EVIDENCE OF LARGE-SCALE SOURCE–SINK DYNAMICS AND LONG-DISTANCE DISPERSAL AMONG WOOD THRUSH POPULATIONS

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Abstract. Source–sink dynamics are commonly thought to occur among Wood Thrush (*Hylocichla mustelina*) and other songbird populations, allowing for the persistence of populations with negative growth rates ("sinks") through immigration from populations with positive growth rates ("sources"). Knowledge of source–sink dynamics is important for management and conservation because the removal of source habitat should result in the extinction of dependent sinks. However, since research has focused on identifying individual sources/sink populations, not source–sink pairs, we cannot predict these effects or the scale over which they occur. We posit that, when dispersal occurs from a source to a sink year after year, there will be a one-year time-lagged correlation in abundance between the two populations. This should occur for populations separated by distances over which juveniles disperse. Using the North American Breeding Bird Survey data, we tested for such time-lagged correlations between paired Wood Thrush populations from 10 to 200 km apart. Populations were linked with a one-year time lag over distances from 60 to 80 km, indicating that dispersal and source–sink dynamics may occur over these long distances. There was also a declining trend in forest cover from sources to sinks. Conservation and management strategies should therefore be designed at large scales, with consideration for source–sink dynamics and forest cover.

Key words: asymmetrical dispersal; dispersal distance; Hylocichla mustelina; *juvenile and natal dispersal; long-distance dispersal; North American Breeding Bird Survey; source–sink dynamics; time lag; Wood Thrush.*

INTRODUCTION

The source–sink model, first presented by Pulliam (1988), suggests that populations that are not self-sustaining can nevertheless persist through immigration from self-sustaining populations. Pulliam defines a sink as a habitat area in which the rate of reproduction is below the level necessary to counterbalance rates of mortality ($\lambda < 1$), and a source as one in which reproduction exceeds that necessary to counterbalance mortality ($\lambda > 1$). He hypothesizes that the excess individuals from the population occupying the source habitat (henceforth referred to as the source population) disperse to the sink habitat, creating a source–sink dynamic through which the population in the sink habitat (or sink population) is maintained.

Since 1988, the source–sink concept has been more or less accepted, incorporated into conservation literature and management (e.g., Meffe and Carroll 1997, Gardenfors et al. 2001), and widely used to explain the presence of individuals in habitats thought to be of low quality (De Groot and Smith 2001, Duguay et al. 2001, Tittler et al. 2001). A search of the ISI Web of Science database yields

1295 published works that cite Pulliam's paper between 1988 and 2005, >25% (325) of which focus on birds.

Knowledge of source–sink dynamics is important for conservation and management, because if such dynamics occur, human activities affecting a source population are likely to influence its dependent sink population(s). Knowledge of source–sink dynamics would increase the ability of managers to predict which sink populations might be negatively affected by the degradation or destruction of source habitat. Knowledge of the distances over which source–sink dynamics occur would allow managers to predict the spatial scale over which removal of source populations might affect dependent sink populations. Without such knowledge, the large-scale effects of changes in habitat may be difficult to predict, and landscape-scale conservation planning will continue to be based on rules of thumb and educated guesses.

One of the North American songbirds most commonly cited in source–sink studies is the Wood Thrush (*Hylocichla mustelina* Gmelin). The Wood Thrush is a neotropical migrant forest songbird that breeds in deciduous and mixed forest (Roth et al. 1996). It is of particular interest because it has been declining steadily across North America over the past decades (Sauer et al. 2005). Researchers have characterized populations of this species as sources or sinks in various locations across North America (Donovan et al. 1995, Anders et

al. 1997, Trine 1998, Weinberg and Roth 1998, Friesen et al. 1999, Burke and Nol 2000, Fauth 2000, 2001, Simons et al. 2000, Duguay et al. 2001, Ford et al. 2001). Sources have been found to occur in areas with more habitat than sinks (Donovan et al. 1995, Burke and Nol 2000). However, this literature focuses on calculating the growth rates of single populations in isolation (i.e., determining the source–sink status of single populations), which does not allow for the identification of source–sink pairs nor the distances over which source–sink dynamics occur. Without this information, we have no way of knowing which populations may be affected by the management of source populations or their habitat, nor over what spatial scales this management may have an impact.

