How far do songbirds disperse?

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Dispersal distances determine the scales over which many population processes occur. Knowledge of these distances may therefore be crucial in determining the appropriate spatial scales for research and management. However, dispersal distances are difficult to measure, especially for vagile organisms like songbirds. For these species, the use of traditional mark–recapture and radio-telemetry methods is problematic. We used positive one-year time-lagged correlations in abundance to estimate natal dispersal distances. Using the North American Breeding Bird Survey database, we examined one-year time-lagged correlations between pairs of North American songbird samples separated by 10–100 km. We submit that consistent positive one-year time-lagged correlations reflect the exchange of individuals through dispersal. We found positive one-year time-lagged correlations between pairs of samples from 25 different songbird species. The median distances of these correlations ranged from 15 to 95 km, depending on the species. These distances were positively correlated with body size and wing length. Dispersal appears to be the most parsimonious explanation for the time-lagged correlations we observed in these species. The putative dispersal distances we measured are generally an order of magnitude longer than those reported in the literature.

Dispersal has been defined as the movement of individuals for the purpose of reproduction (Greenwood 1980). The distance over which dispersal occurs determines the rate of spread of invasive species (Hengeveld 1994), gene flow (Neigel and Avise 1993), and the spatial scales of metapopulation (Harrison 1989) and source-sink dynamics (Paradis et al. 1998, Tittler et al. 2006) and predator-prey interactions (Neubert et al. 1995). However, dispersal distances are difficult or impossible to measure for many organisms. Mark–recapture techniques can be used (Shields 1984), but if most individuals disperse beyond the range of sampling, distances will be underestimated. This is likely the case for natal dispersal among songbirds, for which recapture rates of individuals marked as juveniles are typically low, on the order of 5% or less (Fleischer et al. 1984, Payne 1991, Weatherhead and Forbes 1994). Given the significance of natal dispersal in songbird demography and the difficulty in measuring natal dispersal distances, we applied the one-year time-lagged model presented in Tittler et al. (2006) to estimate typical natal dispersal distances for as many North American songbird species as possible.

This one-year time-lagged model stems from the literature on spatial synchrony in population dynamics or size (see Liebhold et al. 2004 for review). Within-year synchrony has been recorded for many different organisms over many different spatial scales, from protists over tens of centimeters (Holyoak and Lawler 1996) to birds (Paradis et al. 1999) and mammals (Ranta et al. 1997) over hundreds or even thousands of kilometers. The degree of within-year synchrony generally declines with distance (Liebhold et al. 2004). Within-year synchrony is thought to be caused by some combination of Moran effects (synchronized stochastic events), interactions with other species or diseases that are themselves synchronized, and dispersal (Liebhold et al. 2004). Because songbirds disperse between breeding seasons, we expect that these movements will produce one-year time-lagged rather than within-year correlations (Tittler et al. 2006). Thus, if within-year spatial synchrony is controlled for, the distances over which one-year time-lagged effects are detected will reflect dispersal distances.

Dispersal distances have been found to be positively correlated with body mass in birds and other taxa (Paradis et al. 1998, Sutherland et al. 2000). Studies also indicate positive correlations between measures of wing size and flight distance or speed among insects (Suzuki and Kunimi 1981, Peterson 1987) and birds (Kullberg et al. 2005). More specifically, Skjelseth et al. (2007) found a correlation between wing length and dispersal distance in adult female house sparrows *Passer domesticus*. Thus, if the distances over which one-year time-lagged effects are detected correspond to dispersal movements, we predict that measures of bird morphology such as body mass and wing length will be positively correlated with these species-specific lagged correlation distances.

It has been suggested that there should be differences in dispersal distances between migrant and resident birds. It is generally hypothesized that migrants disperse farther than residents because they move greater distances in general (Paradis et al. 1998, Sutherland et al. 2000, Winkler et al. 2005). However, if the process of natal dispersal is carefully considered, we might hypothesize the opposite. Very little is known about when or how young select their first breeding sites, but two modes of dispersal seem possible: 1) the young spend the time between fledging and the onset of winter or migration exploring possible breeding sites for the following year, or 2) the young return to their natal areas in the spring and begin their search from there. If dispersal occurs in either one of these ways, residents would have more time to spend in this search than migrants, and might therefore be expected to disperse farther. Although young residents may be less likely to disperse than young migrants (Weatherhead and Forbes 1994), there is little if any reason to believe that when they disperse, residents do not disperse farther than migrants.

In this study, we examined positive one-year time-lagged correlations in abundance between paired samples of 51 North American songbird species, suggesting that these are estimates of typical natal dispersal distances. We regressed the distances separating these samples (lagged correlation distances) against the wing length and body mass of the corresponding species to test for significant positive correlations, which would strengthen the inference that the distances separating samples linked by positive one-year time-lagged correlations reflect typical dispersal distances. We also tested whether migrants and residents differed in terms of these distances.

Methods

We used the long-term, continent-wide roadside point count data collected by volunteers for the North American Breeding Bird Survey (BBS) (Sauer et al. 2005). From this dataset, we extracted the total abundance of each species at the first 10 stops (defined as a "sample") of each 50-stop route. We restricted our analyses to the first 10 stops because these are run early in the morning; since daily songbird detection rates decline markedly with time since the pre-dawn chorus (Robbins 1981), these first 10 stops are much more reliable than the other 40 stops. We then calculated one-year time-lagged correlations between samples separated by different distances, calculating distances between all pairs of samples based on the latitude-longitude coordinates for each route and using the nearest features extension (Jenness 2002) in Arcview 3.2 (Environmental Systems Research Inst. 1992). The number of correlations examined varied from one species to the next depending on data availability, as described below. We used SPSS 12.0 (Apache Software Foundation 2003) for all statistical analyses unless otherwise stated.

