

**SOURCE-SINK DYNAMICS, DISPERSAL, AND LANDSCAPE EFFECTS ON NORTH
AMERICAN SONGBIRDS**

By

Rebecca Tittler, B.Sc., M.Sc.

A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfillment of
the requirements for the degree of

Doctor of Philosophy

Department of Biology

Carleton University

Ottawa, Ontario

May 20, 2008

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Your file *Votre référence*
ISBN: 978-0-494-40540-6
Our file *Notre référence*
ISBN: 978-0-494-40540-6

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ABSTRACT:

Recent advances in ecology point to the importance of approaching management and research issues from a landscape perspective. However, it is often unclear how large an area the landscape of reference must encompass. Among songbirds, lack of data on dispersal and source-sink dynamics further complicates this issue. In this thesis, I address the following questions: (1) Do source-sink dynamics occur among North American songbird? (2) Over what spatial scales do dispersal and source-sink dynamics occur? (3) Over what spatial scales are songbird abundances most affected by the landscape? (4) Do these scales of landscape effect correspond to dispersal distances? (5) What factors are correlated with source-sink status? I used a novel method to identify sources, sinks, and dispersal distances using the North American Breeding Bird Survey data. I identified species-specific scales of landscape effect by examining correlations between these data and landcover from the National Landcover Database. I found evidence of source-sink dynamics for 25 of the 51 songbird species examined. Estimated dispersal distances ranged from 10 to 100 km, indicating that source-sink dynamics occurred over these distances. Scales of landscape effect ranged from 0.5 to 100 km. They were not correlated with dispersal distances or home range or territory sizes. However, they were correlated with mean distance between habitat patches: species whose habitat tended to be separated by smaller gaps responded at smaller scales than those whose habitat tended to be separated by larger gaps. This likely indicates the importance of some type(s) of movement not examined here. Sources and sinks differed in terms of long-term trend, with sources increasing and sinks declining. In light of the findings on source-sink dynamics, population status should be considered in management; alteration of any

potential source habitat could affect other populations tens of kilometers away, depending on the species. In light of the findings on scale of landscape effect, studies examining the effects of landscape structure on population size should be carried out at correspondingly large scales. Future research should focus on elucidating the mechanism(s) behind the relationship between landscape structure (gap size) and scale of landscape effect.

ACKNOWLEDGMENTS

I dedicate this work to my family:

To the memory of my grandfather, the original Dr. Tittler, for inspiring in me a
fascination with all things living

To my grandmother, for the quickness of her mind and the warmth of her heart

To my parents, for their undying belief in my abilities, and for always being there when I
needed them

To Sasha, for nodding attentively as I talked through every single hypothesis and result,
and for seeing me through these years, for better or for worse

To my children, Anna and Daniel, for inspiring me to finish.

None of this would have been possible without your love and support.

Я вас люблю.

This work would also not have been possible without the constant advice,
encouragement, and friendship of my co-supervisors, Lenore Fahrig and Marc-André
Villard. Thank you for your belief in me and in this project, for reading countless drafts,
and for always being there when I needed you. Votre patience est magnifique. You are
wonderful role models. If this section is not as well-written as the rest of the thesis, it is
only because it is the one section you have not proofread.

Throughout my time here, I have been blessed with wonderful friends and
colleagues:

To Julie Brennan, Felix Eigenbrod, Kringen Henein, and Tom Sherratt, thanks for sharing the teaching load: I learned so much from all of you. Julie, it was fun to share the joys of the student belly-mama with you, and I hope our friendship will be echoed in our children. Felix, you never once turned me away when I asked to “borrow your brain”. The quality of this work has undoubtedly been improved by your input. Kringen, you showed me it was possible to do a Ph.D. and mother young children at the same time. And Tom, you were so kind during my qualifying exam; I’ve appreciated your support over the years.

To Rebecca Barker, Julie Bouchard, Elysia Brunet, Neil Charbonneau, Mark Harvey, Maxim Larrivé, Keith Munro, and Ravi Virk, with whom I shared office space: thank you for putting up with the numerous distractions and interruptions that came with the position. Special thanks to Stéphanie Duguay, who helped me plant my garden in the beginning, and has been there ever since to share my joys and sorrows; and of course to Sara Gagné, who never turned me down when I asked for her ear. I can only hope to be so lucky in my future office-mates!

To Chris Beatty, Dan Bert, Glenn Cunnington, Laura Dingle Robertson, Hume Douglas, Adam Ford, Jeff Holland, Dave Ladd, Jean-Louis Martin, Rachelle McGregor, Ashley McLaren, Leif Olson, Dave Omond, Raphaël Proulx, Krista Ryall, Trina Rytwinski, Adam Smith, Patty Summers, Joerg Tews, Lutz Tischendorf, and Paul Zorn, thanks for your wisdom and friendship over the years. Special thanks to Jochen Jaeger, who failed to tell me I was crazy the night I ran into his office with a cockamamie story about a one-year time-lag. I still hope we’ll work together in the future. Thanks also to

Marija Gojmerac, for helping me sort out all the deadlines and requirements of this degree.

David Currie and Kathryn Lindsay provided their insight throughout as members of my advisory committee. David, I hope I have earned the Ph. I will be reading more Popper over the weekend. Kathy, if I ever publish anything on the pseudo-sources or phylogenetically independent contrasts, it will be thanks to you.

I was honoured to have Kimberly With and Nancy Doubleday read this thesis and sit on my defense committee. Thank you for your interest and your kindness. I hope our paths will cross again in the future.

The tremendous amount of analytical work presented in Chapter 3 was greatly facilitated by some coding done by Matthew Ladd, Ben Lawlor, and Trevor Porter. Kerri Widenmeier also helped with some of the analyses, as did Alexander Drozhzhin.

This research would not have been possible without the thousands of volunteers collecting data for the North American Breeding Bird Survey; their work is invaluable.

Throughout my time as a Ph.D. student, I was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC); the Fonds québécois de la recherche sur la nature et les technologies; the Ontario Ministry of Training, Colleges and Universities; and the Biology Department of Carleton University. Additional funding was provided by NSERC Discovery Grants to Lenore Fahrig and Marc-André Villard, a Canada Foundation for Innovation grant to Lenore, and generous grants from my patient grandmother and my loving parents.

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CHAPTER 1: GENERAL INTRODUCTION

Since the early 1960's, when Rachel Carson warned of a spring without birdsong (Carson 1962), there has been increasing concern about declines in North American songbirds. In ecological research and in management, songbirds are also often used as focal taxa; they are of interest in themselves but, because they are relatively easily surveyed, they are also useful to model general patterns in the response of wildlife to management or landcover changes. As of January 7th, 2008, Cambridge Biological Abstracts listed 4274 publications including the word "songbird", and 449 of these with the words "conservation" or "management" published since 1965. Furthermore, there has been increasing interest in examining and managing for the effects of the surrounding landscape on songbird population size, and an increasingly large body of literature finding the importance of such a landscape-scale approach (e.g., Coreau and Martin 2007).

However, a careful perusal of the literature indicates a general lack of consensus as to the appropriate scale for such landscape study and management. Studies with management implications have been carried out at scales varying from several hectares (e.g. Tittler et al. 2001) to thousands of hectares (e.g., Edenius and Elmberg 1996, Trzcinski et al. 1999). Results on taxa from beetles to birds have been found to vary depending on the spatial scale considered (e.g., Burke and Nol 2000, Mitchell et al. 2001, Holland et al. 2004, Dunford and Freemark 2005, Cunningham and Johnson 2006, Koper and Schmiegelow 2006, Magness et al. 2006, Betts et al. 2007, Buler et al. 2007, Vanbergen et al. 2007). Erroneous conclusions might be drawn based on studies carried out at the wrong spatial scales (e.g., Mitchell et al. 2001). Hence, if we are to effectively

study and manage populations, we must identify appropriate spatial scales of study, or the scales at which populations respond most strongly to the landscape. I refer to this scale as the “scale of landscape effect”, although it has also been called the “characteristic scale” (Holland et al. 2004, 2005).

Many landscape ecologists have assumed that the spatial scales at which populations respond to the landscape correspond to dispersal distances (e.g., Burke and Nol 2000, Villard et al. 1995). Evidence in favour of this approach comes from Holland et al. (2005), who found a correlation between the scale of effect and body size in longhorned beetles; body size has been found to be correlated with dispersal distance in birds and mammals (Paradis et al. 1998, Sutherland et al. 2000, Chapter 3). The theory behind this assumption is that populations are affected by the landscape at the spatial scale(s) at which individuals move through the landscape (Addicott et al. 1987), and that they mostly experience the landscape through dispersal, as opposed to during daily movements (when they likely remain mostly in habitat) or migratory movements (when they likely fly right over the landscape, regardless of landscape structure).