The distance(s) over which source–sink dynamics occur must be the same as the distance(s) over which dispersal occurs. Since adults generally exhibit high site fidelity (Roth et al. 1996), it is likely that sources and sinks are largely linked by juvenile rather than adult dispersal. Therefore, knowledge of juvenile dispersal distances would provide insight into the scales over which management of source populations or habitats may affect other populations. Unfortunately, for the Wood Thrush and most other North American songbird species, there is a lack of reliable information on juvenile dispersal distances. The studies most frequently cited to estimate dispersal distance in the Wood Thrush (Roth et al. 1996, Anders et al. 1998, Rivera et al. 1998) follow fledglings for the first few weeks after they leave the nest, but do not examine true juvenile dispersal (Greenwood 1980) because they do not investigate where these young settle to breed in the following spring (after migration). Dispersal in other North American songbird species has been investigated with mark–recapture studies (Payne 1991, Collister and DeSmet 1997, Wheelwright and Mauck 1998), but these studies are characterized by very low return rates and therefore do not provide a reliable indication of how far most young disperse. The lack of data on dispersal distances has been described as "a major gap in understanding the population dynamics of Neotropical migrants" (Brawn and Robinson 1996).

For insight into source–sink dynamics and into juvenile dispersal distances, we must look beyond the status of single populations and pre-migration dispersal distances. Since source and sink populations must be linked by dispersal, we are led to a prediction not previously tested. If a source–sink dynamic occurs between two populations, it must be marked by asymmetrical dispersal between the populations, i.e., dispersal predominantly from the source to the sink. In the simplest case of a source–sink dynamic that occurs consistently year after year between one source and one sink population, consistent asymmetrical dispersal will lead to a one-year time-lagged correlation in abundance between the two populations. In other words, a decline in abundance in the source population in one year will result in a decline in the sink population in the following

year, as a smaller source population produces fewer young to disperse to the sink. Similarly, an increase in the source population will result in an increase in the sink population with a one-year time lag, as a larger source population will produce more potential immigrants for the sink population the following year. The one-year time lag is crucial, because this is the time it would take for the young born in the source to disperse to and be detected in the sink. Note that these one-year time-lagged patterns could exist between two populations without one depending on the other for persistence, i.e., this is a necessary, but not a sufficient criterion for the simple case of source–sink dynamics described above.

This prediction holds regardless of whether or not dispersal is density dependent. If individuals do not disperse from the source until the source population reaches a certain density, the one-year time-lagged correlation will occur, because in the year following a year in which the source does not produce enough young to disperse to the sink (i.e., abundance in the source population is low), the sink will not benefit from the input of individuals from the source and abundance will be correspondingly low. The opposite will occur in the year after the source does well enough to produce dispersers. Likewise, if more individuals disperse from the source as density in the source becomes higher, the sink will also benefit from these dispersers the year following a year in which the source does well, and will show a lack of these dispersers (and therefore a lower abundance) the year after the source does badly. Finally, if dispersal from the source is in no way dependent on density, the sink will benefit from more dispersers from the source the year after the source does well, and will suffer from fewer dispersers from the source the year after the source does badly.

Based on this prediction, we tested for evidence of consistent asymmetrical dispersal (i.e., one-year time-lagged correlations in abundances) between Wood Thrush populations, to address the following questions: (1) Is there evidence that asymmetrical dispersal and therefore source–sink dynamics occur consistently over time between pairs of Wood Thrush populations? And if so (2), over what distance(s) does this occur? (3) Do identified sources occur in areas with more habitat than their dependent sinks? And (4), are source–sink dynamics clustered in any particular part of the species range?

METHODS

We used data collected by the North American Breeding Bird Survey (BBS) every May and June since 1966 by volunteers working across Canada and the United States (additional information *available online*).[4] Each volunteer runs one or several of the 4462 point count routes (~2900 routes every year), noting all birds

TABLE 1. Results of regression and randomization analyses examining positive, one-year time-lagged correlations between pairs of Wood Thrush populations separated from each other by 10–200 km.

