

Research Article

Population dynamics of songbirds in the boreal mixedwood forests of Alberta, Canada: estimating minimum and maximum extents of spatial population synchrony

Judith D. Toms^{1,*}, Susan J. Hannon¹ and Fiona K.A. Schmiegelow²

¹*Department of Biological Sciences, University of Alberta Edmonton, Alberta, Canada T6G 2E9;* ²*Department of Renewable Resources, University of Alberta Edmonton, Alberta, Canada T6G 2H1;* **Author for correspondence. Current address: Department of Statistics and Actuarial Sciences, University of Waterloo, 200 University Avenue West, Waterloo, Ontario, Canada N2L 3G1 (e-mail: jdtoms@math.uwaterloo.ca)*

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Abstract

Ecological phenomena vary over space and time and interpretation of these processes also varies depending on the measurement scale. As the spatial scale of observation increases and decreases, changes in population abundance will likely exhibit alternating patterns of asynchrony and synchrony. While the study of how and why population dynamics change with spatial scale of measurement is intrinsically interesting, most population ecologists seek to study mechanisms of population change on a discrete study area. Our study develops methods that population ecologists can use to determine spatially appropriate sampling designs, and demonstrates how such spatial scales can be determined for 25 species of songbirds using long-term data from the boreal mixedwood forest of Alberta, Canada. To determine minimum scales of synchrony in population dynamics, we calculated the average correlation of changes in population abundance over time across different numbers of fixed-radius point-count samples. We then used a randomization test to remove the effect of number of replicates from the determination of appropriate spatial scale. The maximum extent of synchrony was estimated as the distance where population dynamics were no longer correlated. Estimates of the minimum scale of synchrony differed between species, ranging from 3.1 to 18.6 ha. The maximum scale of synchrony was estimated to be greater than or equal to 8 km for 14 of the 25 species examined, and to be greater than or equal to 70 km for Tennessee Warbler (*Vermivora peregrina*). Maximum spatial extents were significantly correlated with body mass and territory size.

Introduction

One goal of population ecology is to characterize and understand variation in abundance of organisms over time and space. However, the patterns of abundance observed in any study depend on the

spatial and temporal scale of observation (Allen and Starr 1982; Carlile et al. 1989; Turner et al. 2001). Therefore, it is important to use spatial and temporal scales that are appropriate for the species being studied and the questions being asked. An appropriate temporal scale for studies of

population dynamics could be the length of a generation or breeding cycle (McArdle et al. 1990). Choosing an appropriate spatial scale for studies of population dynamics is more difficult.

Organisms are influenced by processes occurring on several spatial and temporal scales. Hence, observed temporal patterns of abundance will differ depending on the scales of observation (Carlile et al. 1989; Sutcliffe et al. 1996; Turner et al. 2001). Suppose that we wish to study the population dynamics of a species and want to determine the appropriate size of sampling units, the distance between sampling units and the maximum extent of our study area (or the boundary of our population). (For simplicity, here we define population dynamics as the change in population abundance over time, realizing that other demographic parameters are also changing.) Let us assume that there is a true emergent population dynamic at some scale. If we measure changes in population abundance at a spatial scale smaller than this scale, we might expect the true pattern to be confounded by the patchiness of habitats, interspecific competitive exclusion, sampling error or random variation (Sherry 1979; Thomas 1991; Qi and Wu 1996; Steen et al. 1996; Paradis et al. 2000). Similarly, if the bounds of our study area exceed this scale, the true pattern might be obscured due to regional differences in availability of suitable habitat within the study area or from lack of dispersal across the study area (Carlile et al. 1989; Thomas 1991; Sutcliffe et al. 1996). Thus, we expect alternating patterns of asynchrony and synchrony in population abundance as we increase the spatial scale of observation. Note that synchronous dynamics might occur at several spatial scales (e.g. local and regional; Thomas 1991).

