationship for resident species emerged (Table 4). Regressions controlling for additional variables, including body size and POPDEN, yielded identical results.

DISCUSSION

As found in virtually all taxa that have been examined thus far (Hanski and Woiwod 1993, Ranta et al. 1995, Koenig 1999), synchrony declined with distance in all but a handful of species. However, 209 (64.7%) exhibited no significant spatial autocorrelation, even between sites <100 km apart (Table 1 and Appendix), and synchrony was fairly modest even among the 114 species that were significantly autocorrelated at one or more distance categories. Thus, large scale geographic synchrony is not a general phenomenon among wintering North American birds.

This result is unexpected given the relatively high degree of spatial autocorrelation in environmental factors over this same area. For example, mean spatial autocorrelation in annual rainfall (October–September) between sites in North America north of Mexico <100 km apart is 0.70 ($N = 2697$ sites), considerably greater than the value of 0.44 between sites the same distance apart for Pine Grosbeaks, the most highly spatial autocorrelated species in the entire data set. In all, 100% of species were less spatially autocorrelated at the <100 km distance category than annual rainfall, and 99.1% (all but three species) were less spatially autocorrelated than mean spring/summer temperatures (Fig. 2). Similar results were found for all distance categories <2500 km apart. Thus, environmental variation (the Moran effect, Ranta et al. 1995, 1997) is sufficiently synchronous to be the driving force behind much of the synchrony observed in the population dynamics of many of these species.

Other factors also influence the degree of spatial autocorrelation observed in these species, however. Of the nine species that were significantly spatially autocorrelated either across the entire North American continent or at the 1000–<2500 km distance category, for example, five (Common Redpoll, Pine Siskin, Red-breasted Nuthatch, Pine Grosbeak, and Evening Grosbeak) are boreal seed-eating ''eruptive'' species whose population dynamics are dependent to a considerable extent on seed crops of boreal trees, which themselves are spatially autocorrelated over large areas (Bock and Lepthien 1976, Koenig and Knops 1998*b*). This suggests that the large-scale spatial synchrony observed in these species results from tracking of this critical food resource rather than the Moran effect per se.

A variety of other factors also affected the observed degree of spatial autocorrelation. For example, more synchronous species tend to be widely but more northerly distributed, small-bodied species whose populations fluctuate relatively little from year to year. Al-

TABLE 4. Multiple regressions of the mean length of extinction events on spatial autocorrelation (SHORT, <100 km) controlling for the number of sites at which species were recorded and mean latitude. Standardized β and *P* values are listed.

Species category	β	*P*	*N* (species)
All	−0.05	0.35	323
Aquatic	0.09	0.35	109
Terrestrial	−0.05	0.47	214
Resident only	0.27	0.009	85
Migratory only	−0.18	0.05	122

though the ecological basis for these relationships is not entirely clear, small body size and wide geographic distributions seem likely to be associated with greater dispersal, which is expected to increase synchrony and decrease population fluctuations (Hanski and Woiwod 1993). There were no significant differences according to diet or migratory status, but primarily terrestrial species were significantly more autocorrelated at SHORT distances than primarily aquatic species, most likely reflecting the temporally and spatially varying food supplies on which the latter often depend.

Analyses of aquatic and terrestrial species separately reveal that most of the correlations found in the complete data set, with the exception of the inverse correlation with body mass, are apparently due to variation among terrestrial species alone (Table 2). In addition, spatial autocorrelation among terrestrial species differed according to diet, with herbivorous species exhibiting the greatest synchrony (Fig. 3).

These results contrast with those reported earlier for California land birds (Koenig 1998). In the California data set, there was no significant relationship between spatial autocorrelation and either body mass or diet, whereas migrants were significantly more synchronous than residents. These discrepancies are presumably due to differences between the species compositions of the two data sets and indicate that patterns of spatial autocorrelation may vary considerably depending on the region, as well as the scale, of the analysis.

Results can also be contrasted with those reported by Hanski and Woiwod (1993) in a similar analysis for British moths and aphids. No significant relationship with the maximum intrinsic growth rate was found in either study which, combined with a highly positive correlation between spatial synchrony and population variability, was taken by Hanski and Woiwod as providing support for regional stochasticity rather than dispersal playing a dominant role in producing the observed large-scale patterns in spatial synchrony. However, these authors used the mean standard deviation (SD) in population size as a measure of variability, which is sensitive to mean population size, rather than the coefficient of variation, which is not. Reanalyzing the CBC data using the mean SD does, in fact, yield positive correlations with both SHORT and LONG spatial autocorrelation, although not significant at the α level used here ($r = 0.11$ [SHORT] and 0.13 [LONG]; $N = 321$; both $0.02 < P < 0.05$). This suggests that Hanski and Woiwod's (1993) results may be related to differences in mean population density rather than relative variability per se and that at least some of the contrasting results of the two studies are due more to analytical than biological differences.