Distance class (km)	Sample size (N)	P
10–20	76	0.087
20–30	88	0.307
30–40	126	0.315
40–50	106	0.415
50–60	98	0.140
60–70	104	0.007*
70–80	180	0.015*
80–90	194	0.262
90–100	176	0.065
100–110	143	0.062
110–120	162	0.088
120–130	264	0.618
130–140	201	0.870
140–150	159	0.393
150–160	188	0.935
160–170	178	0.740
170–180	199	0.575
180–190	249	0.790
190–200	269	0.735

Note: P values were calculated by comparing the number of significant positive results in the N analyses at each distance class to the expected number, based on 1000 sets of N random pairings of the same populations.

* Significant results ($P \leq 0.05$).

seen or heard in three-minute unlimited-distance point counts at 50 roadside stops per route. Stops are ~800 m apart, making each route ~39.2 km long. We used only routes for which there were at least 29 years of data deemed acceptable by the BBS (Sauer et al. 2005).

To examine patterns of one-year time-lagged correlation between routes, we compared the total abundance at the first 10 stops between routes separated by different distances. We used only the first 10 stops because data collected in the early morning are the most reliable (Robbins 1981). For the purpose of this research, we define a population as the sum of these first 10 stops of each route, and therefore the population abundance as the sum of all the abundances at each of the first 10 stops of each route. We calculated distances between all pairs of these populations based on the latitude–longitude coordinates for each route and using the Nearest Features extension (Jenness 2002) in Arcview, version 3.2 (ESRI 1992). For all statistical analyses, we used SPSS version 12.0 (Apache Software Foundation 2003).

We tested for a one-year time-lagged correlation between populations over the entire time period available for all possible pairs of populations at all distance classes from 10 to 200 km, at 10-km intervals. We did not examine populations separated by distances of <10 km because the distance between the first and last sample points in a population was just under 10 km. We paired the data from year t in each potential sink with that from year $t - 1$ in each potential source to determine whether the abundance in the former at time t was affected by the abundance in the latter at time $t - 1$.

The likelihood of confounding temporal and spatial autocorrelation in the data invalidated the use of simple time-lagged regression or correlation analyses between the potential source and sink populations. Due to weather or other factors that might affect populations on a regional or range-wide scale, we would expect same-year correlations between populations, i.e., correlations between B_t and A_t, and between B_{t-1} and A_{t-1} (where A and B are populations and t is time in years). Note that these correlations are likely to decline with increasing distance between A and B. We would also expect correlations in abundance from one year to the next within individual populations, i.e., between A_t and A_{t-1} and between B_t and B_{t-1}. Therefore, we would expect to find a correlation between B_t and A_{t-1} simply because of the correlations 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 therefore had first to account for the effects of B_{t-1}, which we did by forcing this term into the model before examining the effect of interest (A_{t-1}). Thus, the regression model was

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

where B is the abundance in the potential sink, A is the abundance in the potential source, t is time in years, k and l are coefficients, and m is a constant.

We performed these regression analyses for each pair of routes in each of 19 distance classes, at 10-km intervals. We ran all analyses two ways, the first examining the possible effects of A_{t-1} on B_t, and the second examining the possible effects of B_{t-1} on A_t.

To evaluate our results, we created null distributions using randomization analyses. At each distance class, we compared the number of significant positive results in the actual N analyses at that distance class to the expected number, based on 1000 sets of N random pairings of the same populations. We calculated P as the number of times out of 1000 sets of randomized analyses that we obtained at least as many significant positive results as in the initial N analyses at each distance class. For example, at the 10–20 km distance class, we had 38 pairs of populations, and therefore performed 76 initial analyses ($N = 76$). Of these 76, there were 9 analyses for which we found a significant, positive, one-year time-lagged effect of one population on the other. We then created 1000 sets of 76 randomly paired populations from the initial 38 populations included for this distance class, and performed the corresponding 76 000 regression analyses. We found at least 9 significant, positive, time-lagged effects of one population on the other in 87 of these 1000 sets of 76 analyses, and therefore calculated P as 0.087 (Table 1).