We suggest that appropriate spatial scales for studies of population dynamics are those within a range of spatial scales where the temporal dynamics are synchronous, i.e. a range of spatial scales where a single temporal pattern of population dynamics occurs. We call the smaller end of such a range the minimum extent of synchrony and the larger end of such a range the maximum extent of synchrony, realizing that a different emergent population dynamic may exist at larger or smaller spatial scales. Both measures can be used to design population surveys: the minimum extent of synchrony would be the optimal size of

sample units (Greig-Smith 1952; Kershaw 1957; Mead 1974; Carlile et al. 1989). The maximum extent of synchrony could be used to decide how far apart study areas should be to ensure they are independent, since it defines a region within which sampling units are spatially autocorrelated (Carlile et al. 1989; Lichstein et al. 2002).

The appropriate range of scales for studying population dynamics is expected to be species-specific because of differences in life history characteristics or dispersal abilities of organisms (Paradis et al. 1999, 2000). For example, appropriate spatial scales may be roughly proportional to the size of home ranges or to body size (Wiens 1989; Holling 1992; Roland and Taylor 1997). Larger species often have larger territories due to greater mobility and energy requirements (Holling 1992; Bowman et al. 2002). Wider spacing of individuals in a landscape may, in turn, result in larger spatial scales of synchrony within the population (Roland and Taylor 1997). However, Koenig (1998) found no relationship between body mass and extent of spatial autocorrelation in birds, perhaps because territory sizes can differ widely for species with approximately equal body mass (e.g. Schoener 1968; Sherry and Holmes 1985). Our main objective in this paper was to estimate the minimum and maximum extents of synchrony in population dynamics for 25 species of songbirds in the boreal mixedwood forest. We also tested whether body mass and territory size were associated with the estimated spatial scales. We predicted that both body mass and territory size would be positively correlated with minimum and maximum extents of synchrony. Moreover, since territory size is more closely linked with the motility and spacing of a species in a landscape than body mass, we predicted the correlation with territory size would be stronger than with body mass.

Methods

Study areas and data

We used a subset of data (control sites) from the Calling Lake Fragmentation Study (Schmiegelow et al. 1997; Schmiegelow and Hannon 1999), located in north-central Alberta, Canada (55°15' N, 113°35' W; Figure 1).

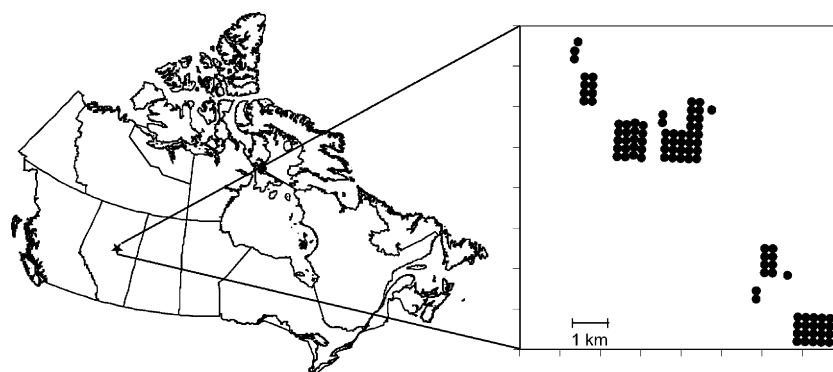


Figure 1. Location of the Calling Lake Fragmentation Study in north-central Alberta and configuration of control point-count stations.

The study area encompassed approximately 14,000 ha of boreal mixedwood forest, dominated by old (80–130) aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*). White spruce (*Picea glauca*), white birch (*Betula papyrifera*), black spruce (*Picea mariana*), jack pine (*Pinus banksiana*) and balsam fir (*Abies balsamea*) were also present. The Calling Lake Study included experimentally fragmented blocks, but we used only data from undisturbed control sites. Thus, sampling stations were not evenly distributed across the study area (Figure 1). Ninety-three stations were sampled from 1993 to 2002 (Schmiegelow et al. 1997; Schmiegelow and Hannon 1999; Schmiegelow, unpublished data).