Another, related reason the scale of landscape effect might correspond to dispersal distances is the possibility of source-sink dynamics. Pulliam (1988) defined sources and sinks based on the population growth equation:

$$\lambda = (1 - M) + SP \quad \text{(Equation 1)}$$

where M is adult mortality, S is juvenile survival, and P is fecundity (Pulliam 1988). If λ is positive, survivorship and fecundity (or, taken together, reproduction) exceed mortality and the population is a source. If it is negative, and mortality exceeds reproduction, it is a sink. Pulliam hypothesized that there might exist a “source-sink dynamic”, such that the

excess individuals from the source population might disperse to the sink population, buffering the effect of the decline of the latter. In a perfectly balanced system, this would result in both the source and the sink having no net change in abundance, i.e.,

$$P + I = (1-S) + M + E \quad \text{(Equation 2)}$$

where I is immigration and E is emigration (Pulliam 1988). The processes of immigration and emigration can also be described as the dispersal, defined as the movement of individuals from one area to another for the purpose of reproduction (Greenwood 1980). Thus, sources and sinks are linked by dispersal, source-sink dynamics must function over the scale(s) over which dispersal occurs, and sink populations are dependent on dispersers from sources. Because of this dependence, it is likely that sinks will be especially affected by the landscape separating them from their sources, or the landscape within dispersal range. Note that, since adult philopatry is high in most songbird species (Poole and Gill 1992-2006), sources and sinks are likely generally linked by natal (juvenile) dispersal rather than adult (breeding) dispersal.

From another perspective, variations in a source population will be echoed in any dependent sinks, i.e., in other populations within natal dispersal distance, thus also highlighting the potential importance of studying and managing populations at scales corresponding to natal dispersal distances. Imagine a situation in which habitat is to be degraded in a particular location. If this habitat housed a source population, effects of this degradation would span far beyond the reaches of the actual degradation, resulting in declines in any dependent sinks. Since these sinks must be within dispersal distance of the source, the degradation of the source habitat would affect populations located within

the dispersal range. Thus, those studying and managing these populations would only see the true effects of the degradation if they examined them over the scale of natal dispersal.

Unfortunately, there is a general lack of data on natal dispersal distances (see Poole and Gill 1992-2006), making it difficult to test for a link between source-sink dynamics, dispersal distances, and scale of effect. Available data are generally collected using either radio-telemetry or mark-recapture studies. Radio-telemetry studies follow birds for the first few weeks after fledging (e.g. Anders et al. 1997) but do not provide true dispersal distances because individuals cannot be tracked over the entire winter to find out where they breed the following spring. Mark-recapture studies rely on the return of banded birds between seasons. Unfortunately, recapture rates for juveniles are generally far too low to provide reliable information on dispersal distances. Although rates as high as 18%, 9%, and 10% have been recorded for the Tree Swallow (*Tachycineta bicolor*), the American Robin (*Turdus americanus*) (Haas 1995), and the Veery (*Catharus fuscens*) (Suthers 1986-1988), rates of 0% (0/42), 1% (2/243), 2% (8/392), 2.1% (154/7375), and 5% (34/68) recorded for the White-eyed Vireo (*Vireo griseus*) (Hopp et al. 1995), Loggerhead Shrike (*Lanius ludovicianus*) (Haas 1995), Brown Thrasher (*Toxostoma rufum*) (Hass 1995), House Wren (*Troglodytes aedon*) (Kendeigh 1941), and Wood Thrush (*Hylocichla mustelina*) (Roth et al. 1996) are much more typical. Intensive mark-recapture studies would likely have to be carried out over much larger spatial scales than is generally practical in order to provide useful indications of how far the majority of young disperse. Stable isotopes and genetic and elemental markers may be useful in examining general patterns of dispersal movement, but the spatial resolution available using these methods is as yet insufficient to estimate typical

dispersal distances (Hobson 2005, Donovan et al. 2006), although these techniques might be refined through the development of chemical signature analysis.

If populations were generally characterized by source-sink dynamics, the ability to identify sources and sinks independently might allow us to circumvent the lack of data on dispersal distances: we could perhaps assume that identified sinks were associated with the closest identified sources, and study and manage populations at appropriate spatial scales. Unfortunately, the identification of sources and sinks is also problematic. Many attempts have been made to identify sources and sinks by examining fledging success as a surrogate for fecundity (P in Equation 1), estimating adult mortality (M) and juvenile survival rates (S) based on mark-recapture data or, in the case of S , on post-fledging, pre-winter survival, and inserting these numbers into the population growth equation (Equation 1) to get an estimate of population growth (λ). The long list of species on which such studies have been carried out includes the Wood Thrush (Roth and Johnson 1993, Donovan et al. 1995a, Anders et al. 1997, Weinberg and Roth 1998, Friesen et al. 1999, Burke and Nol 2000, Fauth 2000 and 2001, Simons et al. 2000, Duguay et al. 2001, Ford et al. 2001), Acadian Flycatcher (*Empidonax virescens*) (Duguay et al. 2001, Ford et al. 2001, Fauth and Cabe 2005, Hoover et al. 2006), and Ovenbird (*Seiurus aurocapilla*) (Donovan et al. 1995a, Porneluzi and Faaborg 1999, Burke and Nol 2000, Flaspohler et al. 2001, Ford et al. 2001).

The use of nesting or fledging success as a measure of fecundity is slightly problematic. To measure nesting or fledging success, researchers do intensive fieldwork in which nests are found and followed throughout the breeding season to determine how many young are produced per adult. This assumes that an indicative sample of the nests

has been found; unless all nests are found, it is likely that the nests that are found are the more obvious ones, and these are also likely more obvious to nest predators and brood parasites. Thus, those nests that are found may also be those more susceptible to parasitism and predation. Furthermore, the regular checking of nests may itself increase the risk of nest predation or brood parasitism (Martin and Roper 1988). Although these data are valuable and may be particularly useful for comparison among populations, they may lead to underestimations of fecundity in general and could therefore cause problems in the careful calculation of population growth rates.

The use of adult return rates as a measure of adult survival is also slightly problematic. This method assumes that all or some proportion of adults that do not return die, but this assumption cannot be tested. This may lead to an overestimation of adult mortality. Furthermore, since adult return rates have been linked to breeding success, with successful adults more likely to return (e.g., Winkler et al. 2004), the error in this estimate may be biased, with higher mortality rates assigned to populations in which individuals experience lower breeding success. Although this may indeed be the case, again, this assumption is difficult to test.

However, the most problematic estimate is that of juvenile survival. Since juvenile recapture rates are far too low to be useful in estimating juvenile survival rates (see above), researchers base this measure on adult return rates or on post-fledging, pre-winter survival rates. The problems with adult return rates are outlined above. Added to these is the difficulty in deciding on the relationship between adult return rates and juvenile survival. Pre-winter survival rates are based on studies using radio-telemetry data to track the newly fledged young in the early fall (Anders et al. 1997). Not only do

small sample sizes make it difficult to base juvenile survival rates on these data, but the assumption that juvenile survival during the early fall is a true reflection of over-winter survival is tenuous. Resident birds are likely to encounter far more difficult conditions and therefore suffer from higher mortality rates during the winter than during the early fall, and mortality rates are likely to be far higher during migration than on the summer or winter grounds for migratory birds (e.g., Sillett and Holmes 2002). This problem in particular makes it very difficult to realistically measure source-sink status.

Not surprisingly, the use of fledging success, adult return rates, and post-fledging survival to identify potential sources and sinks has led to little or no consensus as to when, where, and at what spatial scales source-sink dynamics are likely to occur among songbird populations. A striking example is that of the Wood Thrush, the most commonly studied bird species in this area of research (for review, see Fauth 2001). In south-central Ontario, Burke and Nol (2000) identified fragments of ~93 ha as sinks and those of ~225 ha as sources for the Wood Thrush, while in the nearby Waterloo area, Friesen et al. (1999) found that woodlots ranging from 3 to 140 ha contained self-sustaining populations of the same species, and Roth and Johnson (1993) identified a 15-ha woodlot in Delaware as a population source. In a study performed in 1994 and 1995 in southern Missouri, Anders et al. (1997) considered Wood Thrush populations in the Ozark Mountains as sinks, while studies performed in the same area from 1991 to 1993 by Donovan et al. (1995a) found the area to be a population source for the same species. The variation in these results may indicate that source-sink dynamics occur over different spatial scales in different areas, and/or that some populations may be sources in some years and sinks or self-sustaining populations in others (Fauth 2001), or that the methods

used are flawed. At any rate, they leave us with no clear predictions about when, where, and at what scale a population will function as a source or a sink, and thus with no hints as to the appropriate scale(s) at which to study and manage songbirds.

In an attempt to address the issue of the spatial scale over which songbirds should be studied and managed, I addressed the following questions: (1) Do source-sink dynamics occur among North American songbird populations? (2) Over what spatial scales do natal dispersal and source-sink dynamics occur? (3) Over what spatial scales are songbirds most affected by the landscape? (4) Do identified scales of effect correspond to dispersal distances?

