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SPATIAL SCALING OF AVIAN POPULATION DYNAMICS: POPULATION ABUNDANCE, GROWTH RATE, AND VARIABILITY

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Abstract. Synchrony in population fluctuations has been identified as an important component of population dynamics. In a previous study, we determined that local-scale (<15-km) spatial synchrony of bird populations in New England was correlated with synchronous fluctuations in lepidopteran larvae abundance and with the North Atlantic Oscillation. Here we address five questions that extend the scope of our earlier study using North American Breeding Bird Survey data. First, do bird populations in eastern North America exhibit spatial synchrony in abundances at scales beyond those we have documented previously? Second, does spatial synchrony depend on what population metric is analyzed (e.g., abundance, growth rate, or variability)? Third, is there geographic concordance in where species exhibit synchrony? Fourth, for those species that exhibit significant geographic concordance, are there landscape and habitat variables that contribute to the observed patterns? Fifth, is spatial synchrony affected by a species' life history traits? Significant spatial synchrony was common and its magnitude was dependent on the population metric analyzed. Twenty-four of 29 species examined exhibited significant synchrony in population abundance: mean local autocorrelation (ρ) = 0.15; mean spatial extent (mean distance where $\rho = 0$) = 420.7 km. Five of the 29 species exhibited significant synchrony in annual population growth rate (mean local autocorrelation = 0.06, mean distance = 457.8 km). Ten of the 29 species exhibited significant synchrony in population abundance variability (mean local autocorrelation = 0.49, mean distance = 413.8 km). Analyses of landscape structure indicated that habitat variables were infrequent contributors to spatial synchrony. Likewise, we detected no effects of life history traits on synchrony in population abundance or growth rate. However, short-distance migrants exhibited more spatially extensive synchrony in population variability than either year-round residents or long-distance migrants. The dissimilarity of the spatial extent of synchrony across species suggests that most populations are not regulated at similar spatial scales. The spatial scale of the population synchrony patterns we describe is likely larger than the actual scale of population regulation, and in turn, the scale of population regulation is undoubtedly larger than the scale of individual ecological requirements.

Key words: *bootstrapping; nonparametic convariance functions; North American Breeding Bird Survey; population dynamics; population regulation; spatial synchrony.*

INTRODUCTION

Synchrony in population fluctuations has been identified as an important component of population dynamics (Royama 1992) and has been studied in a wide variety of taxa, including birds (Ranta et al. 1995, Paradis et al. 2000, Koenig 2001, Toms et al. 2005), insects (Hanski and Woiwod 1993, Sutcliffe et al. 1996), and mammals (Moran 1953, Stenseth et al. 1998, 1999, Haydon et al. 2001). One of the most important findings derived from these studies is that population dynamics are best conceptualized as regional phenomena (Bjørnstad et al. 1999*a*, Koenig 1999, Liebhold et al. 2004). Three classes of processes have been identified as contributing to the regionalization of population dynamics: trophic interactions, such as predators synchronizing prey abundances over time or space (Ims and Andreassen 2000); dispersal coupling locally regulated populations (Bjørnstad et al. 1999*a*, Kendall et al. 2000); and spatially correlated density-independent factors, known as the Moran effect (Moran 1953, Royama 1992, Ranta et al. 1995).

In a previous paper (Jones et al. 2003), we documented local-scale (populations separated by ~15 km) spatial synchrony in annual abundances of long-distance, migratory, insectivorous bird populations in New England (see Plate 1) and demonstrated that this synchrony was correlated with synchronous fluctuations in the abundance of lepidopteran larvae, a primary food resource during the breeding season. Lepidopteran larvae, in turn, were influenced by El Niño/La Niña global climate patterns (Sillett et al. 2000). We also found that abundances of year-round resident bird

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PLATE 1. Aerial view of the Hubbard Brook Experimental Forest in the White Mountains of New Hampshire (USA). Research performed at this location provided the basis for the hypotheses and predictions tested in this paper. Photo credit: Peter P. Marra.

species in our local New England study area were related to the North Atlantic Oscillation (Jones et al. 2003) and suggested that winter weather might be having both direct (e.g., via temperature-mediated mortality) and indirect (e.g., via winter food availability) effects on year-round resident species. However, because our data set was limited to bird abundances at local scales, we were unable to determine the broader spatial extent of the spatial synchrony exhibited by our study species, nor were we able to infer whether similar regulatory processes were operating at regional scales.

Here we address five general questions in an attempt to determine if the patterns and potential correlates of spatial synchrony we observed at local spatial scales were representative of larger, regional patterns. First, do bird populations in eastern North America exhibit population synchrony at spatial scales beyond what we have documented locally (Jones et al. 2003)? Second, does the strength and spatial extent of spatial synchrony depend on what population metric (e.g., abundance vs. growth rate) is analyzed? Third, are there synchrony hotspots? In other words, is there geographic consistency among species that exhibit significant spatial synchrony? Fourth, for those species that exhibit significant geographic concordance, are there landscape and habitat variables that contribute to the observed patterns? Fifth, is the strength and geographic extent of spatial synchrony affected by a species' life history traits? Within this latter question we tested the following predictions based on our earlier work (Jones et al. 2003): First, foliage-gleaning insectivore species will exhibit stronger and broader patterns of spatial synchrony than nonfoliage-gleaning insectivore species, given their reliance on a food supply (larval Lepidoptera) that tends to exhibit both cyclical and spatially synchronous population fluctuations (Liebhold and Kamata 2000, Jones et al. 2003, Raimondo et al. 2004). Second, resident species will exhibit stronger and broader patterns of spatial synchrony than will migratory species, by virtue of the strong synchronizing effect winter climate can have on animal populations living year-round in the Northern Hemisphere (Post et al. 1999, Jones et al. 2003).

MATERIALS AND METHODS

The data

Data for this study were obtained for the period 1973–2000 for all routes in 12 physiographic regions from the North American Breeding Bird Survey (BBS: Northern Piedmont, Southern Piedmont, Southern New England, Great Lakes Plains, St. Lawrence River Plain, Cumberland Plateau, Ohio Hills, Blue Ridge Mountains, Allegheny Plateau, Adirondack Mountains, Northern New England, Northern Spruce Hardwoods). (The North American Breeding Bird Survey offers details of its data collection process; *available online*.)[5]

We excluded any routes that had any gaps in coverage of more than two years and that had more than two gaps (regardless of duration) during 1973–2000. We did not include species in our analyses that have traits that render them poorly sampled by BBS protocol (e.g., nocturnal species, gregarious flockers, or nomadic species) or whose populations may have been enhanced by human activity (e.g., box nesters). We excluded species that were present in less than half of our selected routes and excluded routes from a species' data set at

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[5] ⟨http://www.pwrc.usgs.gov/bbs⟩

which a species was detected for <10 years during 1973–2000. Coverage breaks were filled using four-year moving averages. After imposing these restrictions, we were left with 29 species (see Appendix A for scientific names and natural history information) and 128 BBS routes that we included in our analyses. On average, the species we selected were present on 108 routes (range 69–128). The starting points of the routes we included were separated by an average of 827.0 km (range 5.2–2770.6 km).