Birds were surveyed using 100 m fixed-radius point counts at stations located 200 m apart on a grid (Schmiegelow et al. 1997). Each station was surveyed for 5 min, five times each breeding season (every 10 days from the third week of May to late June). The first survey period was not included in this study because most migrants were not yet breeding. We estimated annual abundance at each point as the maximum number of individuals observed over the four survey periods. In another study at Calling Lake, Toms (2004) found that maximum point-count abundance had a higher correlation with spot-mapping abundance estimated on the same grids than did mean point-count abundance. More details of the sampling design are available in Schmiegelow et al. (1997).

We examined extent of synchrony in 25 species that were relatively abundant. Information on

body mass and territory size for each species were obtained from the Birds of North America series (Table 1).

Population abundance data for 12 of these species (Black-capped Chickadee, Blue-throated Vireo, Chipping Sparrow, Connecticut Warbler, Least Flycatcher, Mourning Warbler, Ovenbird, Red-eyed Vireo, Rose-breasted Grosbeak, Tennessee Warbler, White-throated Sparrow and Yellow-bellied Sapsucker) were also available for the same years at another study area, Meanook, located 70 km south of Calling Lake in an agricultural landscape (Hannon 1993 and unpublished data). Forest composition and age were similar to Calling Lake. Seven stations were surveyed in a 140 ha block of forest using unlimited-distance point-counts. Points were surveyed for 6 min over four rounds at roughly 2–3 week intervals. Annual abundance at each station was estimated as the maximum number of individuals observed within 200 m of the station over the four survey periods. Although absolute densities were not comparable between the two study areas due to differences in survey methods, we expected that relative differences in density would be comparable. However, the limited extent of the Meanook study area (140 ha) meant the data were unsuitable for estimating appropriate spatial scales of population dynamics (as described below). We used data from Meanook only to determine if population dynamics there were correlated with those at Calling Lake. This allowed us to estimate maximum extents of synchrony beyond the extent of the Calling Lake study area.

Table 1. Life history parameters used as covariates^a.

Species	Body mass (g)	Territory size (ha)
American Redstart (<i>Setophaga ruticilla</i>)	8.6	0.7
Black-capped Chickadee (<i>Poecile atricapillus</i>)	12.0	3.4
Black-throated Green Warbler (<i>Dendroica virens</i>)	9.0	0.5
Blue-headed Vireo (<i>Vireo solitarius</i>)	15.3	3.0
Brown Creeper (<i>Certhia americana</i>)	8.4	4.3
Chipping Sparrow (<i>Spizella passerina</i>)	13.2	0.6
Connecticut Warbler (<i>Oporornis agilis</i>)	15.3	0.4
Least Flycatcher (<i>Empidonax minimus</i>)	10.5	0.1
Magnolia Warbler (<i>Dendroica magnolia</i>)	8.6	0.7
Mourning Warbler (<i>Oporornis philadelphia</i>)	12.3	0.7
Ovenbird (<i>Seiurus aurocapillus</i>)	22.1	1.0
Philadelphia Vireo (<i>Vireo philadelphicus</i>)	12.2	0.6
Pine Siskin (<i>Carduelis pinus</i>)	12.9	colonial
Red-breasted Nuthatch (<i>Sitta canadensis</i>)	10.5	5.1
Red-eyed Vireo (<i>Vireo olivaceus</i>)	20.4	0.7
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)	46.4	0.8
Swainson's Thrush (<i>Catharus ustulatus</i>)	29.8	1.5
Tennessee Warbler (<i>Vermivora peregrina</i>)	9.4	N/A
Warbling Vireo (<i>Vireo gilvus</i>)	11.9	1.5
Western Tanager (<i>Piranga ludoviciana</i>)	30.0	2.8
White-throated Sparrow (<i>Zonotrichia albicollis</i>)	25.2	1.0
Winter Wren (<i>Troglodytes troglodytes</i>)	9.1	2.4
Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>)	50.3	2.0
Yellow-rumped Warbler (<i>Dendroica coronata</i>)	12.6	0.6
Yellow Warbler (<i>Dendroica petechia</i>)	9.8	0.3

All values were obtained from the Birds of North America series.