For each species, we tested for positive one-year time-lagged correlations (hereafter one-year time-lagged correlations) between samples over the entire time-period available for all possible pairs of samples at each of nine distance classes from 10 to 100 km (i.e. for samples 10–20, 20–30, . . . and 90–100 km apart). We did not consider distances

>100 km because this would have severely limited our sample size. That said, we did examine distances of up to 200 km among wood thrush *Hylocichla mustelina* populations (Tittler et al. 2006), and found that the number of significant positive correlations dropped off beyond 100 km. We could not examine distance classes of <10 km because the samples themselves were composed of transects of ~7.2 km in length (Sauer et al. 2005); it would not make sense for distances between samples to be less than those within samples. We paired the data from year t in one sample with those from year t −1 in the other to determine whether the abundance in the former was influenced by that in the latter.

The likelihood of confounding temporal and spatial autocorrelation in the data invalidated the use of simple regression or correlation analyses. Due to spatial autocorrelation, positive same-year correlations between samples would be expected (Koenig 1998), i.e. correlations between B_t and A_t, and between B_{t-1} and A_{t-1} (where A and B are samples and t is time in years). Due to temporal autocorrelation, positive correlations in abundance from one year to the next within individual samples would also be expected, i.e. between A_t and A_{t-1} and between B_t and B_{t-1}. Therefore, a positive correlation between B_t and A_{t-1} would be expected simply because of the correlation between B_t and B_{t-1} and between B_{t-1} and A_{t-1}. To identify any effect of A_{t-1} on B_t, we first accounted for the effects of B_{t-1} by forcing this term into a multiple regression before examining the effect of interest (A_{t-1}). In other words, we looked for the effect of one sample on the residuals of the other, once the temporal and spatial autocorrelation trends had been removed. In studies of within-year synchrony, this type of analysis has been termed "detrending" (Liebhold et al. 2004) or "prewhitening" (Paradis et al. 1999). The regression equation for each species at each distance class was

$$B_t = kB_{t-1} + lA_{t-1} + m$$

where B is the abundance in one sample, A is the abundance in the other sample, t is time in years, k and l are coefficients, and m is a constant. We ran all analyses two ways, examining the possible effects of A_{t-1} on B_t, and of B_{t-1} on A_t and considering the results separately (i.e. if A_{t-1} was positively correlated with B_t and B_{t-1} was positively correlated with A_t, we considered this to be two separate correlation events).

These analyses were limited in several ways. We included only routes with all of the following three characteristics: 1) at least 29 yr of data deemed acceptable by the BBS (Sauer et al. 2005), 2) 10–100 km from at least one other route with 29 yr of available data, and 3) sufficient non-zero data points for the assumptions of the general linear model to be met (we verified assumptions for a random subset of the analyses). This meant that each analysis had to have a sample size of 28 (because of the one-year time-lag), which is the sample size required to obtain an intermediate level of statistical power (0.75) to detect a large effect (f 2 =0.35) (Cohen 1988) in a multiple regression with two predictors (Faul and Erdfelder 1992). We further limited analyses to species for which there were pairs of routes that could be compared at all nine of the distance classes considered.

For each species at each distance class, we then asked whether samples separated by this particular distance were linked with a positive one-year time-lag. Our null hypothesis was that pairs of samples separated by this particular distance were not more likely to be linked with a positive one-year time-lagged correlation than expected by chance, in other words not more likely to be linked by a positive one-year time-lag than pairs of samples selected at random (not necessarily separated by this particular distance class). To test this, we first examined all possible pairs of samples separated by this distance (N) and noted how many times these samples were linked with a significant positive one-year time-lag (L_{obs}). Although some negative correlations would be expected to occur by chance, we only counted the number of positive correlations because negative correlations would not be expected to be an indication of dispersal. Both analyses resulting in negative correlations and those resulting in positive correlations were included in the sample size N. We examined as many pairs as possible at each distance class to maximize our power to detect any differences. Note that we would not expect all pairs of samples separated by the dispersal distance to show one-year time-lagged correlations in abundance because we would not expect all samples to produce dispersers, nor would we expect dispersers to be able to settle in all areas within their dispersal range. Note also that the sample unit in these analyses was the pairs, not the samples themselves, and the population sampled (the population about which we wished to draw inference) was composed of pairs of areas separated by the particular distance class in question.

Once we had examined all pairs, we created N pairs of samples at random (i.e. not necessarily separated by the distance class in question) and counted how many of these pairs were linked with a one-year time-lag (L). Samples included in these random pairs were selected from the samples included in the initial N pairs, and again all random pairs were analyzed twice, examining the effects of A_{t-1} on B_t and of B_{t-1} on A_t. To create a null distribution, we repeated this procedure 1000 times, and thus produced a frequency distribution of L/N. To test our hypothesis about pairs separated by the particular distance class in question, we examined this frequency distribution to see where L_{obs}/N fell, just as one would compare a calculated F-statistic to an F distribution. Thus, L_{obs}/N was our test statistic. We then calculated a p value in the same way as would be done in the case of an F-statistic: p = the probability of obtaining L_{obs}/N as the test statistic given the frequency distribution of this test statistic (L/N), or, more specifically, the proportion of times out of 1000 sets of randomized analyses in which there were at least as many significant positive results as in the initial N analyses at each distance class.

This process might be best understood through a numerical example. Imagine we were examining the 10–20 km scale for species x. Our null hypothesis would be that one-year time-lagged correlations did not occur more often than expected by chance for this species at the 10–20 km distance class. Imagine we had 100 pairs at the 10–20 km distance class (N = 100). Of these, 10 were linked with a significant positive one-year time-lagged correlation (L_{obs} = 10). The test statistic would be 1/10 (L_{obs}/N = 10/100 or 1/10). We would then have created 100 pairs of samples at random (i.e. not necessarily separated by 10–20 km) from

the samples used in the initial pairings, and counted how many of these random pairs were linked with a one-year time-lag (L). To create a null distribution, we would have done this 1000 times, and thus created a frequency distribution of L/100 (L/N). To test our hypothesis about pairs separated by 10–20 km, we would have examined this frequency distribution to see where 1/10 fell. If, out of 1000 analyses, L/N was 1/10 or larger 25 times, we would have calculated a p-value of 0.025, and would have judged our null hypothesis accordingly.