In Chapter 2, using the example of one focal species, I present a novel way to identify sources, sinks, and dispersal distances based on the long-term, large-scale data provided by the North American Breeding Bird Survey. In Chapter 3, I present results for another 24 species and find correlations between these dispersal distances and wing length and body mass. In Chapter 4, I identify species-specific scales of landscape effect and test for a relationship between these and the dispersal distances from the previous chapters. In Chapter 5, I test for correlates of source-sink status. Overall, my results suggest that source-sink dynamics do occur among North American songbirds; sinks are characterized by declining trends whereas sources tend to be increasing. Furthermore, songbirds do seem to disperse over long distances, allowing these source-sink dynamics to occur over large scales. However, these factors apparently are not important in determining the scale of effect of the landscape. Instead, songbirds responded to the landscape at scales corresponding to those over which the landscape itself was structured.

**CHAPTER 2: TIME-LAGGED CORRELATIONS BETWEEN WOOD THRUSH POPULATIONS
INDICATE LONG-DISTANCE DISPERSAL AND SOURCE-SINK DYNAMICS**

(Adapted from Tittler, R., L. Fahrig, and M.-A. Villard. 2006. Time-lagged correlations between Wood Thrush populations indicate long-distance dispersal and source-sink dynamics. *Ecology* 87: 3029-3036.)

2.1 Chapter summary:

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. I 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, I 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.

2.2 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 counter-balance rates of mortality ($\lambda < 1$), and a source as one in which reproduction exceeds that necessary to counter-balance 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., Gardenfors et al. 2001), and widely used to explain the presence of organisms, often birds, in areas thought to be of low habitat quality (e.g., Tittler et al. 2001, Duguay et al. 2001, DeGroot and Smith 2001, Hoover et al. 2006, Møller et al. 2006, etc.). A search of the ISI Web of Science database brings up a list of 1647 published works that cite Pulliam's seminal paper between its publication in 1988 and January 2008, more than 25% (441) of which contained the word "bird" or "songbird".

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. 1995a, Anders et al. 1997, Trine 1998, Weinberg and Roth 1998, Friesen et al. 1999, Fauth 2000, Simons et al. 2000, Burke and Nol 2000, Fauth 2001, Ford et al. 2001, Duguay et al. 2001). Sources have been found to occur in areas with more habitat than sinks (Donovan et al. 1995a, 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.

As for other species, the distance(s) over which source-sink dynamics occur among Wood Thrush populations 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 natal (juvenile) rather than adult (breeding) 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, as for 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, Vega 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, 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, I 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?

2.3 Methods:

I 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. Each volunteer runs one or several of the 4462 point count routes (~2900 every year), noting all birds seen or heard in 3-minute unlimited-distance point counts at 50 roadside stops per route. Stops are ~800 m apart, making each route ~39.2 km long.

To examine patterns of one-year time-lagged correlation between routes, I compared the total abundance at the first 10 stops between routes separated by different distances. I 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, I 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. I 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 (Environmental Systems Research Institute, Inc. 1992). For all statistical analyses, I used SPSS version 12.0 (Apache Software Foundation 2003)

I 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. I did not examine populations separated by distances of less than 10 km because the distance between the first and last sample points in a population was just under 10 km. I 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, I 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 . I 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, I 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 , I therefore had first to account for the effects of B_{t-1} ,

which I 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.

I performed these regression analyses for each pair of routes in each of 19 distance classes, at 10-km intervals. I 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 .

I included only routes with all of the following three characteristics: (1) at least 29 years of data deemed acceptable by the BBS (Sauer et al. 2005), (2) 10 to 100 km from at least one other route with 29 years of available data, and (3) sufficient non-zero data points for the assumptions of the general linear model to be met (I 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 ($f^2 \geq 0.35$) (Cohen 1988) in a multiple regression with two predictors (Faul and Erdfelder 1992).

To evaluate my results, I created null distributions using randomization analyses. At each distance class, I 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. I calculated P as the number of times out of 1000 sets of randomized analyses that I 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, I had 38 pairs of populations, and therefore performed 76 initial analyses ($N = 76$). Of

these 76, there were 9 analyses for which I found a significant, positive, one-year time-lagged effect of one population on the other. I 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. I 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 2.1).

For the distance classes at which I found more putative source-sink pairs than expected by chance, I 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, I used the USGS's 30-by-30-m-resolution 1992 National Land Cover Data imported into Arcview version 3.2 (Environmental Systems Research Institute, Inc. 1992). I 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 (Tiff 2002), calculated the amount of deciduous/mixed forest per kilometre along this transect. To account for the fact that some putative source-sink pairs are likely in more forested areas than other pairs, I transformed these data by dividing the proportion of forest along each kilometre of each transect by the mean proportion of forest cover per kilometre for that transect. I then ran a linear regression to test whether this relative proportion of forest cover per kilometre of transect decreased with increasing distance from the source to the sink.

For these same distance classes at which I found more putative source-sink pairs than expected by chance, I 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, I first split the Wood Thrush range into two-degree latitude-longitude blocks. I 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.

2.4 Results:

I examined a total of 485 populations across the geographical range of the Wood Thrush (Fig. 2.1). There were 38 to 135 population pairs per distance class (ranging from 10 to 200 km apart), resulting in 76 to 269 analyses per distance class (N : Table 2.1). I found significant, positive, one-year time-lagged correlations between pairs of populations that were 60-70 and 70-80 km apart (Table 2.1).

Of 33 putative source-sink pairs (including both significant distance classes), I 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 I examined the amount of deciduous/mixed forest along transects drawn from each putative source to its corresponding putative sink, I found a significant decrease in forest cover with increasing distance from the putative source to the putative sink ($F = 25.107$; $df = 1,198$; $P < 0.001$). 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.

I 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. 2.2).

2.5 Discussion:

My results indicate that Wood Thrush populations separated by 60 to 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 (Burke and Nol 2000, Donovan et al. 1995a), I 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 I 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 to 80 km.

Interestingly, the 60-80 km dispersal distance I identified here does not correspond to any intrinsic spacing of Wood Thrush habitat. To explore this issue, I examined transitional probabilities (as per Webster and Maestre 2004) at 10 km intervals between deciduous/mixed forest and other types of landcover 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, I counted the number of times two points x distance apart were in different landcover 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 landcover types compared at the spatial lag in question, while a low probability indicates few such transitions. Thus, I 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 peak, I 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 I 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 natal dispersal distances are either limited to postfledgling, premigratory movements (Roth et al. 1996, Anders et al. 1998, Vega Rivera et al. 1998), or are 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 my 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 several 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. 1995a, 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. (1995a) 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 I 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 I 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 is a much more parsimonious explanation for the phenomenon I 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 I 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 approximately 19 km/year, far less than the 60- to 80-km movement distances required to produce the one-year time-lagged correlations observed here. As far as I 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 I 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. I 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 my study. I therefore conclude that the most likely explanation for these time-lagged correlations is between-population dispersal.

A word of caution in labeling these populations as sources and sinks comes from the finding mentioned above that several populations that act as putative sources in some pairs may represent putative sinks in others. This may indicate a multi-year “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 “pseudosources”, surviving only because they are fed by other populations, themselves either true or pseudosources. The danger is that these pseudosource 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 pseudosource 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, I 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 $t + 1$, I would expect abundances in the sink in year t to predict abundances in the source in year $t + 1$. This might lead to the identification of sources as sinks and sinks as sources. However, my 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 (Burke and Nol 2000, Donovan et al. 1995a), indicates that I have likely properly classified my populations. Since I would not expect adults to disperse from sources (in which they generally have high breeding success) to sinks, I 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 my analyses are generally consistent with locations of sources and sinks as identified from demographic data. I 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, I did not have sites to sample at the appropriate distance

classes in areas in which sources and sinks have been identified (Donovan et al. 1995a, Anders et al. 1997, Trine 1998, Friesen et al. 1999, Burke and Nol 2000, Fauth 2000, Simons et al. 2000, Fauth 2001). The one exception is the Wisconsin/Missouri area, where Donovan et al. (1995) found sources and sinks and I found none (Fig. 2.2).

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. I 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 must be made at correspondingly large scales, with consideration for source-sink dynamics.

Table 2.1. Results of regression and randomization analyses examining positive, one-year time-lagged correlations between pairs of Wood Thrush populations separated by 10 to 200 km. *P*-values were calculated based on randomization analyses.