We were also interested in examining landscape-level habitat patterns and how they might interact with population fluctuations. We determined the centroid of each route and buffered these centroids by the length of the route radius (19.7 km, the average distance between the starting point and midpoint of each route). We then downloaded and merged National Land Cover Dataset data (NLCD 1992 [*available online*])[6] for states that overlapped our route buffers. Next, we clipped the land cover data to isolate the landscape features for each buffered BBS route.

We evaluated the following habitat characteristics: deciduous forest (DEC), evergreen forest (EVE), mixed forests (MIX), emergent herbaceous wetland (EHW), woody wetland (WOW), commercial (COM), high-intensity residential (HIR), low-intensity residential (LIR), pasture (PAS), and row crops (ROW). For each of these variables we calculated (using the spatial analysis program FRAGSTATS; McGarigal et al. 2002) percentage of landscape (PER), average patch size (ARE), and Euclidian nearest neighbor distance (ENN). We denoted each habitat metric with a six-letter code; for example, the percentage of the landscape that is deciduous forest is denoted DECPER. We also included three landscape metrics: shape index (LANSHI; a measure of patch aggregation [as LSI increases, patches become less aggregated]), connectedness (LANCON), and patch diversity using a Shannon-Weiner index (LANSHD).

Statistical analyses: birds

For the analyses of spatial scale of population dynamics, we chose three descriptors of population dynamics (following Bjørnstad et al. 1999*b*). First, we used the time series of abundance data, measured on a logarithmic scale [$\mathrm{LN} = \ln(C + 1)$], where C is the measure of abundance, i.e., the count. Second, we calculated annual rates of population change [$R = \ln(C_t + 1) - \ln(C_{t-1} + 1)$]. Third, we quantified the variance in abundance of each time series using the S index: $S = \mathrm{SD}[\log_{10}(C + 1)]$. Hence, each route was characterized by 28, 27, and 1 values, respectively, for these three descriptors for each species included from that route.

Following Bjørnstad et al. (1999*b*), we used spline correlograms to directly estimate spatial covariance functions (Bjørnstad and Falck 2001) and measure the strength and spatial scale of local autocorrelation (i.e., the strength and scale of synchrony; Fig. 1). We applied the spline correlogram to the three population descriptors for all 29 species, using degrees of freedom equal to the square root of the number of routes occupied by a given species. We used 1000 bootstrap resamples to generate the confidence intervals for the covariance functions. All time series analyses were performed using programs written by O. N. Bjørnstad for R/S-plus.

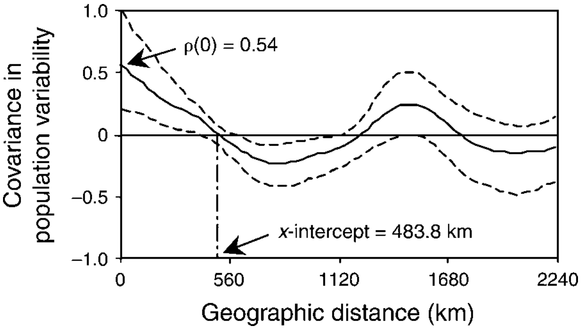

FIG. 1. Spatial synchrony of population variability for the American Crow, as shown by a nonparametric covariance function (solid line) with 95% bootstrap confidence intervals estimated using spline correlograms. Covariance can range from −1 to +1. In this example, local autocorrelation (ρ) is 0.54. The distance at which the local autocorrelation becomes 0 is indicative of the spatial scale of population covariance (x-intercept = 483.8 km). Table 1 provides confidence interval data, and Fig. 3 exhibits the data in a spatially explicit manner.

We tested for concordance in the spatial patterns of autocorrelation (i.e., hotspots) for all species that exhibited a local autocorrelation >0.20. To do so, we performed all possible pair-wise correlations among the time series of significant species, using only those routes where both species of a pair were present. From these correlations, we calculated an average ("global") correlation coefficient for the included species. We tested the significance of this global coefficient using a bootstrap approach. New distributions were generated from the existing values using resampling with replacement within each species, and a new pair-wise correlation coefficient was calculated. The procedure was performed 1000 times for each pair-wise comparison, and the new iteration values were averaged for a bootstrap estimate of the global correlation coefficient. The standard deviation of these 1000 coefficients is the bootstrap estimate of the standard error of the mean ($\mathrm{SE}_{\mathrm{boot}}$). We constructed a 95% confidence interval equal to the global correlation coefficient $\pm 2(\mathrm{SE}_{\mathrm{boot}})$. If this interval did not include zero, we considered the global correlation coefficient to be significantly different from zero (Buonaccorsi et al. 2001).

The influence of life history variables were analyzed between or among guilds using t tests and ANOVAs, after testing for adherence to parametric assumptions. Values of local autocorrelation and spatial extent were averaged across species within each strategy prior to

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[6] ⟨http://landcover.usgs.gov⟩

TABLE 1. Spline correlogram estimates of the local autocorrelation $\rho(\delta = 0)$ and x-intercept, including 95% bootstrap confidence limits for three demographic descriptors for 29 bird species.