In effect, in the initial analyses, we did not use the p-values in the traditional hypothesis-testing sense; we used them simply to characterize the relationship between pairs. The real statistical test was performed at the level of the distance class, addressing the hypothesis of whether or not there were significantly more pairs linked through a one-year time-lagged correlation at that particular distance class than expected by chance given the specific samples included in the initial analyses, i.e. among samples paired at random.

For each species for which there were significantly more positive one-year time-lagged correlations in abundance than expected by chance for at least one distance class, we calculated median correlation distance as the midpoint of the distance classes in question. For example, if species x showed significantly more correlations than expected by chance at the 10–20 km scale, we calculated a median lagged correlation distance of 15 km. If species x also showed significantly more correlations than expected by chance at the 20–30 km scale, we calculated a median correlation distance of 20 km (halfway between 10 and 30). If species y showed significantly more correlations than expected by chance at the 10–20 and at the 50–60 km scale, we calculated a median correlation distance of 35 km.

Because 1000 different sets of pairs could not be obtained with fewer than 6 pairs, we performed randomization analyses only for distance classes for which there were at least 6 pairs of routes. This meant that, for some species, we could not perform randomization analyses at all distance classes.

To test the hypothesis that the lagged correlation distance estimates reflect dispersal movements, we regressed estimated median lagged correlation distance on body mass and wing length (separately) for the species for which there were significant one-year time-lagged relationships between pairs of samples for at least one distance class. We used median body mass and wing length data from the literature (Poole and Gill 1992–2006). We weighted regressions by sample size (number of pairs analyzed at the significant distance class for each species) because, for species with larger sample sizes, we were more confident that sample pairs with significant, positive one-year time-lagged correlations had not been missed, and therefore more confident in the calculation of median lagged correlation distance. For species for which there were significant positive one-year time-lagged correlations between pairs of samples at more than one distance class, we used mean sample size as the weighting variable, i.e. the mean of the number of pairs analyzed at each significant distance class.

We also compared lagged correlation distances to natal dispersal distances reported in the literature. In our examination of the literature, we did not consider measurements of pre-winter, post-fledging dispersal as indicative of

dispersal distances; we only considered cases in which young known to have been born in a specific area were found breeding in subsequent years, either in the same or in a different area.

Multi-species studies such as this can easily be confounded by phylogenetic relatedness among the species studied. If characteristics included in the analyses are likely to be more similar between closely related species than between distantly related species because of common ancestry, it has been argued that the species should not be assumed to be independent data points, but rather that phylogeny should be considered and corrected for in all analyses (Felsenstein 1985). Since morphological characteristics such as body mass and wing length are likely to be related to phylogeny, we corrected for this potential lack of independence by repeating the analyses described above for phylogenetically independent contrasts (Felsenstein 1985) using Mesquite 1.06 (Maddison and Maddison 2004) and PDAP:PDTREE 1.07 (Midford et al. 2005).

We compiled a phylogenetic tree using the general phylogenetic structure presented by Barker et al. (2004), with details filled in for Paridae (Gill et al. 2005), Emberizidae (Carson and Spicer 2003), Parulidae (Lovette and Bermingham 2002), *Cardinalis cardinalis*, and *Piranga olivacea* (Klicka et al. 2003) (Fig. 1). For lack of standardized branch lengths, we assigned all branch lengths a value of 1, then transformed them with a Rho transformation (rho = 0.8) (Grafen 1989). We tested the adequacy of these branch lengths as suggested by Garland et al. (1992). We used the mean sample size of each contrast to calculate a sample size corresponding to each phylogenetically independent contrast. For example, since the sample size for the red-eyed vireo *Vireo olivaceus* was 104 and that for the white-eyed vireo *Vireo griseus* was 8, we calculated a mean sample size of 56 for the red-eyed vireo–white-eyed vireo contrast. This mean sample size of each contrast was then used as the weighting variable in regressions of the phylogenetically independent contrasts of lagged correlation distance on median body mass and wing length. As above, median body mass and wing length values were from Poole and Gill (1992–2006). As recommended (Garland et al. 1992), we forced all regressions of phylogenetically independent contrasts through the origin.

We excluded the American crow *Corvus brachyrhynchos* from the inter-specific analyses described above because the assumptions of general linear models and especially the phylogenetically independent contrasts were violated when this species was included, due to its exceptionally large body mass. Inclusion of this species in the analyses resulted in a lack of homogeneity of variance and in an inability to transform the branch lengths in the calculation of phylogenetically independent contrasts such that there was no correlation between the standardized contrasts and the square route of the sum of the corrected branch lengths, as required (Garland et al. 1992). Note, however, that the results did not change if this species was included in the analyses.