Distance Class (km)	Sample Size (<i>N</i>)	<i>P</i>-value
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

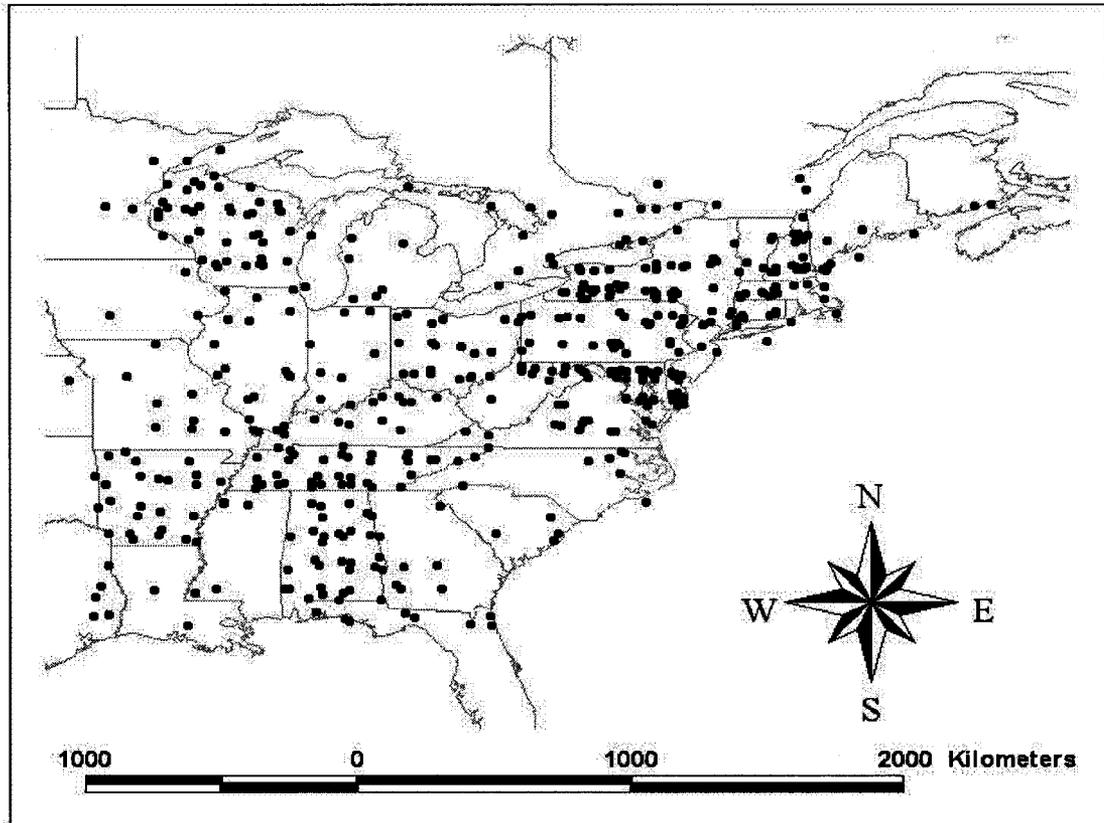


Figure 2.1. Populations of Wood Thrushes analyzed across North America at all distance classes. "Populations" consist of the first 10 stops (pooled) of all Breeding Bird Survey routes that recorded the presence of Wood Thrushes and for which there were at least 28 years of data available.

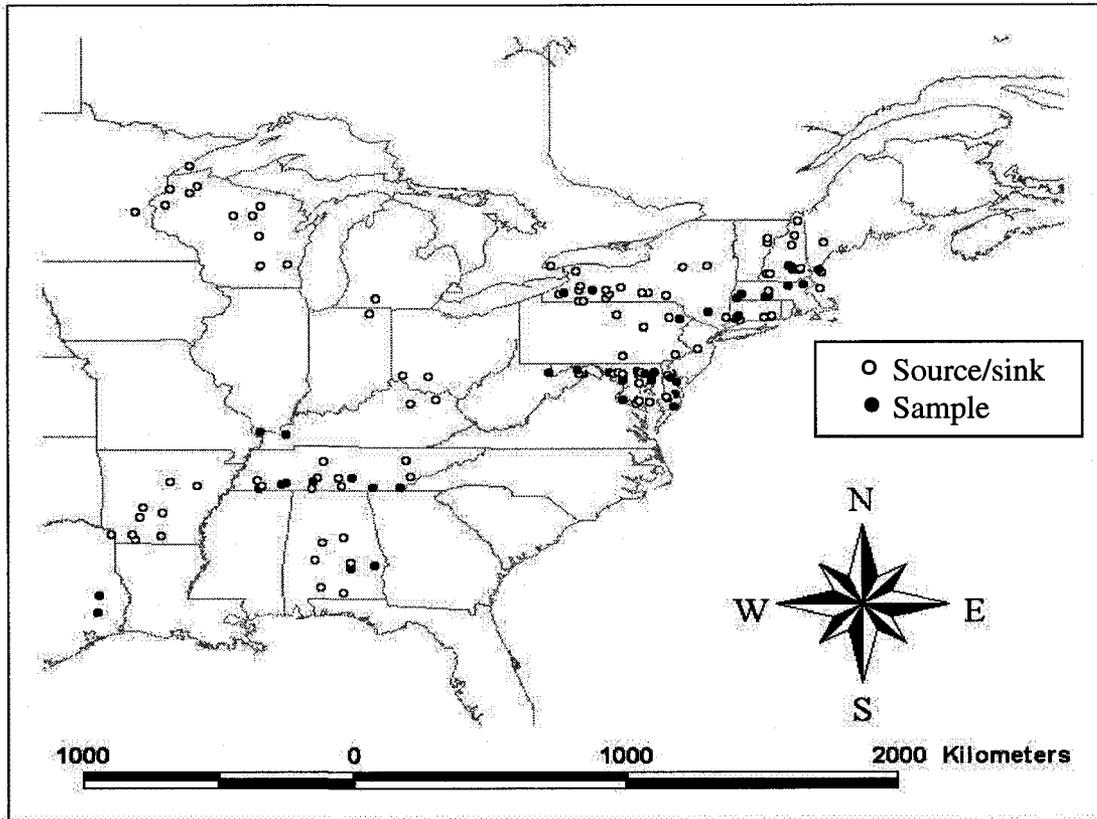


Figure 2.2. Wood Thrush populations included in the analyses at the 60-70 and 70-80 km distance classes, with those found to be putative sources or sinks represented by closed circles and all others represented by open circles. Note a lack of putative sources/sinks in the Midwest, despite the inclusion of several populations in this area in the analyses.

CHAPTER 3: HOW FAR DO SONGBIRDS DISPERSE?

(Adapted from Tittler, R., M.-A. Villard, and L. Fahrig. How far do songbirds disperse? In review.)

3.1 Chapter summary:

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. I used one-year time-lagged correlations in abundance to estimate dispersal distances. Using the North American Breeding Bird Survey database, I examined one-year time-lagged correlations between pairs of North American songbird samples separated by 10 to 100 km. I submit that consistent one-year time-lagged correlations reflect the exchange of individuals through dispersal. I found 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 I measured are generally an order of magnitude longer than those reported in the literature.

3.2 Introduction:

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 (e.g., Shields 1984), but if most individuals disperse beyond the range of sampling, distances will be underestimated. This is likely the case for songbirds, for which recapture rates of individuals marked as juveniles are typically low, on the order of 5% or less (e.g., Fleischer et al. 1984, Payne 1991). Given the significance of dispersal in songbird demography and the difficulty in measuring dispersal distances, I applied the one-year time-lagged model presented in Tittler et al. (2006) and in Chapters 2 and 3 to estimate typical dispersal distances for as many North American songbird species as possible.

This one-year time-lagged model stems from the literature on spatial synchrony (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 (e.g., Paradis et al. 1999) and mammals (e.g., 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 and are mainly detected by their singing during breeding seasons, I expect that songbird dispersal will produce one-year time-lagged

rather than within-year correlations (Tittler et al. 2006, Chapter 2). 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, Jenkins et al. 2007). 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, I predict that measures of bird morphology such as body mass and wing length will be positively correlated with these species-specific lagged correlation distances.

In this study, I examined one-year time-lagged correlations in abundance between paired samples of many North American songbird species, putting forward the idea that these are estimates of typical dispersal distances. I 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 one-year time-lagged correlations reflect typical dispersal distances.

3.3 Methods:

I 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, I extracted the total abundance of each species at the first 10 stops (defined as a "sample") of each 50-stop route. I 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 Institute 1995). I used SPSS 12.0 (Apache Software Foundation 2003) for all statistical analyses unless otherwise stated.

For each species, I tested for 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). I could not examine distance classes of less than 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. I 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, same-year correlations between samples would be expected (e.g., 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, 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 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 , I 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, I 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. I ran all analyses two ways, examining the possible effects of A_{t-1} on B_t , and of B_{t-1} on A_t .

These analyses were limited in several ways. I included only routes with all of the following three characteristics: (1) at least 29 years of data deemed acceptable by the BBS (Sauer et al. 2005), (2) 10 to 100 km from at least one other route with 29 years of available data, and (3) sufficient non-zero data points for the assumptions of the general linear model to be met (I 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 ($f^2 \geq 0.35$) (Cohen 1988) in a multiple regression with two predictors (Faul & Erdfelder 1992). I 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, I then asked whether samples separated by this particular distance were linked with a positive one-year time-lag. My null hypothesis

was that pairs of samples separated by this particular distance were not more likely to be linked with a one-year time-lagged correlation than expected by chance, i.e. pairs of samples selected at random (i.e., not necessarily separated by this particular distance class). To test this, I 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}). Note that the sample unit in these analyses was the pairs, not the samples themselves, and the population sampled (the population about which I wished to draw inference) was composed of pairs of areas separated by the particular distance class in question. I then 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. To create a null distribution, I repeated this procedure 1000 times, and thus produced a frequency distribution of L/N . To test my hypothesis about pairs separated by the particular distance class in question, I 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 my test statistic. I 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 I was examining the 10-20 km scale for species X. My 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 I 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 ($L_{\text{obs}} = 10$). The test statistic would be $1/10$ ($L_{\text{obs}}/N = 10/100$ or $1/10$). I 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, I would have done this 1000 times, and thus created a frequency distribution of $L/100$ (L/N). To test my hypothesis about pairs separated by 10-20 km, I 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, I would have calculated a P-value of 0.025, and would have judged my null hypothesis accordingly.