^aMorse (1993), Pitochelli (1993), Smith (1993), Briskie (1994), Falls and Kopachena (1994), Hall (1994), Van Horn and Donovan (1994), Moskoff and Robinson (1996), Dawson (1997), Pitochelli et al. (1997), Sherry and Holmes (1997), Hunt and Flaspohler (1998), James (1998), Middleton (1998), Rimmer and McFarland (1998), Ghalambor and Martin (1999), Hudon (1999), Lowther et al. (1999), Cimprich et al. (2000), Evans Mack and Yong (2000), Gardali and Ballard (2000), Hejl et al. (2002a, b), Walters et al. (2002) and Wyatt and Francis (2002).

Minimum extent of synchrony

Abundance estimates of a species at adjacent point-count stations may not be identical due to random variation, habitat patchiness or territories that are offset from the sampling grid. This random or sampling variation will obscure trends in spatial autocorrelation of abundance patterns. Therefore, we determined the scale at which synchrony in temporal patterns of abundance developed using 10 years of data from Calling Lake.

Following Greig-Smith (1952); Kershaw (1957) and Mead (1974), we first clustered adjacent point-count stations into sampling units of increasing sizes (e.g. we first used individual point-count stations, then pairs of stations, then four stations, etc.) and for each sampling unit (single point or cluster of points) determined average abundance for each species over the 10 years. We then calculated the correlation of abundance over time

between adjacent sampling units and averaged these correlations over all sampling units at that scale. For example, at the scale of two point-count stations, we would average the maximum abundance of the study species over two adjacent stations for each year, calculate its correlation with abundance over time at the adjacent two stations, and finally calculate the average of these correlations for all adjacent pairs in the study area. However, correlations between averages necessarily increase with the number of stations being averaged (Wiegert 1962). Therefore, we used a randomization test to decouple this effect from the determination of appropriate spatial scale. For each run of the randomization test, we clustered random point-count stations (instead of adjacent stations) and calculated the average correlation between random clusters. Correlations resulting from 1000 runs were then tabulated, and compared with the observed correlation to determine

the significance level. This value represented the probability that a correlation greater than or equal to the observed value would be expected for clusters randomly selected from the study area, and does not measure the degree of synchrony in population dynamics. For example, if the population dynamics were highly synchronous across the entire study area we would expect a high (insignificant) p -value, since adjacent clusters would be only slightly more synchronous than clusters selected at random. Thus, for each species, the cluster size with the smallest p -value (the optimal cluster) was used as a measure of the minimum extent of synchrony, even if the p -value was not significant.

Maximum extent of synchrony

In order to determine the maximum extent of synchrony, we examined the spatial autocorrelation in temporal abundance patterns at Calling Lake. First, we calculated the average temporal pattern of abundance for each optimal cluster, as estimated above. Then we plotted the correlations between these abundance patterns for all pairs of clusters against the distance between these pairs of clusters. The correlation should decrease with increasing distance, until the dynamics are no longer correlated (i.e. are asynchronous).

The spatial autocorrelation was quantified using spline correlograms (Bjørnstad and Falck 2001), a nonparametric technique. This method uses a kernel smoother to estimate the pattern of spatial autocorrelation, rather than assuming any particular parametric function, and is asymptotically equivalent to the spatial Mantel correlogram (Bjørnstad and Falck 2001). Confidence bounds on the estimates were obtained using bootstrapping routines described by Bjørnstad and Falck (2001). The maximum extent of synchrony was defined as the distance where the correlation equaled zero, since confidence bounds were quite wide for most species.