Finally, we compared lagged correlation distances for migrants and residents. We determined migratory status by referring to Poole and Gill (1992–2006), and compared the lagged correlation distance of migrants and residents using a t-test. Because any effect of migratory status on dispersal
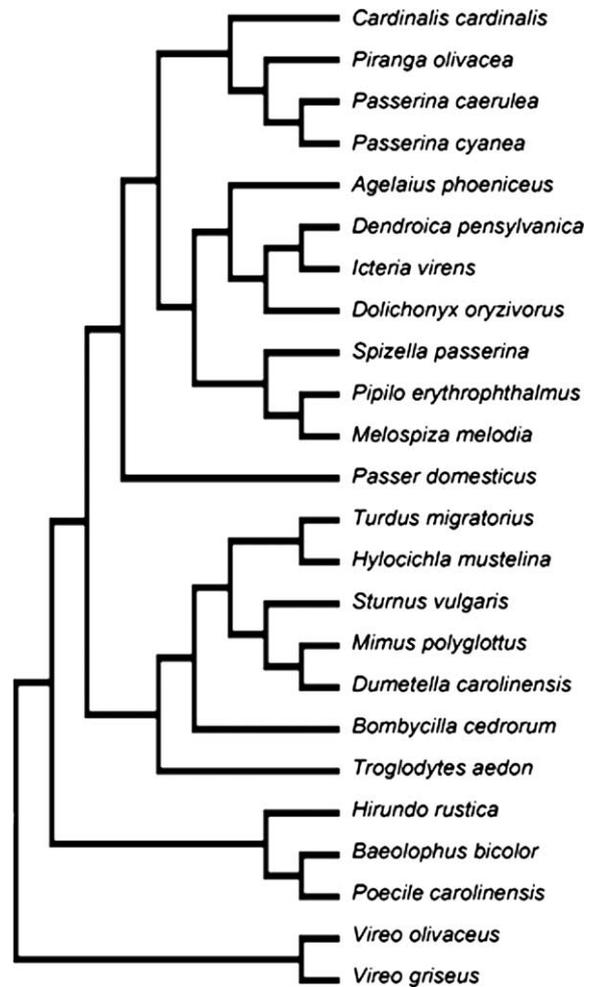

Figure 1. Phylogenetic relationships among songbirds for which there were significantly more one-year time-lagged correlations in abundance than expected by chance at at least one of the distance classes considered. The tree was compiled using the general phylogenetic structure presented by Barker et al. (2004), with details filled in for Paridae (Gill et al. 2005), Emberizidae (Carson and Spicer 2003), Parulidae (Lovette and Bermingham 2002), *Cardinalis cardinalis,* and *Piranga olivacea* (Klicka et al. 2003).

distance may be masked by strong effects of morphological characteristics (Paradis et al. 1998), we performed the t-tests described above on the residuals from the linear regressions of lagged correlation distance on 1) median body mass and 2) median wing length (two analyses). Median body mass and wing length values were from obtained Poole and Gill (1992–2006). From these analyses, we excluded the eastern towhee *Pipilo erythrophthalmus*, red-winged blackbird *Agelaius phoeniceus*, and song sparrow *Melospiza melodia* because they are migrants in some parts of the continental U.S. and residents in others.

Results

Despite the large extent of the BBS data, only 428 routes were included in the analyses (Fig. 2) owing to our strict selection criteria (see above). Coincidentally, these routes were mainly located in the eastern half of the United States,
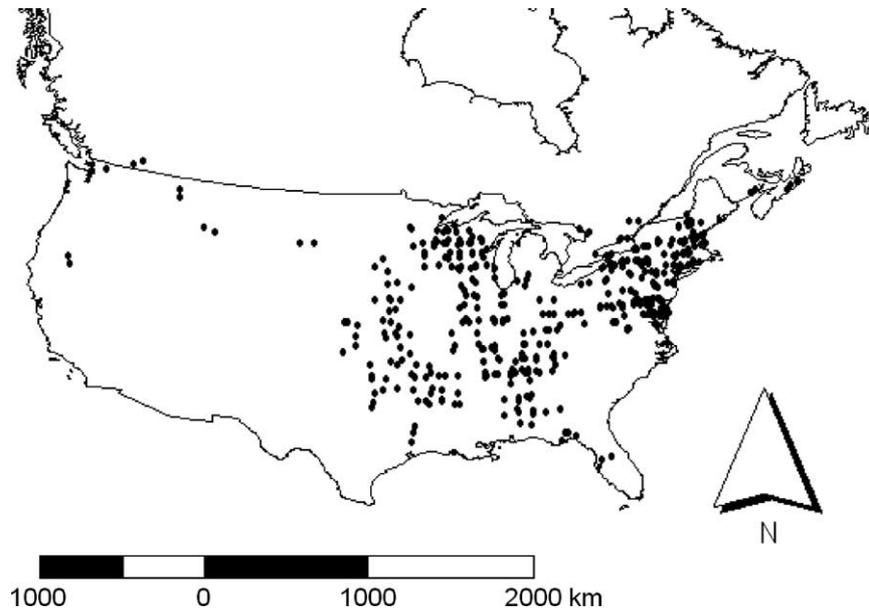
Figure 2. North American Breeding Bird Survey (BBS) routes used in the analyses of time-lagged correlations in abundance. All routes included had at least 29 yr of data available in common with at least one other route at all nine of the distance classes considered.

and the species examined were therefore those common in this part of the continent.

There were significant, positive one-year time-lagged correlations between samples of 25 of the 51 species examined (Table 1). Sample sizes at the distance classes for which we found these correlations varied from 6 to 180 pairs (Table 1). On average, sample sizes were significantly