In effect, in the initial analyses, I did not use the P-values in the traditional hypothesis-testing sense; I 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 one-year time-lagged correlations in abundance than expected by chance for at least one distance class, I 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, I 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, I calculated a median correlation distance of 20 km (halfway between 10 and 30).

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

To test the hypothesis that the lagged correlation distance estimates reflect dispersal movements, I 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. I used median body mass and wing length data from the literature (Poole and Gill 1992-2006). I weighted regressions by sample size (number of pairs analyzed at the significant distance class for each species) because, for species with larger sample sizes, I was more confident that sample pairs with significant, 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 one-year time-lagged correlations between pairs of samples at more than one distance class, I used mean sample size as the weighting variable, i.e., the mean of the number of pairs analyzed at each significant distance class.

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 (e.g. Felsenstein 1985). Since morphological characteristics such as body mass and wing length are likely to be related to phylogeny, I 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). I 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. 3.1). For lack of standardized branch lengths, I assigned all branch lengths a value of 1, then transformed them with a Rho transformation ($\rho = 0.8$) (Grafen 1989). I tested the adequacy of these branch lengths as suggested by Garland et al. (1992). I 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, I 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). Since these analyses did not claim to distinguish between the sexes, these values were calculated based on data from both sexes, regardless of possible

sexual dimorphism for some of the species. As recommended (Garland et al. 1992), I forced all regressions of phylogenetically independent contrasts through the origin.

I 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 root 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.

3.4 Results:

Despite the large extent of the BBS data, only 428 routes could be included in the analyses (Fig. 3.2) owing to the strict route selection criteria (see above). Coincidentally, these routes were mainly located in the eastern half of the United States, and the species examined were therefore those common in this part of the continent.

There were significant, one-year time-lagged correlations between populations of 25 of the 51 species examined (Table 3.1). Sample sizes at the distance classes for which I found these correlations varied from 6 to 180 pairs (Table 3.1). On average, sample sizes were significantly larger for species for which there were significant 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 one-year time-lagged

correlations, no distance classes were excluded from randomization 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, I likely would have found significant time-lagged correlations for at least some of the 26 species for which I found none here. Median lagged correlation distances for the 25 species for which I found significant time-lagged correlations ranged from 15 to 95 km (Table 3.1).

Inter-specific analyses revealed these median lagged correlation distances to be significantly positively correlated with wing length (Fig. 3.3), whether or not phylogenetic relatedness was accounted for (Table 3.2). The positive correlation between lagged correlation distance and median body mass was also significant when phylogenetic relatedness was accounted for, although it was not quite significant when phylogenetic relatedness was not accounted for (Table 3.2). 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 3.2). 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.

3.5 Discussion:

These results indicate that many species of North American songbirds are linked with a one-year time-lag over tens of kilometres (Table 3.1). The correlations between these distances and wing length and body mass support the contention that these distances correspond to dispersal movements.

If these lagged correlation distances are indeed indications of dispersal distances, they are much more extensive than those previously reported for the same species based on mark-recapture and radio-telemetry studies (e.g., Kendeigh 1941, Laskey 1944, Farner 1945, Kessel 1957, Halliburton and Meewaldt 1976, Fleischer et al. 1984, Shields 1984, Moore and Dolbeer 1989, Payne 1991, McGowan 2001). This is not surprising considering the methods used. In contrast with my 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, I sought to draw separate inferences for each distance class, testing independent hypotheses for each species and each distance class, i.e. that there were significantly more one-year time-lagged correlations than expected by chance. Here, I 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, my 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. I 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 my results, since those results judged to be significant at $\alpha = 0.05$ had P-values less than 0.025 ($0.05 / 2$, the cut-off for two comparisons done at $\alpha = 0.05$). In addition, I found one-year time-lagged effects for 49% (25/51) of the species examined, much more than the 5% I might have expected to find by chance. Finally, if my 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, I controlled for within-year synchrony before examining time-lagged synchrony. As far as I know, songbirds are not tightly linked to any other species or disease that is itself synchronized (see 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 my method, all species would be expected to have one-year time-lagged correlations at the smallest scale examined, i.e., at the 10-20 km scale. The fact that most species exhibited 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 one-year time-lagged correlations in abundance between samples observed here are produced by anthropogenic land-use change such as urbanization. My 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 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 (*Hylocichla mustelina*) (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 one-year time-lagged correlations at very different distances (Table 3.1). The forest species (Wood Thrush, Red-eyed Vireo, Scarlet Tanager, Chestnut-sided Warbler, and Tufted Titmouse) showed median lagged correlation distances of 25 to 95 km; the open-area species (Blue Grosbeak, Chipping Sparrow, Bobolink, and Red-winged Blackbird), of 25 to 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 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 I tested for time-lagged correlations at all distance classes between 10 and 100 km, the distance classes at which I found such correlations should correspond to actual

dispersal distances. In addition, if all dispersal were occurring at distances of less than 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 I found (Table 3.1). Dispersal between samples therefore remains the most parsimonious explanation for the observed patterns.

Of course, I would not claim that all individuals of a species disperse over the distances over which I found one-year time-lagged correlations. In referring to these distances as “typical dispersal distances”, I 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 (e.g., Potti and Montalvo 1991). Similarly, I do not doubt the validity of the rare dispersal events that have been recorded over several hundred kilometres (e.g., 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. I do, however, suggest that the lagged correlation distances found here correspond to the distances over which a majority of individuals disperse.

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. For example, as discussed in Tittler et al. (2006), source-sink dynamics should occur over these scales. As such, these findings indicate that the potentially negative effects of land use change on songbirds should be considered over tens of kilometres.

Table 3.1. Median body mass (Mass)[†], median wing length (Wing)[†], distance classes for which there were significantly more 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. Species are ordered as in Fig. 3.1.

Species*	Mass (g) [†]	Wing (cm) [†]	Sig Dist (km)	P	Med Dist (km)
<i>Cardinalis cardinalis</i> (Northern Cardinal)	45.0	28.0	40-50 (11/88)	0.010	70
			50-60 (8/60)	0.018	
			90-100 (12/138)	0.047	
<i>Piranga olivacea</i> (Scarlet Tanager)	30.5	27.0	20-30 (2/13)	0.015	25
<i>Passerina caerulea</i> (Blue Grosbeak)	28.5	28.0	20-30 (1/8)	0.023	25
<i>Passerina cyanea</i> (Indigo Bunting)	15.00	20.5	50-60 (7/58)	0.007	55
<i>Dendroica pensylvanica</i> (Chestnut-sided Warbler)	10.0	19.5	20-30 (5/26)	0.001	35
			40-50 (5/28)	0.008	
<i>Icteria virens</i> (Yellow-breasted Chat)	27.0	25.0	10-20 (5/22)	0.006	40

<i>Agelaius phoeniceus</i> (Red-winged Blackbird)	54.50	35.5	60-70 (5/26)	0.008	85
<i>Dolichonyx oryzivorus</i> (Bobolink)	42.50	27.0	70-80 (2/8)	0.011	85
<i>Spizella passerina</i> (Chipping Sparrow)	13.0	20.0	30-40 (10/98)	0.030	40
<i>Pipilo erythrophthalmus</i> (Eastern Towhee)	42.0	24.0	10-20 (6/30)	0.015	15
45 <i>Melospiza melodia</i> (Song Sparrow)	32.5	21.0	40-50 (18/170)	<0.001	45
<i>Passer domesticus</i> (House Sparrow)	29.0	22.0	30-40 (14/80)	0.046	35
<i>Turdus migratorius</i> (American Robin)	77.0	35.5	70-80 (16/96)	<0.001	75
<i>Hylocichla mustelina</i> (Wood Thrush)	45.0	32.0	60-70 (13/104)	0.007	70
<i>Sturnus vulgaris</i> (European Starling)	78.0	35.5	70-80 (20/180)	0.015	85
<i>Mimus polyglottos</i> (Northern Mockingbird)	51.5	33.0	40-50 (8/66)	0.001	45
<i>Dumetella carolinensis</i> (Gray Catbird)	39.5	26.0	10-20 (7/60)	0.030	15

<i>Bombycilla cedrorum</i> (Cedar Waxwing)	32.0	26.0	20-30 (1/6)	<0.001	25
<i>Troglodytes aedon</i> (House Wren)	11.0	17.0	70-80 (5/58)	0.031	75
<i>Hirundo rustica</i> (Barn Swallow)	18.5	30.5	60-70 (8/76)	0.030	65
<i>Baeolophus bicolor</i> (Tufted Titmouse)	22.0	23.0	70-80 (15/74)	<0.001	75
<i>Poecile carolinensis</i> (Carolina Chickadee)	10.0	17.5	30-40 (1/8)	<0.001	35
<i>Corvus brachyrhynchos</i> (American Crow)	465.0	92.5	80-90 (13/120)	0.024	85
<i>Vireo olivaceus</i> (Red-eyed Vireo)	19.0	24.0	90-100 (14/104)	0.001	95
<i>Vireo griseus</i> (White-eyed Vireo)	12.0	17.0	50-60 (3/8)	0.001	55

* See Ehrlich et al. (1988) for authorities.