Bird species	LN		*R*	
	ρ(0)	*x*-intercept	ρ(0)	*x*-intercept
AMCR	**0.19** (0.12, 0.26)	281.7 (127.5, 1884.3)	0.03 (−0.02, 0.09)	448.5 (0, 891.5)
AMRE	**0.13** (0.03, 0.24)	439.4 (126.8, 899.1)	0.02 (−0.04, 0.07)	54.3 (0, 691.5)
AMRO	**0.15** (0.07, 0.25)	568.5 (152.6, 1282.3)	0.02 (−0.02, 0.06)	806.9 (0, 1069.2)
BAOR	**0.10** (0.04, 0.15)	548.1 (164.2, 814.5)	0.04 (−0.03, 0.10)	139.7 (0, 1048.4)
BCCH	**0.21** (0.12, 0.32)	485.9 (0, 1428.1)	0.06 (0, 0.13)	665.9 (0, 1107.1)
BLJA	**0.11** (0.06, 0.17)	548.7 (305.0, 774.9)	0.05 (0, 0.10)	686.2 (0. 1161.5)
BOBO	**0.09** (0.02, 0.16)	105.6 (0, 625.4)	0.03 (−0.03, 0.09)	132.9 (0, 1049.2)
CHSP	**0.18** (0.09, 0.28)	283.8 (80.5, 2001.4)	0 (−0.05, 0.04)	0 (0, 787.4)
COYE	**0.15** (0.08, 0.22)	355.9 (239.8, 484.4)	**0.06** (0.01, 0.12)	251.9 (44.9, 878.1)
DOWO	0.05 (0, 0.10)	333.0 (0, 1193.3)	0.05 (0, 0.10)	311.4 (0, 1431.7)
EAKI	**0.08** (0.02, 0.15)	425.9 (0, 1327.9)	0.01 (−0.05, 0.07)	92.2 (0, 683.8)
EAPH	**0.20** (0.13, 0.28)	325.2 (0, 583.6)	**0.10** (0.03, 0.18)	406.6 (0, 1251.8)
EATO	**0.37** (0.20, 0.54)	425.1 (163.2, 1045)	0 (−0.05, 0.08)	0 (0, 705.1)
EWPE	0.06 (0, 0.14)	245.2 (0, 1212.8)	0.01 (−0.05, 0.08)	0 (0, 705.1)
GCFL	0.04 (−0.01, 0.01)	636.0 (0, 768.2)	0 (−0.05, 0.08)	0 (0, 777.3)
GRCA	**0.17** (0.09, 0.25)	358.7 (251.3, 712.3)	**0.07** (0.02, 0.12)	741.7 (158.3, 1017.6)
HOWR	**0.12** (0.04, 0.21)	456.7 (0, 671.1)	0.02 (−0.04, 0.09)	0 (0, 719.0)
INBU	**0.14** (0.05, 0.24)	451.6 (127.8, 1006.0)	0.05 (−0.01, 0.12)	254.1 (0, 653.8)
LEFL	**0.24** (0.11, 0.38)	408.2 (86.5, 987.7)	0.03 (−0.03, 0.12)	412.8 (0, 957.5)
NOFL	**0.21** (0.15, 0.28)	626.8 (277.3, 1155.2)	0.03 (−0.02, 0.08)	437.9 (0, 907.2)
OVEN	**0.17** (0.09, 0.27)	700.3 (0, 1204.9)	0.04 (−0.01, 0.10)	196 (0, 965.7)
RBGR	**0.14** (0.06, 0.24)	720.8 (0, 1205.3)	0.06 (−0.02, 0.13)	709.0 (0, 1021.3)
REVI	**0.18** (0.09, 0.26)	307.2 (180.7, 845.9)	**0.02** (0.03, 0.07)	483.2 (0, 1163.8)
SCTA	0.06 (0, 0.13)	375.1 (0, 742.8)	0.02 (−0.05, 0.09)	272.1 (0, 744.2)
SOSP	**0.18** (0.01, 0.27)	306.3 (183.8, 836.9)	0.03 (−0.03, 0.08)	483.2 (0, 1289.0)
VEER	0.10 (0, 0.22)	386.9 (0, 1132.9)	0.04 (−0.04, 0.12)	463.8 (0, 747.5)
WBNU	**0.18** (0.11, 0.26)	226.9 (83.8, 986.3)	0.07 (0, 0.15)	343.1 (0, 860.6)
WOTH	**0.28** (0.15, 0.40)	380.9 (207.3, 755.3)	**0.07** (0.01, 0.14)	405.6 (0, 843.4)
YWAR	**0.09** (0.02, 0.19)	358.5 (0, 1137.5)	0.03 (−0.02, 0.08)	402.8 (0, 1256.3)

Notes: Boldface values are significant (i.e., 95% CI does not include zero). The abbreviations are as in the main text (LN is log-transformed time series, *R* is annual population growth, and *S* is standard deviation of the $\log_{10}$ time series). See Appendix A for species codes.

analysis. Pair-wise differences were assessed using Tukey-Kramer tests.

Statistical analyses: landscape

Using multiple linear regression and model selection methods based on Akaike's information criterion (AIC; Akaike 1973, Lebreton et al. 1992, Burnham and Anderson 1998) we examined the effects of habitat variables on bird population dynamics for those metrics and species that exhibited significant spatial concordance. Following Burnham and Anderson (1998), models in each candidate set were ranked by second-order AIC differences (ΔAIC_c), and the relative likelihood of each model i was estimated with AIC weight (w_i).

In our first set of habitat information theoretic models, we entered each class of variables as a set. For example, if a model contained forest and urban variables, it included all nine forest and six urban variables. We used the weight sums ($\Sigma\ w_i$) of each variable class to rank them in terms of relative importance. As each variable class was entered into the same number of models, we did not feel it was necessary to weight w_i by the number of models containing a given class. We took the highest ranked class of habitat variables and used it in a second set of habitat information theoretic models. In this second set, the models ranged in parameter space from one variable to all variables in a given class.

We used spline correlograms to estimate spatial characteristics of habitat variables from the top-ranked information theoretic models ($\Delta AIC = 0$) for species that exhibited significant spatial concordance. We used 1000 bootstrap resamples to generate the confidence intervals for the covariance functions. We then compared the spatial scale of habitat synchrony with the spatial scale of avian synchrony. If the mean spatial scale of the habitat variable was larger than the mean of a bird's spatial scale, we considered the habitat variable to be a potential contributor to the bird pattern.

RESULTS

Regional population synchrony

Twenty-four of the 29 species exhibited significant local autocorrelation in population abundance over the 28-yr period (mean $\rho(0) = 0.15$, $SE = 0.01$; Table 1). The mean spatial extent (i.e., the x-intercept where $\rho = 0$) of local autocorrelation in population abundance for these 24 species was 420.7 km (SE = 30.0). The mean lower 95% CI spatial extent (hereafter "minimum spatial extent") was 114.9 km (SE = 20.4 km). Five of the 29 species exhibited significant local autocorrelation in annual population growth (mean $\rho(0) = 0.06$, SE =

TABLE 1. Extended.

S	
ρ(0)	*x*-intercept
0.54 (0.20, 1.0)	483.8 (386.9, 573.7)
0.14 (−0.07, 0.44)	401.8 (0, 519.6)
0.10 (−0.07, 0.34)	822.2 (0, 1093.8)
0.08 (−0.19, 0.45)	635.8 (0, 884.3)
0.35 (0, 0.86)	196.7 (0, 523.1)
0.36 (0.10, 0.71)	269.7 (165.8, 521.7)
−0.04 (−0.25, 0.21)	0 (0, 729.1)
0.12 (−0.01, 0.29)	711.7 (0, 876.0)
0.12 (−0.01, 0.28)	412.8 (0, 1291.6)
−0.05 (−0.22, 0.14)	0 (0, 588.5)
−0.11 (−0.30, 0.10)	0 (0, 317.7)
0.12 (−0.14, 0.43)	466 (0, 576.1)
0.99 (0.34, 1.0)	498.5 (437.1, 760)
0.27 (−0.01, 0.62)	285.0 (0, 613.2)
−0.02 (−0.17, 0.20)	0 (0, 906.9)
0.48 (0.21, 0.86)	233.0 (151.2, 722.3)
0.68 (0.24, 1.0)	393.2 (220.5, 491.0)
0.44 (0.15, 0.77)	554.9 (433.6, 716.4)
−0.09 (−0.40, 0.25)	325.0 (0, 591.9)
0.08 (−0.09, 0.33)	540.3 (0, 731.0)
0.32 (0.06, 0.35)	592.3 (196.6, 732.8)
0.22 (−0.04, 0.52)	149.6 (0, 627.7)
0.25 (0.03, 0.52)	318.2 (119.1, 486.9)
0.12 (−0.12, 0.27)	459.8 (0, 844.1)
0.41 (0.15, 0.82)	207.7 (137.4, 628.1)
0.06 (−0.20, 0.36)	82.7 (0, 529.6)
0.18 (−0.10, 0.54)	230.2 (0, 359.8)
0.46 (0.15, 0.49)	586.7 (240.6, 689.7)
0.19 (−0.02, 0.50)	213.1 (0, 665.8)