An even more diverse set of ecological factors was found to correlate with the mean length of local disappearances in individual species (Table 3). Species in which disappearances lasted longer tended to be rare, locally distributed species with relatively high population variability from year to year. The positive relationship between population variability and local disappearance is intuitive, since increasing probability of populations achieving zero abundance can scarcely fail to correlate with greater overall population variability. Of greater interest are the positive correlations between disappearances and both abundance and distribution. These relationships are expected if demographic rescue is a cause of interspecific variation in the length of disappearance events since rescue should be more frequent in widely distributed, common species. Less expected are the relationships with ecological factors, with aquatic, migratory, vertebrate predators tending to be more prone to local disappearances than terrestrial residents that feed on insects, fruit, or vegetable material (Table 3; Fig. 3).

The positive correlation between population variability and local disappearances was observed among all subsets of species. Beyond this, other factors applied to some groups of species but not others (Table 3). More widespread, terrestrial, and migratory species were less prone to local disappearances, whereas there was no significant relationship between the length of disappearances and distribution among aquatic or resident species. Local disappearances were significantly longer among migrant than resident terrestrial species, but not among other categories of species (Table 3). Only among resident species did the length of disappearances increase as winter distributions became more northerly.

In multivariate analyses controlling for confounding factors, there was a significant positive relationship between spatial autocorrelation at SHORT distances and length of disappearances in resident species (Table 4). Thus, for at least this group of species, population rescue is consistent with the observed relationship between spatial synchrony and length of local disappearances, the latter of which are more likely to reflect true local extinctions than they are for migratory species. Given that residents in general disperse less than migratory species (Weatherhead and Forbes 1994), the finding that metapopulation-like processes are more characteristic of residents than migrants is not surprising.

Although dispersal capabilities of most of the species analyzed here have not been studied, dispersal events up to 100 km in length are certainly within the capabilities of most, if not all of them, and thus the sites analyzed are not so distant from one another as to preclude recolonization. Combined with the low spatial autocorrelation exhibited by many of the species and the frequent disappearances often lasting long enough to be attributable to mortality rather than local movement of individuals (Harrison and Taylor 1997), three of Hanski's (1997) four conditions characterizing metapopulations are satisfied by a high proportion of the species analyzed. The only condition that may not be met for most of the species is that suitable habitat be restricted to discrete patches, although, with increasing fragmentation of natural landscapes even this criterion may be met in more cases than might otherwise be expected.

I conclude that, regardless of whether they are limited to discrete, localized patches of habitat or not, wintering populations of many avian species, and particularly of resident species, exhibit dynamics characteristic of metapopulations. Thus, for many avian species, it may be possible to model patterns of colonization and disappearance, even during the winter, using the kinds of spatially explicit models commonly used in metapopulation biology (Hanski 1998). Species for which this is unlikely to be true include many of the migrants that are in general too vagile to conform to the assumptions of these models (Haila and Hanski 1993), although it is still possible that breeding populations of these species may conform more closely to the conditions needed for a metapopulation approach than the wintering populations analyzed here.

Regardless of the degree to which these populations can be modeled using a metapopulation approach, patterns of spatial autocorrelation as measured here are potentially important to the design and interpretation of monitoring programs since the degree to which year-to-year trends detected by local monitoring efforts are generalizable to larger areas is dependent on the magnitude and geographic extent of spatial autocorrelation among sites. Such analyses do not tell the whole story because long-term trends (which themselves may or may not be synchronous among sites) were eliminated here by using residuals from regressions of year on relative population size. However, short-term spatial autocorrelation values using residuals, as used here, were highly correlated with long-term values derived from the raw, untransformed data and thus are generally a good index of synchrony between sites on a long-term, as well as a short-term, basis.

Consequently, the patterns of spatial autocorrelation reported here are potentially important in interpreting the significance of local population changes at larger geographic scales and for inferring the kinds of demographic and environmental factors that are important to particular species. Specifically, species exhibiting high spatial autocorrelation are either likely to have relatively high dispersal rates or be affected by environmental factors that are themselves synchronous over large geographic areas. Conversely, species exhibiting low spatial autocorrelation are likely to be sedentary, affected by relatively local environmental conditions, or both. On a short-term, and usually on a long-term scale as well, population trends of species with strong spatial autocorrelation over large distances can be inferred from results of local population surveys, since by definition population sizes of such species are correlated even when the sites are far apart. In contrast, those of species exhibiting no spatial autocorrelation cannot, since populations separated by even relatively short distances apart are uncorrelated.

Species differences in spatial autocorrelation (see Appendix) are thus an important guide to the degree that large-scale trends can be inferred from local population surveys. All things being equal, more effort will be needed to establish global population trends of species with low spatial autocorrelation than those exhibiting high spatial autocorrelation over large geographic distances. Since increased spatial synchrony is expected to correlate with the probability of global extinction (Heino et al. 1997), this indicates that monitoring efforts aimed at species most vulnerable to global extinction can in some cases be performed efficiently by extrapolating from data acquired at relatively few sites.

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APPENDIX

A table presenting spatial autocorrelation results and basic ecological data for the 323 species used in the analyses is available in ESA's Electronic Data Archive: *Ecological Archives* E082-026.