† Reviewed in Poole and Gill (1992-2006).

Table 3.2. 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	R²
Body mass	0.405	3.778	0.065	0.108
Wing length	1.846	7.492	0.012	0.220
PICBodyMass	0.723	6.826	0.016	0.202
PICWingLength	2.2379	7.135	0.014	0.211

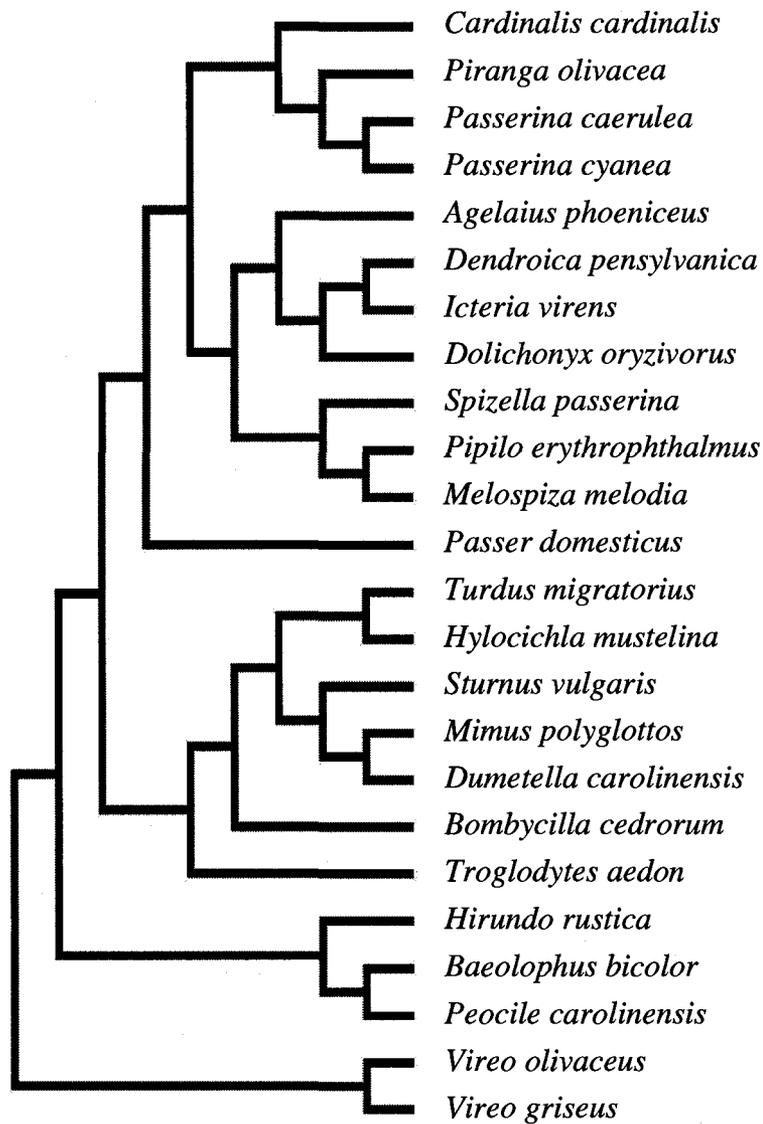


Figure 3.1. Phylogenetic relationships among songbirds for which there were lagged correlation distance estimates. The tree was compiled using the general phylogenetic structure presented by Barker et al. (2004), with details filled in for Paridae (Gill et al. 2005), Emberizidae (Carson and Spicer 2003), Parulidae (Lovette and Bermingham 2002), *Cardinalis cardinalis*, and *Piranga olivacea* (Klicka et al. 2003).

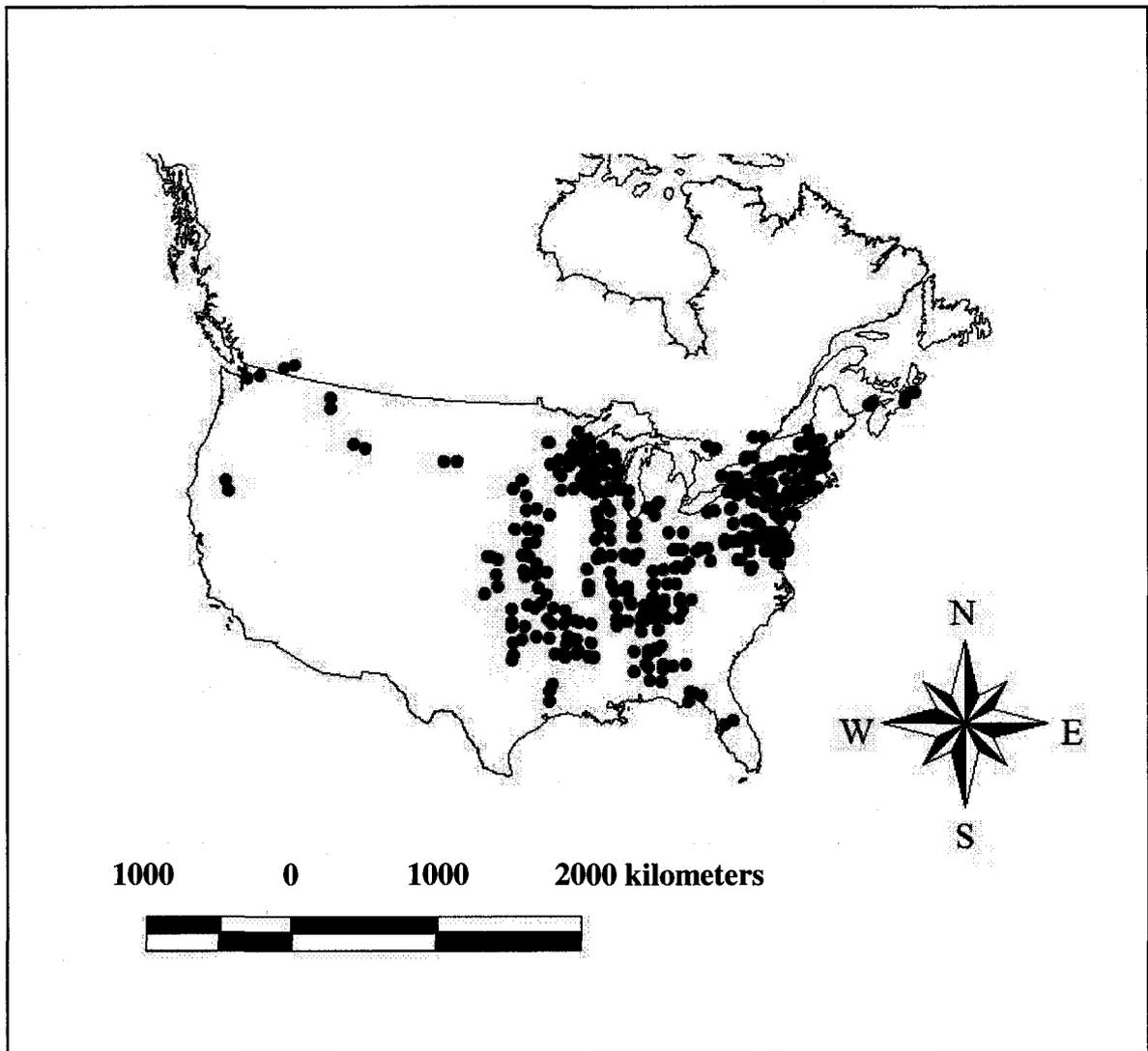


Figure 3.2. North American Breeding Bird Survey (BBS) routes used in the analyses of time-lagged correlations in abundance. All routes included had at least 29 years of data available in common with at least one other route at all nine of the distance classes considered.