Population dynamics for twelve species were also obtained at Meanook. For these species, we fit another set of spline correlograms using data from both study areas to determine whether significant spatial autocorrelation occurred at distances ≥ 70 km (i.e. beyond the 10 km extent of the Calling Lake study area).

Covariates

We determined whether the minimum and maximum extents of synchrony were correlated with body mass and territory size using Spearman's rank correlation tests.

Results

The estimated minimum extents of synchrony comprised 3.1 or 6.2 ha (i.e. one or two point-count stations) for approximately half the species examined (13 of 25; Table 2).

However, over a quarter of the species (7 of 25) had optimal cluster sizes of 18.6 ha, the largest minimum scale examined due to sample-size restrictions. At these scales, the average correlation in population dynamics within a cluster ranged from 0.03 to 0.61. Population dynamics of most species were not more highly correlated within a cluster than would be expected by randomly creating clusters in the study area.

Estimates of maximum scale of synchrony were greater than or equal to 8 km for 15 of 25 species at Calling Lake, where sample sizes became severely restricted due to the bounds of the study area (Table 2, Figure 2).

Lower confidence bounds indicated that Blue-headed Vireo, Red-breasted Nuthatch, Red-eyed Vireo, Tennessee Warbler and White-throated Sparrow were significantly correlated at distances greater than 8 km.

Population dynamics for twelve of these species were also surveyed at Meanook, so we could determine whether dynamics at Calling Lake and Meanook were correlated. Of these species, only Tennessee Warbler was significantly autocorrelated to distances ≥ 70 km. Least Flycatcher, Mourning Warbler, Ovenbird, White-throated Sparrow and Yellow-bellied Sapsucker had correlations in population dynamics between study areas that were consistent with those at Calling Lake, but not significantly different from zero.

Maximum scales of synchrony were positively correlated with body mass ($\rho = 0.407$, $p = 0.051$) and territory size ($\rho = 0.402$, $p = 0.066$). However, minimum scales were not related to either covariate (body mass $\rho = -0.044$, $p = 0.826$; territory size $\rho = -0.100$, $p = 0.639$).

Table 2. Estimated minimum and maximum scales of synchrony in population dynamics of boreal songbirds at Calling Lake in north-central Alberta.

Species	Minimum scale			Maximum scale (km)	
	Area (ha)	Corr. (r)	<i>p</i> -value	Estimate	Lower CI
American Redstart	3.1	0.08	0.20	2.0	1.2
Black-capped Chickadee	6.2	0.19	0.10	> 10.0	6.5
Black-throated Green Warbler	6.2	0.03	0.75	4.6	3.1
Blue-headed Vireo	3.1	0.09	0.20	> 10.0	8.7
Brown Creeper	18.6	0.18	0.28	0.0	0.0
Chipping Sparrow	18.6	0.25	0.55	> 10.0	4.2
Connecticut Warbler	15.5	0.23	0.45	> 10.0	0.0
Least Flycatcher	3.1	0.11	0.40	9.6	3.3
Magnolia Warbler	18.6	0.24	0.10	4.6	0.0
Mourning Warbler	9.3	0.22	0.02	> 10.0	2.8
Ovenbird	18.6	0.56	0.01	> 10.0	6.0
Philadelphia Vireo	6.2	0.10	0.25	6.1	0.0
Pine Siskin	6.2	0.21	0.30	> 10.0	0.0
Red-breasted Nuthatch	3.1	0.31	0.01	> 10.0	> 10.0
Red-eyed Vireo	3.1	0.14	0.15	> 10.0	> 10.0
Rose-breasted Grosbeak	6.2	0.28	< 0.01	> 10.0	1.5
Swainson's Thrush	12.4	0.15	0.30	5.1	0.0
Tennessee Warbler	3.1	0.61	0.17	> 10.0	> 10.0
Warbling Vireo	9.3	0.19	0.02	6.7	0.0
Western Tanager	12.4	0.11	0.35	6.0	0.0
White-throated Sparrow	6.2	0.43	0.31	> 10.0	8.6
Winter Wren	18.6	0.49	0.30	> 10.0	7.4
Yellow-bellied Sapsucker	6.2	0.18	0.05	> 10.0	2.3
Yellow-rumped Warbler	18.6	0.27	0.15	2.2	0.0
Yellow Warbler	18.6	0.48	0.05	2.4	1.6