0.01; Table 1). The mean spatial extent of local autocorrelation in population growth for these five species was 457.8 km (SE = 80.3 km). The mean minimum spatial extent was 40.6 km (SE = 30.7 km). Ten of the 29 species exhibited significant local autocorrelation in population variability (as measured by time series SD; mean ρ(0) = 0.49, SE = 0.07; Table 1). The mean spatial extent of local autocorrelation in population variability for these 10 species was 413.8 km (SE = 47.1 km). The mean minimum spatial extent was 248.9 km (SE = 39.2 km).

When we included all species in our analysis, local autocorrelation was highest for population variability and population abundance, which were significantly different than growth rate ($F_{2,84} = 12.8$, $P < 0.0001$; Fig. 2A). There were no significant differences in the spatial extent of local autocorrelation among the three descriptors ($F_{2,84} = 1.36$, $P = 0.26$; Fig. 2B). However, there were significant differences in the minimum spatial extent ($F_{2,84} = 6.69$, $P = 0.002$; Fig. 2C); population abundance and variability exhibited greater minimum spatial extents of local autocorrelation than did rates of population change.

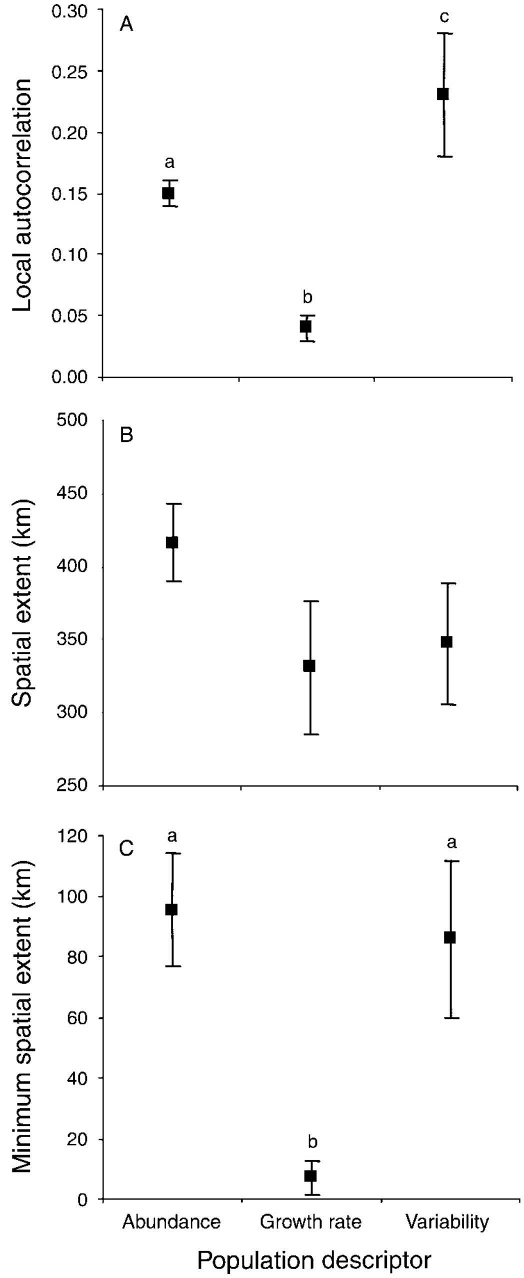

FIG. 2. (A) Strength and (B and C) extent of local autocorrelation (i.e., spatial synchrony calculated using nonparametric covariance functions) vary among population descriptors. Values presented are means ± SE ($n = 29$ species in each category). Lowercase letters denote significant differences between means as determined by Tukey-Kramer post hoc tests.

Spatial concordance

There was no significant concordance among the spatial distributions of population abundance for the six species with mean ρ(0) > 0.20 (global correlation = 0.09; 95% CL, −0.03, 0.21). There was significant concordance among the spatial distributions of population variability for the 10 species that exhibited a strong SD local autocorrelation (global correlation = 0.15; 95% CL, 0.12, 0.18; Fig. 3]. However, visual inspection reveals no consistent geographic pattern to where the foci of these areas of concordance were (Fig. 3).