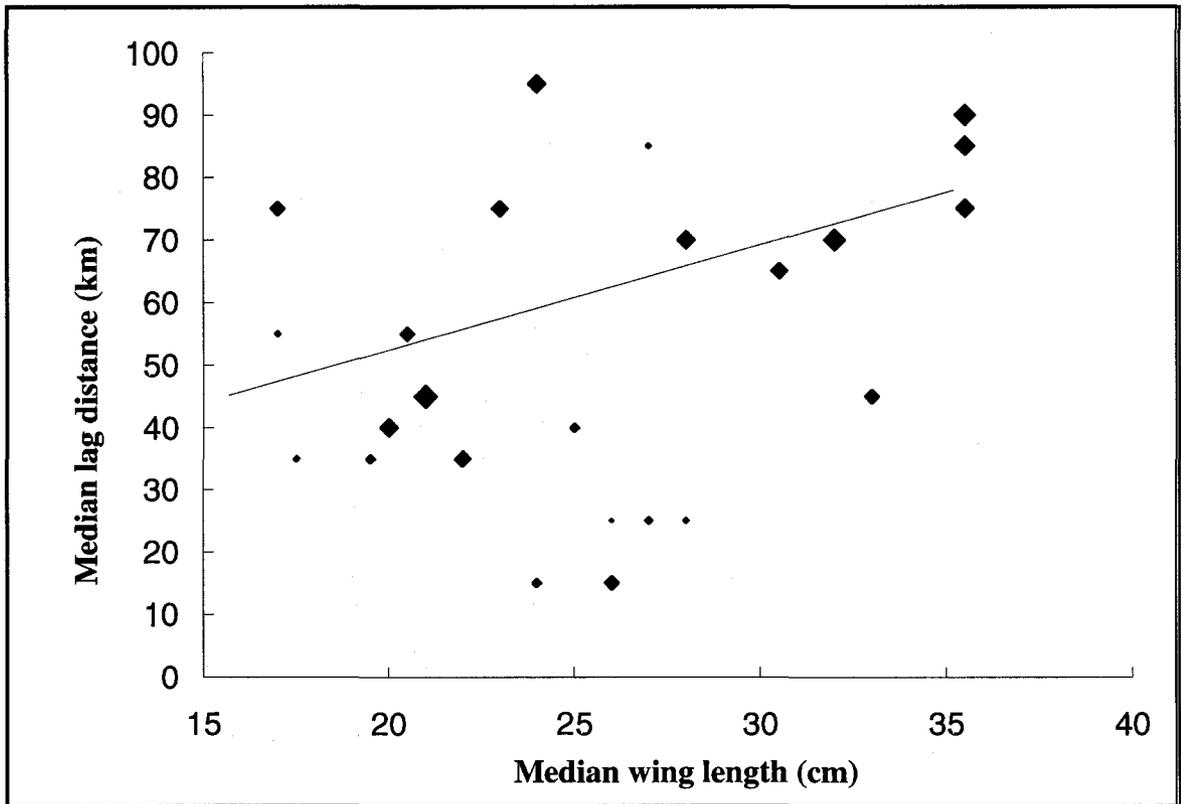


Figure 3.3. Median lagged correlation distance vs. wing length, weighted by sample size, as indicated by the size of the dots. See Table 3.2 for associated statistics.

CHAPTER 4: NORTH AMERICAN SONGBIRDS AND THE SCALE OF LANDSCAPE EFFECTS:

HOW LARGE IS A LANDSCAPE?

4.1 Chapter summary:

In studies on the effects of landscape structure on species abundances, results have been shown to differ depending on the spatial extents considered. It is thus important to select spatial scales relevant to the focal species. These scales of effect may be correlated with scales of dispersal or daily movement, or with the scales over which landscapes are structured. I tested these hypotheses using abundance data on 71 songbird species from the North American Breeding Bird Survey and landcover data from the 1992 National Landcover Database. I examined correlations between bird abundances and landcover within distances of 0.5 to 100 km. I identified species-specific scales of landscape effect for each species as the scale at which this correlation was strongest, then tested for correlations between this scale and dispersal distance and correlates thereof (body mass and wing length), territory and home range size (daily movement), and mean distance between habitat patches (gap width, a parameter of landscape structure). Scales of effect ranged from 0.5 to 100 km. The only significant correlation was between scale of effect and gap width: species whose habitat was separated by larger gaps were affected by the landscape over larger spatial scales. This likely indicates the importance of some type(s) of movement not examined. Population models should not assume that movement is independent of landscape structure. Further research on the relationship between landscape structure and movement could elucidate the mechanism underlying these results and lead to the improvement of population models and conservation strategies.

4.2 Introduction:

Over the past few decades, there has been increasing focus on the importance of studying and managing populations on a landscape scale rather than on a patch scale (e.g., Villard et al. 1995; Fahrig 2003; Betts et al. 2006). However, the effects of landcover on population size have been found to depend on the spatial scale (extent) considered, and different species are most strongly affected by landcover measured at different scales (e.g., Mitchell et al. 2001; Cunningham and Johnson 2006). Thus, it is crucial to identify the appropriate scales for landscape studies.

The scale at which landscape structure affects population size (“scale of landscape effect”) most likely reflects the distance over which individuals move (e.g., Addicott et al. 1987), either within or between seasons. Landscape ecologists have often assumed that scales of effect correspond to species-specific dispersal distances for songbirds and other taxa (e.g., Haila et al. 1993; Villard et al. 1995; Parris 2006), where dispersal is the movement of individuals for the purpose of reproduction (Greenwood 1980).

Unfortunately, very little is known about the behaviour of songbirds during dispersal. For example, it is not known whether individuals actually interact with the landscape during dispersal or simply fly some distance irrespective of the landscape structure before they begin prospecting for suitable habitat. If individuals move through the landscape during dispersal and dispersal success strongly affects population size, the scale of effect of the landscape should be correlated with species-specific dispersal distances.

Scales of effect could also correspond to species-specific scales of daily movement, during which individuals may move through and therefore be affected by the

landscape. For many species, the breeding territory encompasses individual daily movement during the breeding season, although some species have larger home ranges through which they regularly travel to forage (Poole and Gill 1992-2006) or for extra-pair copulations (Hanski et al. 1992; Norris and Stutchbury 2001). Thus, the scale of landscape effect could correspond to territory size or home range size.

If movement is strongly influenced by landscape structure, its extent should not simply reflect a species-specific attribute, but would arise through the interaction of the species' movement behaviour and landscape structure (Fahrig 2007). In this case, the scale of effect of the landscape should be influenced by the structure of the landscape itself. For example, I might expect species whose habitat is generally spread out (patches separated by large gaps) to travel farther during dispersal, as individuals must bridge the distance between patches of habitat (e.g., Hein et al. 2004).

In this study, I document species-specific scales of effect of the landscape for 71 North American songbird species and test the hypotheses that these scales of effect are (1) positively correlated with species-specific dispersal distance and/or with wing length or body mass (themselves correlates of dispersal distance; Chapter 3; Paradis et al. 1998), (2) positively correlated with species-specific scales of daily movement (territory or home range sizes), and (3) related to the structure of the landscape itself, or, more specifically, positively correlated with the average distance between habitat patches (gap width).

4.3 Methods:

I used songbird count data collected by the North American Breeding Bird Survey (BBS). I obtained landcover data of the from the United States Geological Survey's 1992

National Land Cover Database (NLCD). This dataset consists of 30- x 30-m resolution landcover data for the entire continental United States, based on satellite data from the early 1990s (USGS 2007). The data are provided for 21 landcover types (USGS 2007) (Appendix 1).

Of the ~4462 BBS point count routes that have been run since 1966 (Sauer et al. 2005), I randomly selected a set (a) that were at least 200 km apart, because I sought to examine the effects of landscape composition at scales of up to 100 km and did not want landscapes to overlap; (b) that were at least 100 km from any national borders, since the 1992 NLCD covers only the continental United States; and (c) for which bird count data deemed acceptable by the BBS were available from 1992 to 2002 (Sauer et al. 2005). I felt that eleven years would be sufficient to see effects of landcover while not being so long that landcover would likely change significantly. I used the Random Point Generator extension (v. 1.3, Jenness 2005) in Arcview 3.2 (Environmental Systems Research Institute, Inc. 1992) in this selection process, which yielded a set of 82 routes meeting these requirements (Fig. 4.1).

For each of these routes, I created digitized buffers of 0.5, 1, 5, 10, 20, 30, 40, 50, 60, 70, 80, 90, and 100 km radius around the first 10 stops (Fig. 4.1). I then calculated the percentage of each landcover type within each of these buffers. I used the Buffer With Attribute script (Tilton 2000) to create the buffers and the Grid Clip to Polygon script (Plummer 1998) to assign the appropriate landcover data to each buffer in Arcview 3.2. For each species, I created a subset of these 82 BBS samples that fell within its breeding range, and subsequently excluded any species with fewer than 30 of these landscapes

within this range. This left a total sample size of 71 species. I used digitized breeding range data compiled by Ridgely et al. (2005).