larger for species for which there were significant positive time-lagged correlations than for species for which there was no evidence of such correlations [mean $N = 68.7 \pm 10.01$ (standard error) and 30.0 ± 4.39, respectively; $U = 192.5$, $n = 51$, $p = 0.012$]. Among the 25 species for which there were significant positive one-year time-lagged correlations, no distance classes were excluded from randomization
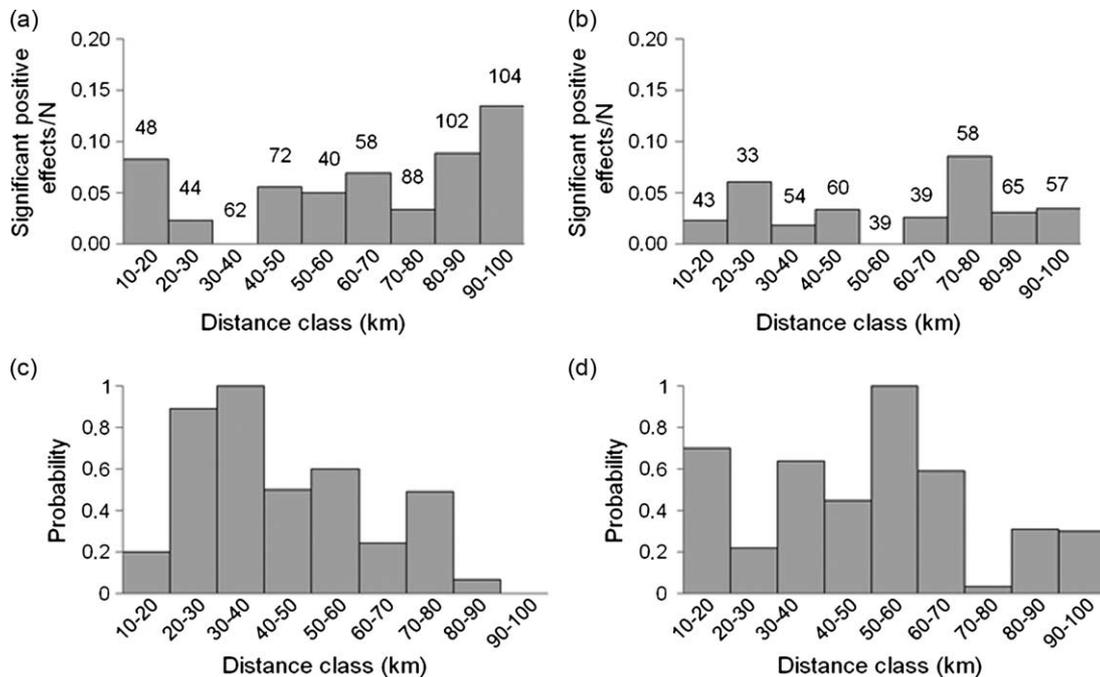

Figure 3. (a–b) Proportion of all initial paired analyses that resulted in significant, positive one-year time-lagged correlations at each distance class (number of significant, positive one-year time-lagged correlations divided by N, the number of pairs analysed at each distance class), and (c–d) corresponding probabilities (p) of obtaining these proportions given the samples included in the analyses at each scale, calculated based on randomization analyses. Results are presented for two species: (a and c) the red-eyed vireo and (b and d) the house wren. Sample sizes (N, number of analyses carried out at each distance class) are presented above each bar in (a–b); the same sample sizes apply to (c–d).

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Table 1. Median body mass (Mass)[†], median wing length (Wing)[†], migratory status (Migrat; M for migrants, R for residents)[†], and distance classes for which there were significantly more positive one-year time-lagged correlations between samples than expected by chance (Sig Dist), corresponding p-values (p) based on randomization analyses (see Methods), and median lagged correlation distance (Med Dist) for the 25 songbird species for which the results allowed for such estimates. In parentheses after the significant lagged correlation distance classes, the number of analyses with these effects over number of pairs of samples analysed at this distance class is included. Where available, mean (or, in the case of the song sparrow, median) natal dispersal distances and sample sizes (N) reported in the literature from mark-recapture studies are listed in parentheses (Disp Dist). Species are ordered as in Fig. 1.

Species*	Mass (g)[†]	Wing (cm)[†]	Migrat[†]	Sig Dist (km)	p	Med Dist (Disp Dist [†], N) (km)
Cardinalis cardinalis (northern cardinal)	45.0	28.0	R	40–50 (11/88)	0.010	70 (1.5, 26)
				50–60 (8/60)	0.018	
				90–100 (12/138)	0.047	
Piranga olivacea (scarlet tanager)	30.5	27.0	M	20–30 (2/13)	0.015	25
Passerina caerulea (blue grosbeak)	28.5	28.0	M	20–30 (1/8)	0.023	25
Passerina cyanea (indigo bunting)	15.0	20.5	M	50–60 (7/58)	0.007	55
Dendroica pensylvanica (chestnut-sided warbler)	10.0	19.5	M	20–30 (5/26)	0.001	35
				40–50 (5/28)	0.008	
Icteria virens (yellow-breasted chat)	27.0	25.0	M	10–20 (5/22)	0.006	40
				60–70 (5/26)	0.008	
Agelaius phoeniceus (red-winged blackbird)	54.50	35.5	R	80–90 (16/112)	0.009	85 (32.1)
Dolichonyx oryzivorus (bobolink)	42.50	27.0	M	70–80 (2/8)	0.011	85
				90–100 (1/8)	0.047	
Spizella passerina (chipping sparrow)	13.0	20.0	M	30–40 (10/98)	0.030	40
				40–50 (13/106)	0.010	
Pipilo erythrophthalmus (eastern towhee)	42.0	24.0	M/R	10–20 (6/30)	0.015	15
Melospiza melodia (song sparrow)	32.5	21.0	R	40–50 (18/170)	<0.001	45 (0.225, 36; 0.185, 34)
Passer domesticus (house sparrow)	29.0	22.0	R	30–40 (14/80)	0.046	35
Turdus migratorius (American robin)	77.0	35.5	R	70–80 (16/96)	<0.001	75
Hylocichla mustelina (wood thrush)	45.0	32.0	M	60–70 (13/104)	0.007	70
				70–80 (20/180)	0.015	
Sturnus vulgaris (European starling)	78.0	35.5	R	80–90 (15/156)	<0.001	85
Mimus polyglottos (northern mockingbird)	51.5	33.0	R	40–50 (8/66)	0.001	45
Dumetella carolinensis (gray catbird)	39.5	26.0	M	10–20 (7/60)	0.030	15
Bombycilla cedrorum (cedar waxwing)	32.0	26.0	R	20–30 (1/6)	<0.001	25
Troglodytes aedon (house wren)	11.0	17.0	M	70–80 (5/58)	0.031	75
Hirundo rustica (barn swallow)	18.5	30.5	M	60–70 (8/76)	0.030	65 (1.6, 5)
Baeolophus bicolor (tufted titmouse)	22.0	23.0	R	70–80 (15/74)	<0.001	75
Poecile carolinensis (carolina chickadee)	10.0	17.5	R	30–40 (1/8)	<0.001	35
Corvus brachyrhynchos (American crow)	465.0	92.5	R	80–90 (13/120)	0.024	85 (3.2, 49; 3.2, 8)
Vireo olivaceus (red-eyed vireo)	19.0	24.0	M	90–100 (14/104)	0.001	95
Vireo griseus (white-eyed vireo)	12.0	17.0	M/R	50–60 (3/8)	0.001	55