For the distance classes at which we found more putative source–sink pairs than expected by chance, we then examined whether the putative source populations identified occurred in areas with more habitat (i.e., deciduous and mixed forest) than their associated putative sinks. For this analysis, we used the USGS's
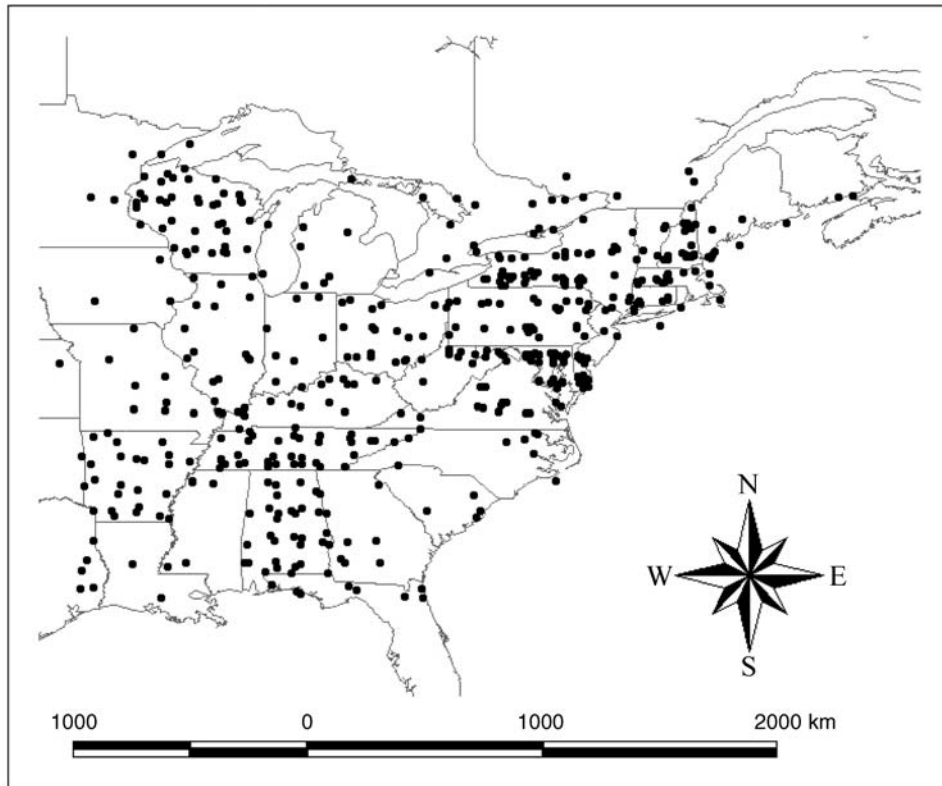
Fig. 1. Populations of Wood Thrushes analyzed across North America at all distance classes. "Populations" consist of the first 10 stops (pooled) of all Breeding Bird Survey routes that recorded the presence of Wood Thrushes and for which there were at least 29 years of data available.

30×30 m resolution 1992 National Land Cover Data (USGS 1992) imported into ArcView version 3.2. We drew a transect between the first point of each putative source population and its associated sink, and, with the help of the Cross Section Utility extension (Tifft 2002), calculated the amount of deciduous/mixed forest per kilometer along this transect. To account for the fact that some putative source–sink pairs are likely in more forested areas than other pairs, we transformed these data by dividing the proportion of forest along each kilometer of each transect by the mean proportion of forest cover per kilometer for that transect. We then ran a linear regression to test whether this relative proportion of forest cover per kilometer of transect decreased with increasing distance from the source to the sink.

For the same distance classes at which we found more putative source–sink pairs than expected by chance, we also investigated whether the putative sources and sinks were more likely to be found in some parts of the breeding range than in others. To address this issue, we first split the Wood Thrush range into 2° latitude–longitude blocks. We then performed a log-likelihood test of association comparing the proportion per block of all populations included in the analyses at these distance classes to the proportion of putative source and sink populations found in these same blocks, expecting

to see no effect if the putative sources and sinks were randomly distributed as opposed to clustered throughout the species range.

RESULTS

We examined a total of 485 populations across the geographical range of the Wood Thrush (Fig. 1). There were 38–135 population pairs per distance class (ranging from 10 to 200 km apart), resulting in 76 to 270 analyses per distance class (Table 1: sample size N). We found significant, positive, one-year time-lagged correlations between pairs of populations that were 60–70 and 70–80 km apart (Table 1).

Of 33 putative source–sink pairs (including both significant distance classes), we identified 3 populations as putative sources in more than one pair (i.e., they appeared to feed more than one putative sink), and 5 populations as putative sinks in more than one pair (i.e., they appeared to be fed by more than one putative source). Six populations were identified as putative sources in some population pairs and putative sinks in others.