The minimum scale estimated the area required for correlation in population dynamics to develop; also tabulated are the average correlation between adjacent point-count stations, and the probability that correlation was greater than expected for random clusters of stations. The maximum scale estimated the distance where correlations in population dynamics were no longer significantly correlated, and the lower 90% confidence bound on this estimate.

Discussion

The appropriate spatial scale for a given study depends on the questions and organisms being studied. Here, we demonstrated an approach that estimated appropriate spatial scales for examining changes in abundance of a population over multiple years. Most analyses of spatial autocorrelation of abundance in songbirds have used a single year of data for each location (e.g. Brown et al. 1995; Beard et al. 1999; Moskát 2000; Lichstein et al. 2002), although some have applied multi-year approaches (e.g. Koenig 1998, 2001). Methods that estimate spatial scales using a single year of data on population abundance do not estimate scales of synchrony in population dynamics. Thus, they may not be a reliable predictor of the extent of spatial autocorrelation in the future, since environmental variables and species interactions

might influence the scale observed in any single year.

We found that the optimal area of sampling units (i.e. minimum extent of synchrony) differed between species, ranging from 3.1 to 18.6 ha. However, sampling units greater than 18.6 ha were not examined, so optimal sizes could be larger than estimated. Estimating the minimum extent of synchrony should reduce the variation due to sampling with smaller than optimal units and thus improve estimates of the maximum extent of synchrony. The randomization procedure we applied permitted selection of the best cluster size available. The *p*-values associated with this test should not be used as an indication of the strength of synchrony in population dynamics, however. The test compared the observed synchrony with that expected under a random distribution within the region or study area. Thus, if population dynamics