*See Ehrlich et al. (1988) for authorities.
[†]Reviewed in Poole and Gill (1992–2006).

analyses due to low sample size (<6 pairs). However, for five of the 26 species for which there were no such correlations, sample sizes were too small for randomization analyses to be performed for at least one distance class. This suggests that, given larger sample sizes, we might have found significant positive time-lagged correlations for at least some of the 26 species for which we found none. Median lagged correlation distances for the 25 species for which we found significant positive time-lagged correlations ranged from 15 to 95 km (Table 1). Although we only found mean and median natal dispersal distances in the literature for 5 species, lagged correlation distances were much greater than published natal dispersal distances in all cases (Table 1).

However, interspecific analyses revealed median lagged correlation distances to be significantly positively correlated with wing length (Fig. 4), whether or not phylogenetic relatedness was accounted for (Table 2). The positive correlation between lagged correlation distance and median body mass was also significant when phylogenetic related-

ness was accounted for, although it was not quite significant at alpha = 0.05 when phylogenetic relatedness was not accounted for (Table 2). In any case, there was a greater and more significant correlation between median lagged correlation distance and wing length than between median lagged correlation distance and body mass (Table 2). Body mass and wing length were themselves highly correlated ($R^2 = 0.86$, N = 24, p < 0.001). This suggests that median lagged correlation distance may be better predicted by wing length than by body mass. None of the correlations examined were significant if regressions were not weighted by mean sample size (results not shown).

There was no significant difference in lagged correlation distance for migratory and resident species when body mass was controlled for (t = −0,273, DF = 20, p = 0.788), nor when wing length was controlled for (t = −1,58, DF = 20, p = 0.876). The 13 migratory species had a mean lagged correlation distance of 52.3 km (±6.88 standard error), while the 9 residents had a mean lagged correlation distance of 59.4 (±8.14).
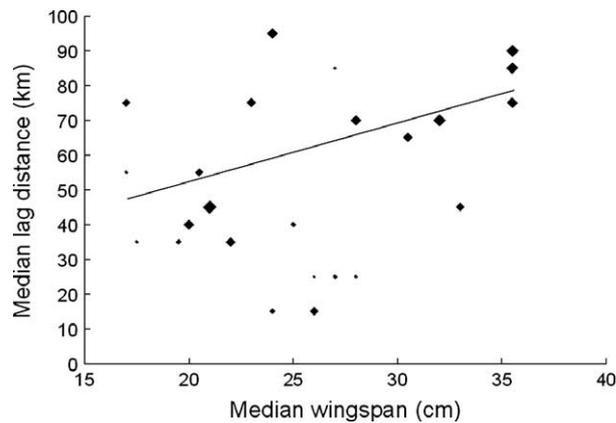
Figure 4. Median distance between North American Breeding Bird Survey (BBS) samples linked by one-year time-lagged correlations in abundance ("median lagged correlation distance") vs wing length, weighted by sample size, as indicated by the size of the dots. See Table 2 for associated statistics.

Discussion

These results indicate that many species of North American songbirds are linked with a one-year time-lag over tens of kilometres (Table 1). The correlations between these distances and wing length and body mass support the contention that these distances correspond to dispersal movements. The fact that these correlations were not significant when analyses were not weighted by sample size is not surprising considering the great variation in sample size (from 6 to 180 pairs); it is this variation that we were attempting to account for with the weighting.

If these lagged correlation distances are indeed indications of dispersal distances, they are much longer than those reported in the literature for the same species. These reported distances are based on mark-recapture and radio-telemetry studies, so this difference is not surprising. In contrast with our method, mark-recapture and radio-telemetry studies are severely limited in the spatial extent over which they can be carried out. Interestingly, an analysis of data obtained from the British bird ringing scheme yielded estimates of songbird dispersal distances that are similar to ours (Paradis et al. 1998).

Although the issue of multiple comparisons should be considered whenever many statistical analyses are done (Abdi 2007), it does not present a problem in this study. Multiple comparisons are only a problem if many analyses are done on the same statistical population, i.e. on the population about which we want to draw inferences (Zar 1984). For each species, we sought to draw separate

Table 2. Results of linear regression of median lagged correlation distance on body mass and wing length (N=24 species), with and without the use of phylogenetically-independent contrasts (PIC). All analyses are weighted by sample size, i.e. the mean number of pairs examined per distance class.