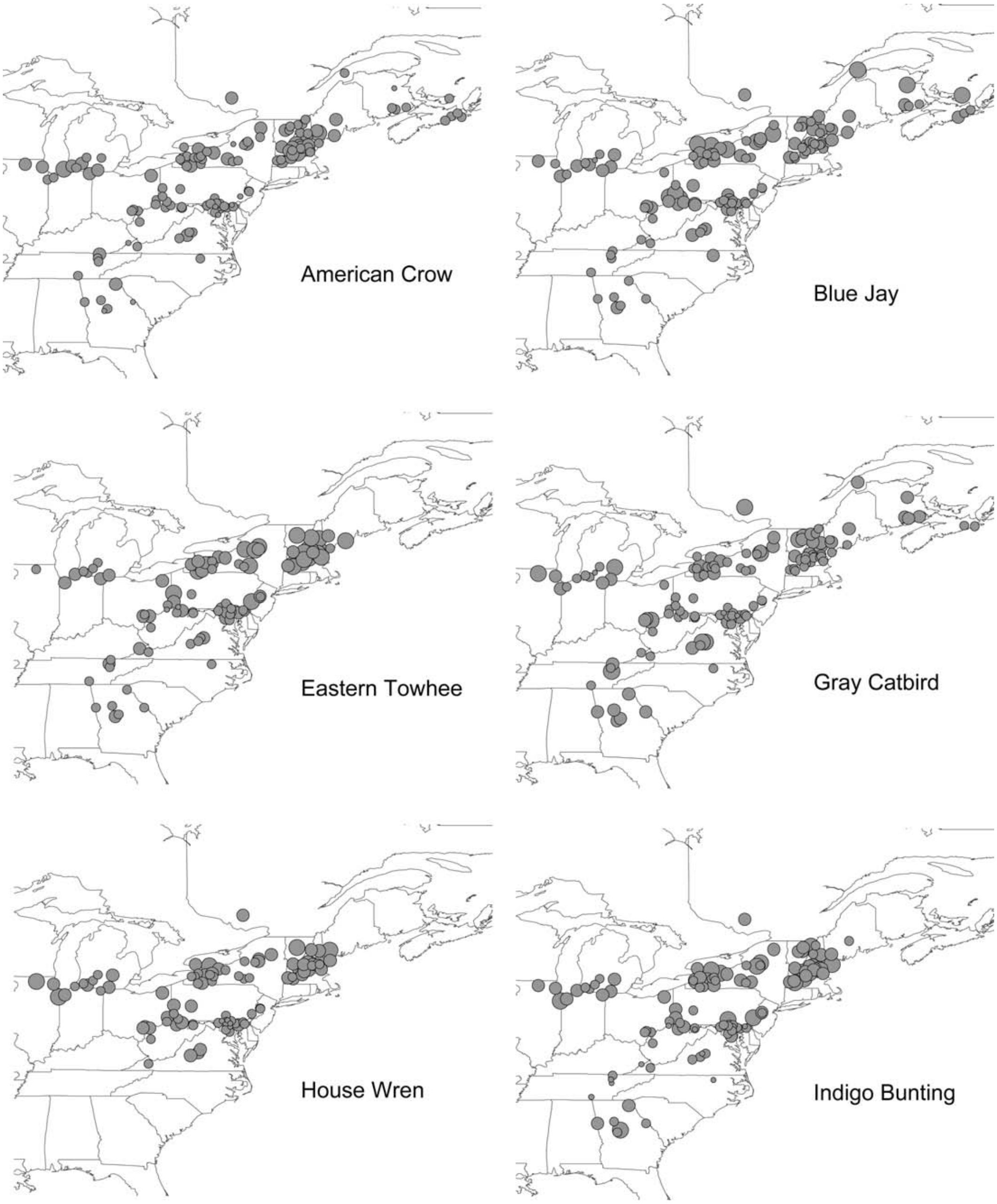

FIG. 3. Geographical distribution of population variability (SD values) for the 10 bird species in eastern North America with statistically significant spatial structure in population variability, based on North American Breeding Bird Survey (BBS) data from 1973 to 2000. Larger circles indicate higher population variability at a given BBS route. Within each of these species, BBS routes with high population variability tend to be located near one another, as do routes with low population variability.

Landscape effects

Analyses of the relationships between landscape and population variability data for the 10 species we included uncovered no clear relationships between bird population fluctuations and habitat features (detailed results are available in Appendix B). Briefly, in the first set of our habitat information theoretic models, wetland and urban variables had the highest weight sums in six of the 10 species (for wetland, Eastern Towhee, Grey Catbird, and Wood Thrush; for urban, House Wren, Ovenbird, and Red-eyed Vireo), while forest and cultivated variables had the highest weight sums in the other four (forest, American Crow and Blue Jay; cultivated, Indigo Bunting and Song Sparrow). Despite never being the most "important" class of variables, however, landscape variables (e.g., patch aggregation)

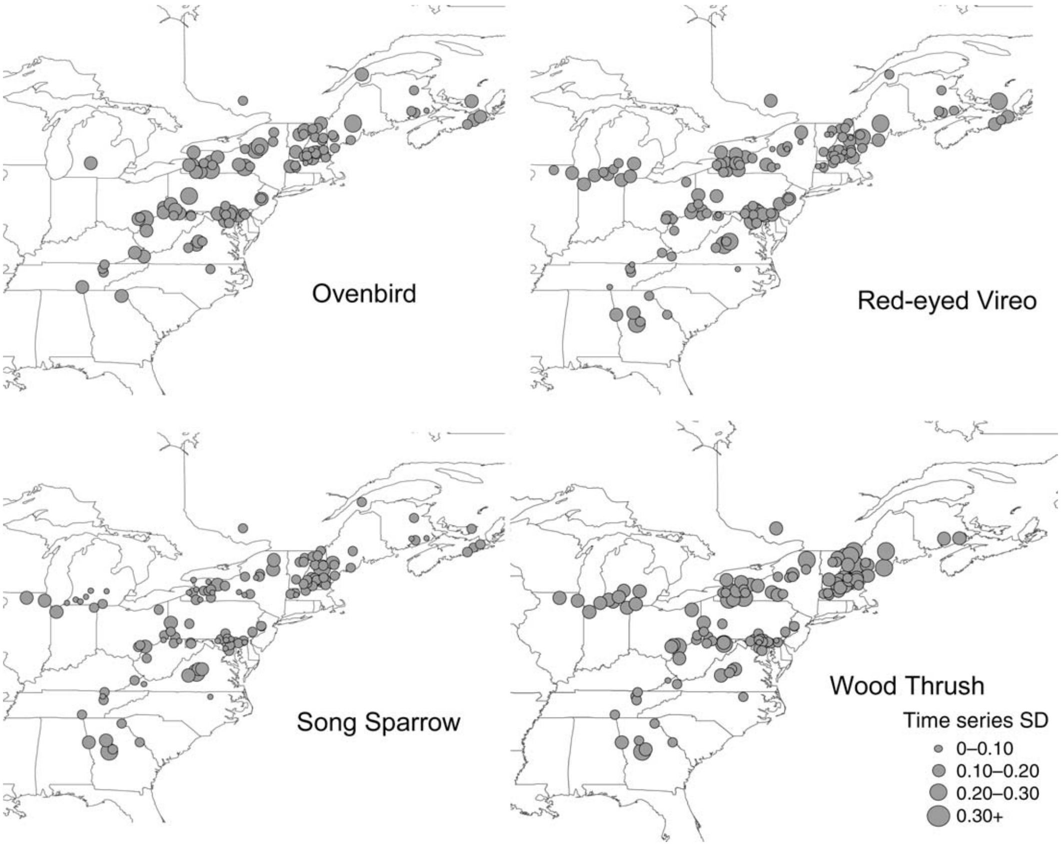

FIG. 3. Continued.

were the only class to be included in all 10 of the top ($\Delta\mathrm{AIC} = 0$) models.

For the two species with forest as the dominant habitat type (American Crow and Blue Jay), three habitat variables (EVEARE, MIXPER, and MIXARE) exhibited significant spatial synchrony at a scale that could have contributed to avian synchrony (Appendix B, Tables 2 and 3). American Crow population variability was positively affected by average evergreen forest patch size (EVEARE), while Blue Jay variability was negatively affected by average mixed forest patch size (MIXARE). For the three species with wetland as the dominant habitat type (Eastern Towhee, Gray Catbird, and Wood Thrush), four habitat variables (EHWPER, EHWARE, EHWENN, and WOWPER) exhibited significant spatial synchrony at a scale that could have contributed to avian synchrony (Appendix B, Tables 2 and 3), but only for the Gray Catbird. Gray Catbird variability was negatively affected by average woody wetland patch size (WOWPER) and by average distance between emergent wetland patches (EHWENN). For the three species with urban habitats as the dominant habitat type (House Wren, Ovenbird, and Red-eyed Vireo), two habitat variables (HIRARE and LIRARE) exhibited significant spatial synchrony at a scale that could have contributed to avian synchrony (Appendix B, Tables 2 and 3), but only for the Red-eyed Vireo. However, neither of these variables was ranked as one of the top two for this species. For the two species with cultivated habitats as the dominant habitat type (Indigo Bunting, and Song Sparrow), four habitat variables (PASPER, PASARE, PASENN, and ROWARE) exhibited significant spatial synchrony at a scale that could have contributed to avian synchrony (Appendix B, Tables 2 and 3), but only for the Song Sparrow. However, neither of these variables was ranked as one of the top two for this species.