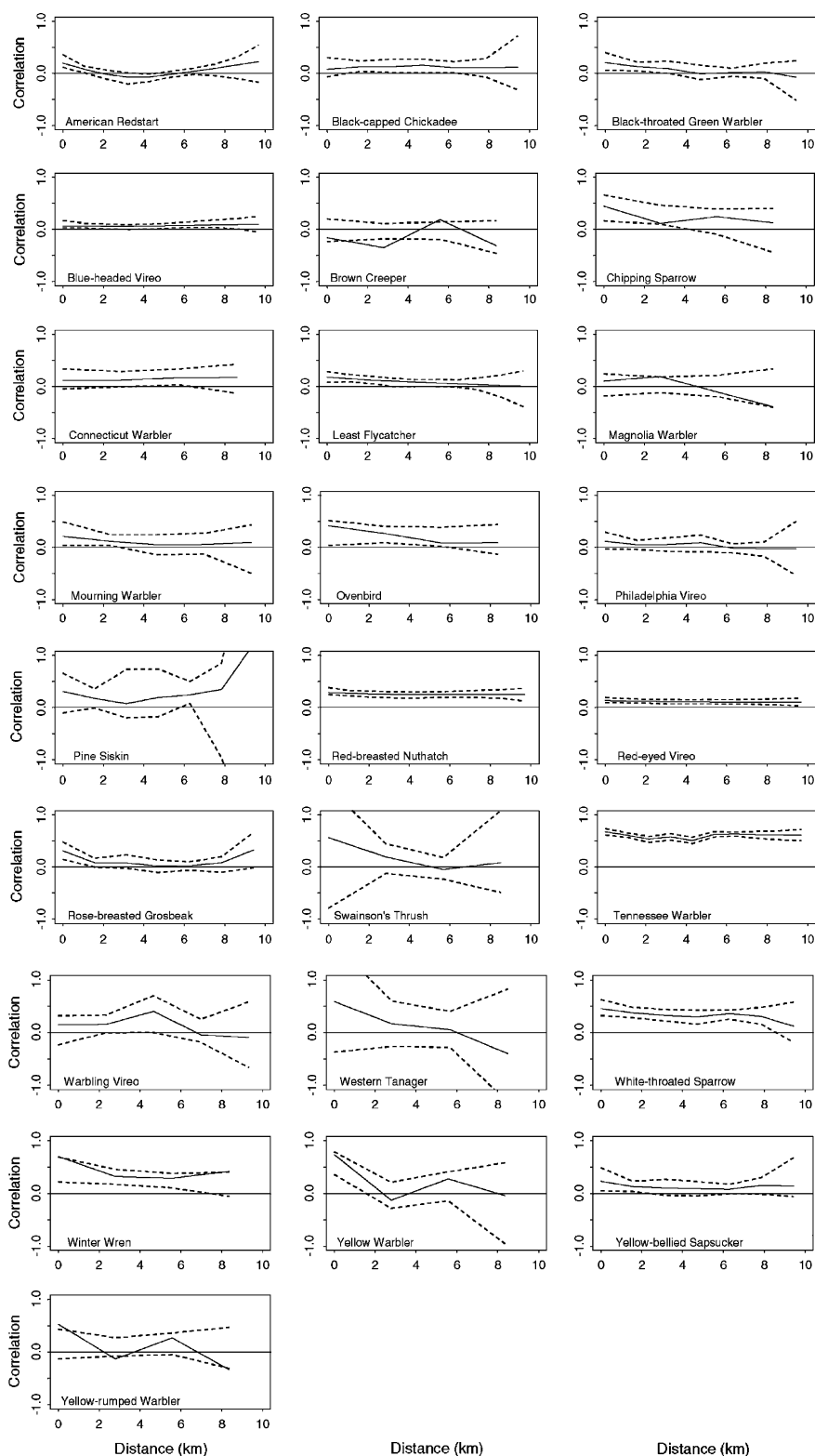


Figure 2. Spatial autocorrelation of temporal patterns of population dynamics (10 years) for 25 species at Calling Lake used to estimate maximum extents of synchrony. Solid lines are estimates, dotted lines are 90% confidence intervals.

were homogeneous across the entire study area, adjacent clusters would be only slightly more synchronous than clusters selected at random.

Koenig (1998, 2001), using multiple years of data from California and across North America, found significant autocorrelation (maximum extents of synchrony) in abundance of some wintering songbird species over very large distances (hundreds of kilometers), but not in others. There was no evidence for significant autocorrelation in abundance of breeding bird populations in California at the scales examined (but the first distance interval was 0–100 km; Koenig 1998). Using only single years of data, others have found significant correlations (i.e. maximum extents of synchrony) in abundance of breeding songbirds at a few hundred metres (data from Hungary; Moskát 2000), a minimum of 3 km (data from Tennessee and North Carolina, USA; Lichstein et al. 2002) and over several hundred kilometers (data from across North America; Brown et al. 1995). Our estimates of the extent of synchrony in population dynamics are consistent with the variation seen previously in estimates of the extent of synchrony in population abundance; estimated maximum extents of synchrony in population dynamics vary widely across species, with little or no spatial autocorrelation for some species, but significant autocorrelation to a minimum of 8 km for 15 of the 25 species examined at Calling Lake, Alberta.