Predictor	Coefficient	F	p	R^2
Body mass	0.405	3.778	0.065	0.108
Wingspan	1.846	7.492	0.012	0.220
PICBodyMass	0.723	6.826	0.016	0.202
PICWingspan	2.2379	7.135	0.014	0.211

inferences for each distance class, testing independent hypotheses for each species and each distance class, i.e. that there were significantly more positive one-year time-lagged correlations than expected by chance. Here, we did not perform multiple analyses on the same statistical population since for each species at each distance class, the statistical population was composed of pairs of areas separated by the particular distance in question. At the interspecific level, our hypotheses were that median lagged correlation distances would be correlated with body mass and wing length. For these analyses, the statistical population was either the species or the phylogenetically independent contrasts of the species. We performed two analyses on each population, one with body mass, the other with wing length. Thus, in this case, Bonferroni adjustments may be appropriate. However, these adjustments do not change the interpretation of our results, since those results judged to be significant at alpha=0.05 had p-values <0.025 (0.05/2, the cut-off for two comparisons done at alpha = 0.05). In addition, we found one-year time-lagged effects for 49% (25/51) of the species examined, much more than the 5% we might have expected to find by chance. Finally, if our results were simply spurious, it is unlikely there would have been any significant correlations between median lagged correlation distances and wing length or body mass.

As described in the Methods, for each species at each distance class, we controlled for within-year synchrony before examining time-lagged synchrony. As far as we know, songbirds are not tightly linked to any other species or disease that is itself synchronized (Tittler et al. 2006), and synchrony caused by songbird dispersal should be time-lagged (see above). Therefore within-year synchrony is likely caused by Moran effects or by large-scale trends in abundance. If these within-year synchrony or spatial autocorrelation effects were not properly controlled for by our method, all species would be expected to have positive one-year time-lagged correlations at the smallest scale examined, i.e. at the 10–20 km scale. The fact that most species exhibited positive one-year time-lagged correlations only at larger scales supports the idea that the effects of within-year synchrony have been efficiently controlled.

It could be argued that the positive one-year time-lagged correlations in abundance between samples observed here are produced by anthropogenic land-use change such as urbanization. Our results, however, are not consistent with this explanation. Such land-use change typically spreads over a period of years, leading to corresponding spatio-temporal changes in songbird abundances. However, any resulting positive one-year time-lagged correlations would be expected to occur at the same spatial scale for all species with similar habitat requirements; this scale would be determined by the scale over which the spread in land-use change was occurring. For example, forest species such as the wood thrush (Roth et al. 1996), red-eyed vireo (Cimprich et al. 2000), and the scarlet tanager *Piranga olivacea* (Mowbray 1999) would be expected to show lagged correlation distances corresponding to similar spatial scales. Contrary to this prediction, even species with very similar habitat requirements showed positive one-year time-lagged correlations at very different distances (Table 1). The forest species (wood thrush, red-eyed vireo, scarlet tanager, chestnut-sided warbler, and tufted titmouse)

showed median lagged correlation distances of 25–95 km; the open-area species (blue grosbeak, chipping sparrow, bobolink, and red-winged blackbird), of 25–85 km.

It might also be suggested that spatial autocorrelation could result in apparent dispersal distances that are larger than the actual dispersal distances. For example, if individuals were actually dispersing 20 km, abundances in sample A would show a one-year time-lagged correlation with those of B 20 km away, and those of sample B with those of C another 20 km away (40 km away from A). If only the relationship between A and C were examined, it would be concluded that individuals were dispersing 40 km as opposed to 20 km. However, in this scenario, the strongest positive time-lagged correlations should occur at the distances where dispersal is actually occurring (between A and B and between B and C). The time-lagged correlation between A and C should be much weaker. Since we tested for positive time-lagged correlations at all distance classes between 10 and 100 km, the distance classes at which we found such correlations should correspond to actual dispersal distances. In addition, if all dispersal were occurring at distances of <10 km (the shortest dispersal distance evaluated), all species would be expected to show time-lagged correlation distances at the 10–20 km distance class. This is not what we found (Table 1). Dispersal between samples therefore remains the most parsimonious explanation for the observed patterns.

The one-year time-lagged model used to estimate dispersal distances assumes that there is a positive relationship between abundance (measured as number of males singing during point counts) and the number of individuals dispersing. We know of no studies that have examined this relationship, possibly because natal dispersal is such a difficult process to study. However, abundance does seem to be an indication of territory density (Svensson 1981, Cyr et al. 1995, Howell et al. 2004, Toms et al. 2006), and in most cases, density either has a positive or a neutral effect on natal dispersal (reviewed in Matthysen 2005). In either case, a more densely populated area (or one with higher abundance) would produce more dispersers than a less densely populated area (or one with a lower abundance).

Of course, we would not claim that all individuals of a species disperse over the distances over which we found positive one-year time-lagged correlations. In referring to these distances as "typical dispersal distances", we make no claims to any knowledge about the variance around the peak in the distribution of dispersal distances. Obviously, adults that are found breeding for the first time relatively close to their natal sites have dispersed over relatively short distances (Potti and Montalvo 1991). Similarly, we do not doubt the validity of the rare dispersal events that have been recorded over several hundred kilometres (Kendeigh 1941, Farner 1945, Moore and Dolbeer 1989, Payne 1991). Natal and breeding dispersal distances are undoubtedly distributed over wide ranges in each of the species studied. We do, however, suggest that the lagged correlation distances found here correspond to the distances over which a majority of individuals disperse.

Lagged correlation distances did not differ significantly between migratory and resident songbird species. This finding is consistent with the fact that there is little if any evidence that dispersal distance varies with migratory status.

In their extensive review of the literature on the dispersal distances of 77 bird species (largely based on mark–recapture studies), Sutherland et al. (2000) found no significant differences in dispersal distances. Such a relationship has only been found by Paradis et al. (1998); in their estimates of dispersal distance based on band-recovery data in Europe, these researchers found migrants moved significantly farther than residents when body size was controlled for. However, they cautioned against placing too much confidence in this result because the banding data used did not necessarily provide a clear indication of where young were born (unless banded as nestlings, it is difficult to ascertain that captured juveniles have not already travelled substantial distances from their natal sites).