Life history effects

Neither foraging strategy nor migratory strategy affected strength or spatial extent of local autocorrelation in population abundances (all $F < 1.87$, all $P > 0.17$). Similarly, there were no significant guild-based differences in the strength or spatial extent of local autocorrelation in rates of population change (all $F < 1.00$, all $P > 0.16$).

Foraging guilds exhibited no significant differences in the degree of local autocorrelation of population variability, although foliage and ground gleaners do appear higher than aerial and bark foragers ($F_{3,25} = 2.70$, $P = 0.07$; Fig. 4A). We detected no significant differences among foraging guilds for either spatial extent ($F_{3,25} = 1.15$, $P = 0.35$; Fig. 4B) or minimum spatial extent

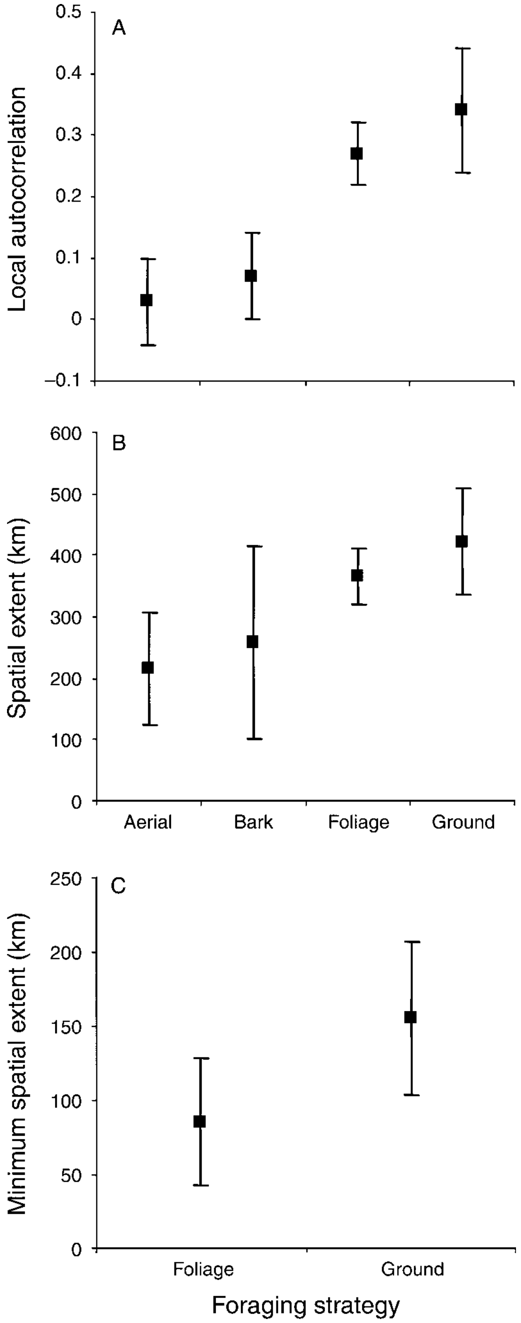

FIG. 4. (A) Strength and (B and C) extent of local autocorrelation (i.e., spatial synchrony calculated using nonparametric covariance functions) of population variability do not vary among foraging locations. Values presented are means ± SE.

($t_{19,0.05} = 1.05$, $P = 0.31$; all members of the aerial and bark guilds were 0 km for this metric; Fig. 4C).

We detected no significant differences among migratory guilds in the degree of local autocorrelation of population variability ($F_{2,26} = 2.74$, $P = 0.08$), although long-distance migrants do appear to show a weaker signal (Fig. 5A). There was a significant difference among migratory guilds in the spatial extent of local autocorrelation ($F_{2,26} = 5.02$, $P = 0.01$; Fig. 5B), with short-distance migrants having more extensive areas of local autocorrelation, but there were no significant differences in the minimum spatial extent of local

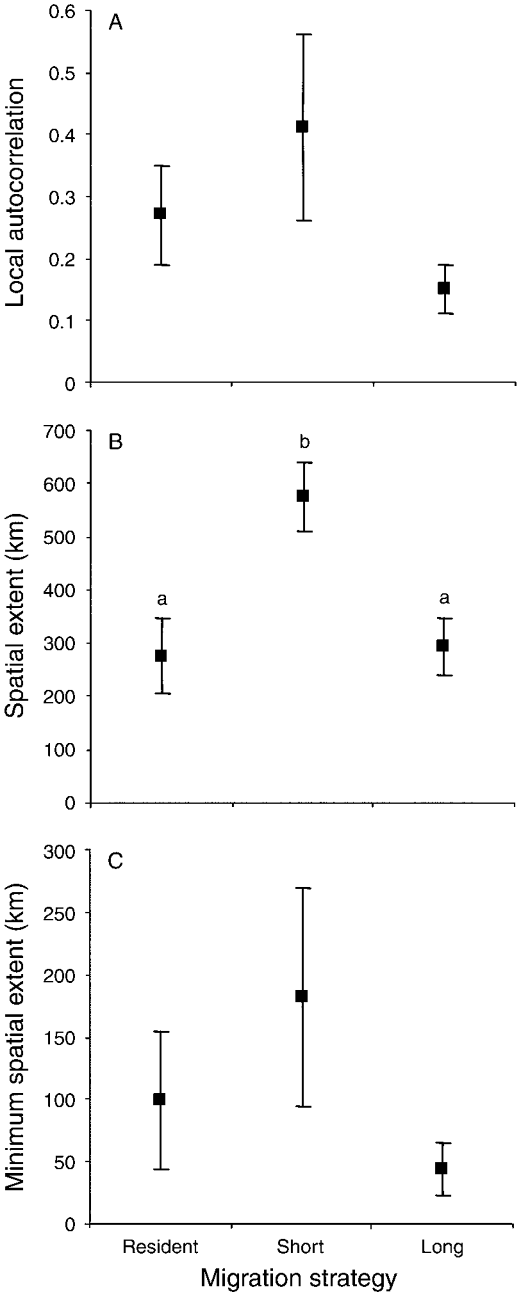

FIG. 5. The mean spatial extent of local autocorrelation (i.e., spatial synchrony calculated using nonparametric covariance functions) of population variability varies among (B) migratory strategies, but (A) local autocorrelation strength and (C) minimum spatial extent do not. Values presented are means ± SE. Lowercase letters denote significant differences between means as determined by Tukey-Kramer post hoc tests.

autocorrelation among migratory guilds ($F_{2,26} = 2.38$, $P = 0.11$; Fig. 5C).