Moreover, analyses using data from both study areas showed that Tennessee Warblers were significantly autocorrelated to distances ≥ 70 km. Tennessee Warblers are thought to be specialist predators on spruce budworm (*Choristoneura fumiferana*), and exhibit large annual changes in breeding density (Morris 1958; Rimmer and McFarland 1998). Tennessee Warblers have relatively low breeding-site fidelity compared with other warbler species (Rimmer and McFarland 1998), suggesting that they may have higher vagility. Hence, its population dynamics may be synchronized over larger areas than are typical for a bird of this body mass. Five additional species (Least Flycatcher, Mourning Warbler, Ovenbird, White-throated Sparrow and Yellow-bellied Sapsucker) had insignificant but positive correlations in population dynamics between study areas. Given the limited number of point-count stations available for comparison, it is possible that some of these species have population dynamics that are corre-

lated over greater distances than 10 km. Autocorrelation at these scales could result from dispersal or from external stochastic events synchronizing dynamics of neighbouring areas (Paradis et al. 1999, 2000). However, the cause of the spatial autocorrelation was not addressed in this study.

Both body mass and territory size were significantly correlated with the maximum extent of synchrony in population dynamics, but not with the minimum extent of synchrony. Estimation of minimum spatial scales was limited by sample sizes, so appropriate minimum scales could be larger than estimated. This could have affected the strength of any relationship between minimum scales and covariates, although correlations were estimated to be near zero. Territory size had a slightly weaker correlation than body mass, counter to what we predicted. However, the estimates of territory sizes used were largely derived from studies in other parts of North America, and may not be typical of territory sizes in this region. Koenig (1998) found no relationships between body mass and maximum scales of synchrony in abundance of wintering bird populations in California. Our study differs in many respects, which might explain these differences (i.e. we studied dynamics of breeding populations in a different suite of species and a different ecosystem). Nevertheless, our results should be corroborated before body mass or territory size alone are used to predict appropriate spatial scales.

Given the limited extent of the area surveyed in this study (ca. 140 km²), neither minimum nor maximum extents of synchrony could be estimated with certainty. It would be useful to conduct similar analyses with stations scattered over a larger spatial extent and with larger groups of stations to improve the estimates of minimum and maximum extents of synchrony for these species. Nevertheless, we conclude based on these and previous results, that the appropriate spatial scale for examining temporal changes in abundance seems to be species-specific.

Multi-year approaches are necessary to provide reliable estimates of the spatial extents of synchrony in population dynamics. However, when designing a monitoring program in a new area or for new species, it is not desirable to spend several years estimating appropriate spatial scales for sampling. Therefore, is there any way to predict appropriate scales *a priori*? We found that both body mass and territory size were correlated with

the maximum scale of synchrony in population dynamics. However, rank correlations were approximately 0.4, so this provides only a rough approximation. Furthermore, only a limited range of body masses and territory sizes were examined in this study, and the result may not hold when extrapolated outside the ranges observed here. Clearly, more study is required on a broader array of species, on larger areas, and in different regions.

Population dynamics can become synchronized in space through Moran effects (stochastic events that perturb reproductive success or survival over a large area) or dispersal (Ranta et al. 1995, 1999). If the environmental or habitat variables that synchronize population dynamics are known, one could use the spatial scales of these variables to estimate the appropriate scales for monitoring systems. However, results from a complementary study in the same region described here suggest that population dynamics of the study species may be independent of several potential synchronizing factors, namely weather during breeding and wintering seasons, insect outbreaks, cone crops, and fires (Toms 2004).

Therefore, the simplest and most robust approach may be to directly estimate appropriate spatial scales using available data. For example, in North America, Breeding Bird Survey data (<http://www.mbr-pwrc.usgs.gov/bbs>) could be used to estimate maximum extents of synchrony in population dynamics of birds, even though they are not amenable to estimating minimum extents of synchrony. If no data are available for the species or region of interest, data for nearby regions and similar species may provide a rough gauge of the spatial scales that are appropriate for examining changes in abundance of a population over multiple years. Body mass or territory size could also be cautiously used to predict these scales. Despite these difficulties, we feel that the analytical approaches outlined here will provide more robust estimates of appropriate spatial scales for studies of population dynamics than ad-hoc or single-year estimation approaches.

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