When we examined the amount of deciduous/mixed forest along transects drawn from each putative source to its corresponding putative sink, we found a significant decrease in forest cover with increasing distance from
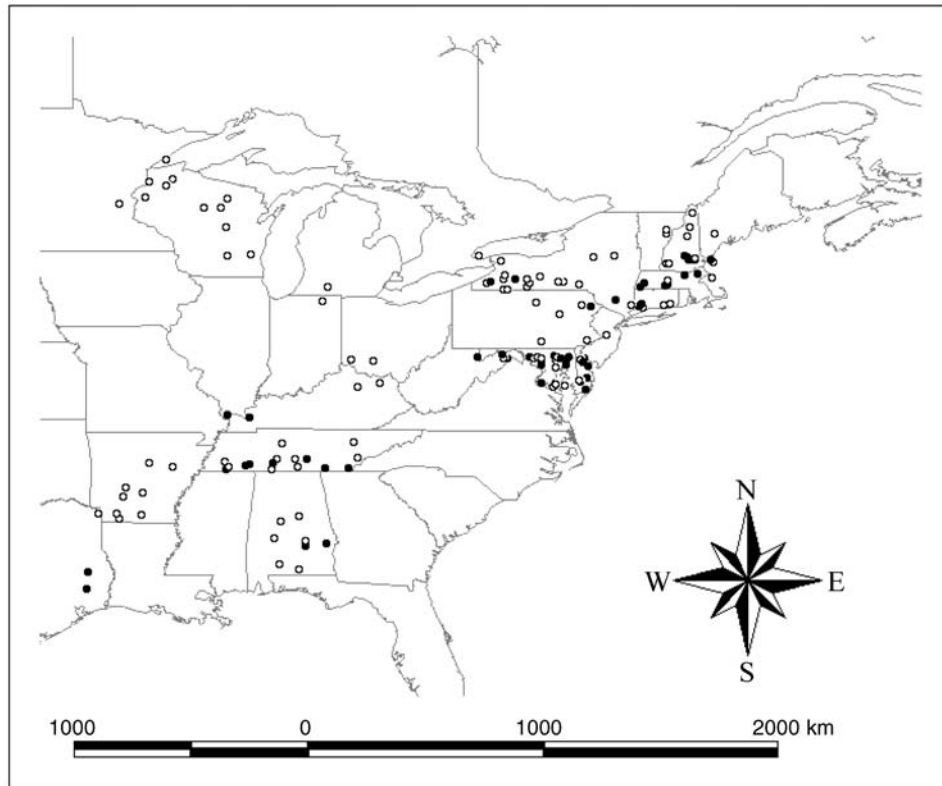
Fig. 2. Populations included in the analyses at the 60–70 and 70–80 km distance classes, with those found to be putative sources or sinks represented by solid circles and all others represented by open circles. Note a lack of putative source/sink populations in the Midwest, despite the inclusion of several populations in this area in the analyses.

the putative source to the putative sink ($F = 25.107$; df = 1, 1983; $P < 0.001$). In other words, there was a declining trend in forest cover from sources to sinks, sources existing in more forested areas than their associated sinks.

We also found evidence of spatial clustering of the putative source and sink populations ($G = 72.316$, df = 36, $P < 0.001$). The putative source/sink populations identified in this study were absent from the Midwest and clustered in the South and Northeast of the United States (Fig. 2).

DISCUSSION

Our results indicate that Wood Thrush populations separated by 60–80 km show significant one-year time-lagged correlations. This supports the idea that consistent asymmetrical dispersal occurred between Wood Thrush populations separated by these distances, which in turn supports the idea that Wood Thrushes frequently disperse over such distances. These findings also support the hypothesis that source–sink dynamics occur consistently over time between pairs of Wood Thrush populations over long distances. Furthermore, in keeping with the literature (Donovan et al. 1995, Burke and Nol 2000), we found a significant decline in habitat amount with increasing distance from each putative

source to its associated putative sink, i.e., the sources identified were in more forested areas than their associated sinks. Note that the fact that we did not find significant time-lagged patterns for distance classes below 60 and above 80 km does not indicate that Wood Thrushes do not disperse over shorter or longer distances. Rather, it suggests that they frequently disperse over distances of 60–80 km.