DISCUSSION

Do bird populations in eastern North America exhibit spatial synchrony at regional scales?

The majority (83%) of the species tested exhibited significant spatial synchrony in abundance. While the average strength of this synchrony was low ($\rho(0) = 0.15$), it was spatially extensive; the average spatial extent of synchrony in abundance encompassed an area ~550 000 km^2 (diameter, ~840 km), and the average minimum spatial extent encompassed an area ~40 000 km^2 (diameter, ~230 km).

We know of only one other study that has examined North American breeding songbird population synchrony at similar spatial scales (Koenig 1998). Using a modified correlogram approach to analyzing North American Breeding Bird Study (BBS) data for California land birds (1968–1996), Koenig (1998) detected significant spatial synchrony in only a single species, the Mourning Dove (*Zenaida macroura*), out of 88 species tested. The striking differences between breeding population synchrony in California and eastern North America warrant further discussion, especially given the considerable overlap in the species tested; we detected significant spatial synchrony for eight species that did not exhibit significant patterns in California: American Crow, American Robin, Chipping Sparrow, Common Yellowthroat, House Wren, Northern Flicker, Song Sparrow, and Yellow Warbler. One possibility for these differences is a difference in the sensitivities of our analytical techniques; perhaps spatial nonparametric covariance functions are more appropriate for this type of data than are more traditional approaches (e.g., modified correlograms). If the differences are real (i.e., not a statistical artifact), they are a clear demonstration of how the appearance of spatial synchrony is strikingly scale and location dependent (Bjørnstad et al. 1999*a*).

Does the strength and spatial extent of spatial synchrony depend on which metric is analyzed?

While no species showed significant synchrony in growth rate or variability without also showing significant synchrony in abundance, there was a large discrepancy in the number of species displaying significant synchrony for each of the three population metrics (LN $> S > R$). Perhaps it is "easier" to regulate abundance and variability than growth rate, in the sense that more factors can potentially generate synchrony in abundance than in growth rate (Bjørnstad et al. 1999*a*). For example, it is easier to envision how climate patterns or weather patterns affect general conditions (e.g., good year vs. bad year), than it is to envision how the same patterns could influence the precise number of individuals being recruited into or leaving multiple populations.

Is there spatial concordance among species that exhibit spatial synchrony?

There was significant spatial concordance of population variability, the metric that showed the strongest signal among the 10 species with significant coefficients. However, very few habitat metrics exhibited significant spatial structure at a scale larger than that of the avian spatial synchrony or spatial concordance; consequently, most of these habitat variables likely are not significant contributing factors to the synchrony we detected (see Appendix B). We were only able to identify four habitat features for three bird species that may be contributing to spatial synchrony in population variability. American Crow populations tended to fluctuate more in landscapes characterized by large patches of evergreen forests. Blue Jay populations tended to fluctuate more in landscapes characterized by small patches of mixed forests. Gray Catbird populations tended to fluctuate more in landscapes characterized by small patches of woody wetland and less in landscapes characterized by widely dispersed emergent wetland patches. In general, percentage of landscape variables tended to exacerbate population variability, average patch area variables tended to minimize population variability, and the effect of nearest-neighbor distance was equivocal.

Is the strength and geographic extent of spatial synchrony affected by life history traits?

The species that exhibited significant spatial concordance of population variability represent a wide array of life history traits, including three of the four foraging categories and all migration categories (see Appendix A). However, the evidence for synchrony-generating effects of life history traits was equivocal and contrary to our expectations. Earlier studies have documented synchrony differences among dietary guilds (e.g., Koenig 2001; herbivores exhibit the strongest synchrony), while others have not (e.g., Paradis et al. 2000). In our study, there were very few differences in the strength or extent of spatial synchrony that we could attribute to differences in foraging strategies. There were suggestive differences in population variability among guilds, with foliage- and ground-gleaning birds exhibiting higher local autocorrelation then aerial or bark foragers. Foliage- and ground-gleaning birds in eastern North America tend to be insectivorous, with a strong reliance on a food resource (lepidopteran larvae) that tends to exhibit synchronous population fluctuations (Liebhold and Kamata 2000, Jones et al. 2003, Raimondo et al. 2004). The spatial extent of lepidopteran synchrony generally exceeds the values detected in this study (Liebhold et al. 2004); for example, North American gypsy moth populations exhibit significant synchrony at distances approaching 1200 km (Johnson et al. 2005). Therefore, if synchronous population fluctuations in food resources were solely influencing synchronous population fluctuations in bird populations, we would have expected a stronger association, similar to that found in Jones et al. (2003).

We did uncover significant differences in the spatial extent of synchrony among migratory guilds in population variability; all three synchrony descriptors showed the same pattern, with short-distance migrants showing stronger signals than either resident species or long-distance migrants. Koenig (1998) found that terrestrial migratory birds in California tended to exhibit stronger synchrony than nonmigratory species, but, in a later analysis of a different data set (continental North America; Koenig 2001), he uncovered no effect of migration. Other long-term, large-scale efforts have not detected significant migration effects (Paradis et al. 1999, 2000). Any effect of migration on spatial synchrony is likely due to the effect of dispersal. However, while dispersal's positive influence on spatial synchrony has been predicted in theory (Holmes et al. 1994, Ranta et al. 1995, Kendall et al. 2000), empirical evidence has been slow to accumulate (Paradis et al. 1999, Bellamy et al. 2003). In birds, breeding (i.e., adult) dispersal and natal dispersal are positively correlated with the strength of synchrony (Paradis et al. 1999), and migrants tend to disperse farther than residents (Sutherland et al. 2000). Based on these expectations, it is puzzling why, in our study, short-distance migrants consistently exhibited the strongest synchrony signals. One possibility is that populations of short-distance migrants may be additionally synchronized by harsh winter conditions in the southeastern United States (Holmes and Sherry 1988, Mehlman 1997). This latter hypothesis, however, does not explain why short-distance migrants exhibited higher synchrony than year-round residents in this data set; this difference is likely due to high dispersal tendencies of short-distance migrants and indicates that dispersal may be a stronger synchronizing agent than climate (i.e., a Moran effect) for these birds.

The tendency of short-distance migrants to have higher synchrony than long-distance migrants in this study is the opposite of what we found in our earlier, more local study (Jones et al. 2003). One possible explanation may lie in the scale of synchronizing factors (e.g., weather vs. prey availability). Another is that the difference is a sampling artifact; due to sampling and statistical constraints, we were unable to include many short-distance migrants in our earlier analyses and manuscript, and those we did include were generally found at low abundance, thereby limiting our ability to detect significant spatial synchrony.