Our results may have implications in terms of source-sink dynamics (sensu Pulliam 1988). In general, source-sink dynamics should occur over the distances over which dispersal occurs (Tittler et al. 2006). If positive one-year time-lagged correlations occur between pairs of samples in only one direction (i.e. A_{t-1} is correlated with B_t but B_{t-1} is not correlated with A_t), this may indicate the net movement of individuals from one area to another (from A to B) necessary for source-sink dynamics. If positive one-year time-lagged correlations occur between pairs of samples in both directions, we considered this to be potential evidence of dispersal, but it is not likely to be evidence of source-sink dynamics because it implies an exchange of individuals rather than a net flow from one area to another.

Because we used point count data in our analyses, the dispersal distances estimated may be more relevant for males than for females. The point count procedure largely detects singing males (Gibbs and Wenny 1993, Rosenstock et al. 2002), and natal dispersal distances may be longer (Drilling and Thompson 1988, Wheelwright and Mauck 1998, Winkler et al. 2005) or shorter (Payne 1991) for females than for males, depending on the species.

Furthermore, for those study species whose geographical ranges extend far beyond the area studied (e.g. song sparrow, red-winged blackbird, American crow, American robin), the dispersal distances estimated here may not apply to all populations throughout the range. The areas included in our study may be characterized by particularly high levels of habitat loss, more so than the boreal forest to the north, for example. If habitat loss leads to greater dispersal distances, as individuals must travel farther between habitat patches, dispersal distances might be expected to be longer in areas characterized by extensive habitat loss than in areas where habitat is more readily available, as found for bush crickets (Hein et al. 2004). On the other hand, if remaining habitat is separated by an inhospitable matrix through which individuals are hesitant to move, dispersal distances might be shorter in areas characterized by extensive habitat loss. Van Houtan et al. (2007) found area-sensitive species of tropical birds dispersed shorter distances after than before habitat loss, while the opposite was true for species not found to be area-sensitive. Since our far-ranging species are not likely to be area-sensitive, they might be expected to disperse over shorter distances in areas with more habitat.

Our findings suggest that the distribution of dispersal distances may not necessarily correspond to the distribution generally assumed. Whether they are Gaussian (Turchin 1998), leptokurtic (Kot et al. 1996), inverse

power (Hill et al. 1996), negative exponential (Hanski et al. 2000), or extended negative exponential (Chapman et al. 2007), the distribution of dispersal distances is generally thought to peak close to the point of origin and trail off as distance from this point increases, with most young settling close to their natal sites. This assumption is largely based on data from passive dispersers like plants (Howe and Westley 1986, Okubo and Levin 1989) or from insects (Taylor 1978). The three species with significant time-lagged correlation distances at the smallest distance class examined (10–20 km) (eastern towhee *Pipilo erythrophthalmus*, gray catbird *Dumetella carolinensis*, and yellow-breasted chat *Icteria virens*) may have dispersal distributions corresponding to the commonly accepted idea that the young settle preferentially close to their natal habitat. However, for most of the species studied we did not find positive one-year time-lagged correlations between samples at the smallest distance class examined (10–20 km), which is what would be expected if dispersal rates decreased monotonically with distance. This should not be terribly surprising considering that mark–recapture studies carried out over relatively small spatial scales generally result in juvenile recapture rates of 5% or less (Fleischer et al. 1984, Payne 1991, Sutherland et al. 2000, Winkler et al. 2005, Hosner and Winkler 2007). The implication of these low recapture rates is that most young disperse farther than the relatively limited spatial range of mark–recapture studies. This implies that the dispersal distance distribution may peak at larger scales than those covered by most mark–recapture studies.

In this study, we make no assumptions about the dispersal distance distribution. Our approach is purely phenomenological; we ask simply whether we can gain some information about typical dispersal distances from the time-lagged correlations. The correlations do not tell us a lot about the actual distribution of dispersal distances but what they do say is that, for some songbird species, there are peaks in the distribution at relatively large distances. This is not what we would have expected based on what others have hypothesized about dispersal distances (see above).

There are several possible explanations for the patterns we observe: 1) young songbirds may in fact move to the closest available territory, but healthy populations (those that produce most of the young) are large (i.e. they span over large areas) and competition for territories in these areas is quite fierce, so that most young end up moving quite a distance before they reach the next available territory. It has certainly been suggested that natal dispersal distances are related to habitat availability (Hansson et al. 2002), but habitat availability is difficult to quantify. 2) Young songbirds tend to move a certain distance before beginning to search for a breeding territory, which would serve to limit the chance of inbreeding. It has been suggested that juveniles generally disperse farther than adults for just this reason (Johnson and Gaines 1990). 3) Some or even most young may disperse over distances of less than the smallest scale examined here (i.e. <10 km), but our results imply that those that disperse farther tend to go quite a bit farther. This implies two types of dispersal behavior. Perhaps young that fledge early enough in the season have enough time to prospect for potential breeding territories near their natal areas before preparing for winter,

while those born later lack this time, and therefore use another mechanism such as conspecific attraction to find a breeding territory the following spring. This would lead to a two-peaked distribution of dispersal distances. Such a pattern may be indicated by the band-recovery data presented by Paradis et al. (1998; Fig. 2) and Paradis et al. (2002; Fig. 4), in which 5 of 6 species seem to show a peak in natal dispersal distance between 20 and 80 km as well as one below 10 km. In general, we know so little about dispersal behavior and movement that it is difficult to do more than speculate about the possible mechanisms that might lead to the patterns observed here, or indeed about the expected distributions of dispersal distances. However, we feel that these patterns are strong enough to merit further consideration.

Regardless of whether the lagged correlation distances found here indicate median, mean, maximum, or simply common dispersal distances, they do indicate the scales over which samples are linked, most likely by dispersal, and therefore the scales over which samples influence one another. As such, these findings indicate that the effects of land use change on songbirds should be studied and managed over tens of kilometers, at least in the areas studied.

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