Interestingly, the 60–80 km dispersal distance we identified here does not correspond to any intrinsic spacing of Wood Thrush habitat. To explore this issue, we examined transitional probabilities (as per Webster and Maestre 2004) at 10-km intervals between deciduous/mixed forest and other types of land cover along transects stretching 200 km out from each putative source–sink pair and spanning the distance between each pair. In other words, along each transect, for each distance x from 10 to 200 km, we counted the number of times two points x distance apart were in different land cover types (deciduous/mixed forest or other), and divided this by the number of pairs of points compared at x distance apart to get a transition probability for each distance. A high transition probability indicates many changes between the two land cover types compared at the spatial lag in question, while a low probability indicates few such transitions. Thus, we

would expect to see a peak in transition probability at 60–80 km if this distance corresponded to some intrinsic pattern of habitat spacing. Transitional probabilities averaged ~0.21, gradually increasing from 0.17 at 10 km to 0.24 at 200 km, but there were no particular peaks at any distance. Because of the lack of any such peaks, we concluded that there was no characteristic spacing between forested and less forested landscapes in the areas of the Wood Thrush geographic range examined.

The dispersal distances we identified (60–80 km) seem large in the context of the literature on juvenile dispersal distances for this and other species of North American songbirds (Weise and Meyer 1979, Payne 1991, Collister and DeSmet 1997, Wheelwright and Mauck 1998). As a typical example, Roth et al. (1996) cite a juvenile dispersal distance of 1–6.8 km for the Wood Thrush, which is more than an order of magnitude shorter than the distances suggested here. However, as discussed above, most of the studies on juvenile dispersal distances were either limited to postfledgling, premigratory movements (Roth et al. 1996, Anders et al. 1998, Rivera et al. 1998), or were based on mark–recapture protocols with extremely low return rates (Payne 1991, Collister and DeSmet 1997, Wheelwright and Mauck 1998). Finally, the spatial extent of study areas used in most songbird dispersal studies is also order(s) of magnitude smaller than the dispersal distances found here, which may explain the low recapture rates. The dispersal distances implied by our findings do not seem quite so large when considered in the context of band recovery data collected in Great Britain by the British Trust for Ornithology. For example, Paradis et al. (1998) found much greater juvenile dispersal distances for some songbirds than have been found for any comparable species in North America. Unpublished radio-tagging data from six birds first captured in the spring in Illinois also support the idea that Wood Thrushes may disperse over large distances. Twenty flights of 20–375 km (mean 125 km, duration 15 minutes to several hours) were recorded for 11 individual Wood Thrushes. Because these "wandering" flights were in random compass directions, they likely represent dispersal, in contrast with the 7 other individuals (13 flights) recorded moving northward, likely in the final stages of migration (W. W. Cochran, *personal communication*).

These relatively large dispersal distances are also consistent with the idea that source–sink dynamics may occur over regional or even continental scales, as has been suggested (Maurer and Villard 1994, Donovan et al. 1995, Robinson et al. 1995, Curnutt et al. 1996, Anders et al. 1997). In fact, these distances might be relatively short to account for such patterns. Donovan et al. (1995) and Robinson et al. (1995) suggest that much of the American Midwest acts as a sink fed by healthy source populations in the Ozark Mountains, northern Wisconsin, and south-central Indiana. Such source–sink dynamics would probably not occur with a one-year time lag, as one generation of young disperse from the source to the sink.

Rather, they might occur over several years, as generations of birds move farther and farther from the source year after year. The fact that we found some populations to be putative sinks in some pairs and putative sources in others supports this idea of large-scale source–sink dynamics occurring with greater time lags.

One alternative explanation for the one-year time-lagged correlations we found between populations is the possible existence of traveling waves of predators or disease, which in turn could create traveling waves in Wood Thrush abundances. Such traveling waves have been documented in field voles across northern England (Lambin et al. 1998, Mackinnon et al. 2001), microtine rodents in Finland (Ranta and Kaitala 1997), and measles among humans in England and Wales (Grenfell et al. 2001). However, asymmetrical dispersal appears to be a much more parsimonious explanation for the phenomenon we document here. There is some evidence in the literature of a one-year time-lagged quadratic relationship between Wood Thrush abundances and those of rodents (potential nest predators) (Schmidt and Ostfeld 2003), but as far as we know, these rodents do not display wave-like patterns of abundance across space in the North American range of the Wood Thrush. In addition, the rate of movement of the small-mammal abundance waves found in northern England was ~19 km/yr, far less than the 60–80 km movement distances required to produce the one-year time-lagged correlations observed here. As far as we know, there is also no evidence that Wood Thrush population sizes are controlled by any particular disease that might cause such one-year time-lagged correlations.