The dissimilarity of the spatial extent of synchrony both within and across species suggests that most of the species we tested are not regulated at the same spatial scales. Our study shows that species differed in the strength and extent of spatial synchrony, despite, for the most part, being surveyed at the same place and time with the same methodology: species do have species-specific scaling. Finally, it is important to acknowledge that the scale of the covariance patterns we have described is likely much larger than the actual scale of population regulation and that, in turn, the scale of population regulation is larger than the scale of individual spatial requirements (Bjørnstad et al. 1999*b*).

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LITERATURE CITED

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petrov and F. Csaki, editors. Second international symposium on information theory. Akademiai Kiado, Budapest, Hungary.

Bellamy, P. E., P. Rothery, and S. A. Hinsley. 2003. Synchrony of woodland bird populations: The effect of landscape structure. Ecography 26:338–348.

Bjørnstad, O. N., and W. Falck. 2001. Nonparametric spatial covariance functions: Estimation and testing. Environmental and Ecological Statistics 8:53–70.

Bjørnstad, O. N., R. A. Ims, and X. Lambin. 1999*a*. Spatial population dynamics: Analyzing patterns and processes of population synchrony. Trends in Ecology and Evolution. 14: 427–432.

Bjørnstad, O. N., N. C. Stenseth, and T. Saitoh. 1999*b*. Synchrony and scaling in dynamics of voles and mice in northern Japan. Ecology 80:622–637.

Buonaccorsi, J. P., J. S. Elkinton, S. R. Evans, and A. M. Leibhold. 2001. Measuring and testing for spatial synchrony. Ecology 82:1668–1679.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Hanski, I., and I. P. Woiwod. 1993. Spatial synchrony in the dynamics of moth and aphid populations. Journal of Animal Ecology 62:656–668.

Haydon, D. T., N. C. Stenesth, M. S. Boyce, and P. E. Greenwood. 2001. Phase coupling and synchrony in the spatiotemporal dynamics of muskrat and mink populations across Canada. Proceedings of the National Academy of Sciences, USA 98:13149–13154.

Holmes, E. E., M. A. Lewis, J. E. Banks, and R. R. Veit. 1994. Partial differential equations in ecology: Spatial interactions and population dynamics. Ecology 75:17–29.

Holmes, R. T., and T. W. Sherry. 1988. Assessing population trends of New Hampshire forest birds: Local versus regional patterns. Auk 105:756–768.

Ims, R. A., and H. P. Andreassen. 2000. Spatial synchronization of vole population dynamics by predatory birds. Nature 408:194–196.

Johnson, D. M., A. M. Liebhold, O. N. Bjørnstad, and M. L. McManus. 2005. Circumpolar variation in periodicity and synchrony among gypsy moth populations. Journal of Animal Ecology 74:882–892.

Jones, J., P. J. Doran, and R. T. Holmes. 2003. Climate and food synchronize regional forest bird abundances. Ecology 84:3024–3032.

Kendall, B. E., O. N. Bjørnstad, J. Bascompte, T. H. Keitt, and W. F. Fagan. 2000. Dispersal, environmental correlation, and spatial synchrony in population dynamics. American Naturalist 155:628–636.

Koenig, W. D. 1998. Spatial autocorrelation in California land birds. Conservation Biology 12:612–620.

Koenig, W. D. 1999. Spatial autocorrelation of ecological phenomena. Trends in Ecology and Evolution 14:22–26.

Koenig, W. D. 2001. Spatial autocorrelation and local disappearances in wintering North American birds. Ecology 82:2636–2644.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecological Monographs 62:67–118.

Liebhold, A., and N. Kamata. 2000. Are population cycles and spatial synchrony a universal characteristic of forest insect populations? Population Ecology 42:257–266.

Liebhold, A., W. D. Koenig, and O. N. Bjørnstad. 2004. Spatial synchrony in population dynamics. Annual Review of Ecology, Evolution and Systematics 35:467–490.

McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: Spatial pattern analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst, Massachusetts, USA. ⟨http://www.umass.edu/landeco/research/fragstats/fragstats.html⟩

Mehlman, D. W. 1997. Change in avian abundance across the geographical range in response to environmental change. Ecological Applications 7:614–624.

Moran, P. A. P. 1953. The statistical analysis of the Canadian lynx cycle. II. Synchronization and meteorology. Australian Journal of Zoology 1:291–298.

Paradis, E., S. R. Baillie, W. J. Sutherland, and R. D. Gregory. 1999. Dispersal and spatial scale affect synchrony in spatial population dynamics. Ecology Letters 2:114–120.

Paradis, E., S. R. Baillie, W. J. Sutherland, and R. D. Gregory. 2000. Spatial synchrony in populations of birds: Effects of habitat, population trend, and spatial scale. Ecology 82: 2112–2125.

Post, E., M. C. Forchhammer, and N. C. Stenseth. 1999. Population ecology and the North Atlantic Oscillation (NAO). Ecological Bulletins 47:117–125.

Raimondo, S., M. Turcani, J. Patoeka, and A. M. Liebhold. 2004. Interspecific synchrony among foliage-feeding forest Lepidoptera species and the potential role of generalist predators as synchronizing agents. Oikos 107:462–470.

Ranta, E., V. Kaitala, J. Lindström, and H. Lindén. 1995. Synchrony in population dynamics. Proceedings of the Royal Society of London B 262:113–118.

Royama, T. 1992. Analytical population dynamics. Chapman and Hall, New York, New York, USA.

Sillett, T. S., R. T. Holmes, and T. W. Sherry. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288:2040–2041.

Stenseth, N. C., et al. 1999. Common dynamic structure of Canada lynx populations within three climatic regions. Science 285:1071–1073.

Stenseth, N. C., W. Falck, K.-S. Chan, O. N. Bjørnstad, M. O'Donoghue, H. Tong, R. Boonstra, S. Boutin, C. J. Krebs, and N. G. Yoccoz. 1998. From patterns to processes: Phase and density dependence in the Canadian lynx cycle. Proceedings of the National Academy of Sciences, USA. 95:15430–15435.

Sutcliffe, O. L., C. D. Thomas, and D. Moss. 1996. Spatial synchrony and asynchrony in butterfly population dynamics. Journal of Animal Ecology 65:85–95.

Sutherland, G. D., A. S. Harestad, K. Price, and K. P. Lertzman. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. Ecology and Society 4:16. ⟨http://www.ecologyandsociety.org/vol4/iss1⟩

Toms, J. D., S. J. Hannon, and F. K. A. Schmiegelow. 2005. Population dynamics of songbirds in the boreal mixedwood forests of Alberta, Canada: Estimating minimum and maximum extents of spatial population synchrony. Landscape Ecology 20:543–553.

APPENDIX A

Species included in synchrony analyses and their associated guilds (*Ecological Archives* E088-151-A1).

APPENDIX B

Detailed results for landscape–bird relationships (*Ecological Archives* E088-151-A2).