It also seems unlikely that the one-year time-lagged correlations we observed could be caused by some environmental or climatic factor such as weather or resource pulses (e.g., Jones et al. 2003, Koenig and Liebhold 2005). It is easy to imagine that the weather in one population could be correlated within the same year to the weather in another population 60–80 km away. This could lead to within-year correlations in abundance in the two populations through, for example, correlated fluctuations in resource availability. However, it is much more difficult to imagine that the weather or resource availability in one population in one year would be consistently correlated with the weather or resource availability in another population 60–80 km away in the following year. This is what would have to occur for environmental correlations to be the cause of the consistent one-year time-lagged correlations in abundance reported here. We cannot think of any environmental factor that would cause one-year time-lagged correlations at the 60–80 km distances found over the large geographic area of our study. We therefore conclude that the most likely explanation for these time-lagged correlations is between-population dispersal.

A word of caution in labelling these populations as sources and sinks comes from the finding mentioned above that several populations that act as putative

sources in some pairs act as putative sinks in others. This may indicate a multiyear "spatial cascade" effect, whereby a source feeds a sink in one year, and that sink then feeds another sink in the following year. Hence, some of the putative source populations identified may in fact be "pseudo sources," surviving only because they are fed by other populations, themselves either true or pseudo sources. The danger is that these pseudo source populations might be thought to be self-sustaining, when in fact they are dependent on other sources. Nonetheless, there is no reason to believe that management of such pseudo source populations would have a different effect on any dependent sink populations than would management of true source populations.

It has been pointed out that, since adult philopatry is somewhat dependent on breeding success (Roth et al. 1996), and breeding success is lower in sinks than in sources (e.g., Burke and Nol 2000), adults might in fact disperse from sinks to sources rather than from sources to sinks. If juveniles follow the leads of adults in dispersing, they might also tend to move from sinks to sources. In this case, we would expect the one-year time-lagged correlation in abundance to function in the opposite direction: instead of abundances in the source in year t predicting abundances in the sink in year $t + 1$, we would expect abundances in the sink in year t to predict abundances in the source in year $t + 1$. This might lead us to identify sources as sinks and sinks as sources. However, our finding that forest cover decreased with increasing distance from the predictor populations to the predicted populations, in keeping with the studies that find higher forest cover around sources than sinks (Donovan et al. 1995, Burke and Nol 2000), indicates that we have likely properly classified our populations. Since we would not expect adults to disperse from sources (in which they generally have high breeding success) to sinks, we conclude that these source–sink dynamics are likely caused by the dispersal of juveniles away from their natal source populations, as suggested above. Adult and some juvenile dispersal in the opposite direction would only dampen the signals detected.

The locations of the putative source and sink populations identified in our analyses are generally consistent with locations of sources and sinks as identified from demographic data. We found several putative sources and sinks in the general vicinity of the Delaware sites identified as sources and sinks by Weinberg and Roth (1998), and one in the vicinity of the Monongahela National Forest sites identified as sources by Duguay et al. (2001). In several other cases, we did not have sites to sample at the appropriate distance classes in areas in which sources and sinks have been identified (Donovan et al. 1995, Anders et al. 1997, Trine 1998, Friesen et al. 1999, Burke and Nol 2000, Fauth 2000, 2001, Simons et al. 2000). The one exception is the Wisconsin/Missouri area, where Donovan et al. (1995) found sources and sinks and we found none (Fig. 2).

The most important finding of this research is that populations of Wood Thrushes are linked consistently through time with a one-year time lag over distances from 60 to 80 km. We suggest that this indicates that young Wood Thrushes frequently disperse over such distances, and thus that source–sink dynamics occur over such distances. Management decisions concerning this species and its habitat should therefore be made at correspondingly large scales, with consideration for source–sink dynamics.

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