For each species, I identified the scale of landscape effect as the radius of the buffer (0.5 – 100 km) at which percentage landcover was most highly correlated with mean bird count. Since the data did not meet the assumption of homogeneity of variance, I used Spearman's rank correlations. More specifically, for each species, I took the scale of landscape effect to be the scale at which there was the highest absolute correlation (absolute value of rho) between the mean count per year and any one of the landcover variables. In an attempt to render the landcover variables more meaningful biologically, I created several compound landcover variables. For example, since some species are associated with forest in general, irrespective of tree species composition, I created the compound landcover variable "allforest", which was the sum of all deciduous, evergreen, and mixed forest in each buffer. Based on information on species-specific habitat requirements (Poole and Gill 1992-2006), I also created specific landcover variables to correspond to the habitat of each species. All landcover variables used are defined in Appendix 1. For each species, I examined correlations between count per year and all 21 initial landcover variables, 13 general compound variables, and one species-specific habitat variable. The landcover variable with the highest correlation with mean bird count is henceforth referred to as the "landcover type of importance" for that species. I provide further rationale for this method and consider possible alternatives in the Discussion.

Once I had identified a scale of landscape effect for each species, I tested whether these scales were correlated with dispersal distances with two Pearson's correlation analyses: one of the log scale of landscape effect against estimated juvenile dispersal

distances from Tittler et al. (2006 and in review), and the other of the log scales of landscape effect against juvenile dispersal distances reported in Poole and Gill (1992-2006). I used juvenile dispersal distances because adult philopatry is generally high among these songbird species (Poole and Gill 1992-2006). I also conducted Pearson's correlation analyses between log scale of landscape effect and territory size, home range size, body mass, and wing length (from Poole and Gill 1992-2006). In all analyses, I used the log-transformed scale of landscape effect (\log_{10}) so that the assumptions of parametric statistics were met.

For the movement variables taken from Poole and Gill (1992-2006) – dispersal distance, territory size and home range size – I used mean values when available. Where only ranges of these measurements were available, I used the mid-points of the reported ranges. When only median dispersal distances were available, I used these. Since these analyses did not distinguish sex-specific patterns, all values were based on data from both sexes. For the first analysis testing the dispersal distance hypothesis, sample size was limited to the 25 species for which I had estimates of dispersal distance from Tittler et al. (2006 and in review). Of these, two species could not be included in the present analyses because of low sample sizes within the area for which landcover data were available. Thus, the sample size for the dispersal distance analysis using estimates from Tittler et al. (2006 and in review) was 23 species. For the dispersal distance analysis based on Poole and Gill (1992-2006), I used only the 17 species for which mean, median, or ranges of dispersal distances were available. To test the territory-size hypothesis, I used only the 55 species for which data were available, and for the home-range hypothesis, only the 17 species for which data were available.

To correct for the fact that closely-related species may not represent statistically independent data points in terms of dispersal distance, territory size, home range size, body size, and wing length, I repeated these analyses for phylogenetically independent contrasts (Felsenstein 1985) using Mesquite 1.06 (Maddison and Maddison 2004) and PDAP:PDTREE 1.07 (Midford et al. 2005). I compiled a phylogenetic tree using the general phylogenetic structure presented by Barker et al. (2004), with details filled in for Emberizidae (Carson and Spicer 2003), Parulidae (Lovette and Bermingham 2002), Tyrannidae (Cicero and Johnson 2002), Vireonidae (Murray et al. 1994), Certhiidae and *Poliophtila caerulea* (Barker 2004), Hirundinidae (Sheldon et al. 2005), Turdinidae (Klicka et al. 2005), Icteridae (Lanyon and Omland 1999), *Loxia curvirostra* (Arnaiz-Villena et al. 2001), and *Cardinalis cardinalis*, and *Piranga olivacea* (Klicka et al. 2003) (Fig. 2). For lack of standardized branch lengths, I assigned all branch lengths a value of 1, then conducted a Rho transformation ($Rho = 0.85$) (Grafen 1989), testing the adequacy of these branch lengths as suggested by Garland et al. (1992). I then conducted Pearson's correlation analyses of the phylogenetically independent contrasts of scale of landscape effect on estimated dispersal distance, territory size, home range size, median body mass, and median wing length (separately). As above, I used mean or mid-point territory and home range sizes and median body mass and wing length values from Poole and Gill (1992-2006). I excluded the American Crow (*Corvus brachyrhynchos*) from all wing length and body mass analyses because it was an extreme outlier in terms of these two characteristics.

To examine the hypothesis that scale of effect was correlated with landscape structure, I first calculated mean gap width over the landscapes examined for each

species. I used gap width as a measure of landscape structure because I expected that scales of effect would be positively related to the distance between habitat patches. For those species for which the correlation between abundance and the landcover type of greatest importance at the scale of landscape effect was positive (56 species), I assumed that this landcover type corresponded to habitat. I defined anything other than this landcover type as gap. To estimate mean gap width, I first drew a 100-km transect in a random direction from the center of each BBS sample and identified the landcover type present at points separated by 0.25-km intervals along each transect. I calculated the size of each gap by counting the number of consecutive points that fell within any but the landcover type of greatest importance to the species. Since sample points were 0.25 km apart, multiplying the number of consecutive points by 0.25 yielded approximate gap widths in kilometres. For each species, I then calculated mean gap width in kilometres. As above, for each species, I based these analyses only on the BBS samples that fell within the breeding range. This yielded a mean gap width per species, but meant that two species with the same landcover type of greatest importance but with different breeding ranges might have different mean gap widths because different BBS samples were included in calculating these gap widths. In this part of the study, I excluded species for which the correlation between abundance and the landcover type of greatest importance at the scale of landscape effect was negative (15 species) because this landcover type could not be defined as habitat.

I tested the hypothesis that scale of effect was correlated with gap width using a Pearson's correlation analysis. As above, I used the log-transformed scale of landscape effect (\log_{10}) so that the assumptions of parametric statistics were met. I did not analyze

phylogenetically independent contrasts of gap width and scale of landscape effect because I saw no reason for gap width to be related to phylogeny.

4.4 Results:

Most predictor variables had fairly large ranges (Appendix 2). Mean gap width ranged across species from 1.4 to 100.0 km (mean 18.76 km, standard error 2.500 km; Table 4.1). Scales of landscape effect ranged from 0.5 to 100 km across the 71 species examined (mean 34.40 km, standard error 4.760 km; Table 4.1).

For nine of the 71 species, abundance was most highly correlated with a species-specific compound landcover variable created to represent habitat use by that species based on information from the literature. For the other 62 species, abundance was most highly correlated with an individual landcover type; for most of these, the landcover type of greatest importance corresponded to a key habitat component mentioned in the literature (Poole and Gill 1992-2006). For 56 of 71 species, scale of landscape effect represented the scale at which there was the highest positive correlation with whatever landcover type was most important to that species; for the remaining 15 species, the highest correlations were negative. Forty-two species (59%) exhibited scales of effect of 10 km or less and 18 species (25%) exhibited scales of effect of 90 km or more (Table 4.1).

Because there was a danger that the scale of landscape effect identified was simply the scale at which the landcover type of importance varied the most, I did a Spearman's rank correlation between the scale of landscape effect and the scale at which variation in landcover type of importance was highest. I found no significant correlation

(Spearman's rank correlation coefficient = 0.07, N = 71 species, P = 0.540), indicating that the scales of landscape effect did not reflect this kind of statistical anomaly.

Scales of effect were not correlated with dispersal distance estimates (Table 4.2). The scale of landscape effect was less than the dispersal distance estimates provided in Chapter 3 in 14 of 25 cases (56%), and less than those provided by Poole and Gill (1992-2006) in 6 of 17 cases (~35%). These scales were not correlated with territory or home range size, wing length, or body mass (Table 4.2). Results did not change when phylogenetic relatedness was accounted for (Table 4.2). However, scale of landscape effect was positively correlated with mean gap width (Table 4.2, Fig. 4.3).

4.5 Discussion:

The lack of correlations between scales of landscape effect and dispersal distances, territory size, home range size, body mass, and wing length does not support the predictions that the spatial scale at which songbirds are most affected by landscape structure (scale of landscape effect) is determined by species-specific dispersal or daily movement distances. However, the positive correlation between scales of landscape effect and gap widths, my index of landscape spatial structure, supports the hypothesis that movement distances are influenced by the spatial structure of the landscape at the species level. In other words, species whose habitat tends to be more aggregated (i.e., larger gaps) respond to the landscape at larger spatial scales than those whose habitat is less aggregated.

To my knowledge, no research has indicated a link between species-specific landscape structure and movement. However, several studies have indicated effects of landscape structure on the movement of individuals within species. In their modelling

study on bush crickets, Hein et al. (2004) found that, unless movement was completely random, decreasing the number of patches (and thus increasing the gap width) resulted in an increase in dispersal distance. Among birds, a behavioural response to landscape structure is suggested by the ability of certain species (e.g., Pileated Woodpecker, *Dryocopus pileatus*) to increase the size of their home range as their habitat becomes more fragmented (Renken and Wiggers 1989). Van Houtan et al. (2007) also found that many tropical forest bird species travelled farther in fragmented than in continuous forest. Finally, in the damselfly *Calopteryx maculata*, Taylor and Merriam (1995) found that individuals living in areas where gaps between habitat patches were larger and had longer wings, suggesting that wider gaps selected for more vagile individuals. This implies that natural selection could lead to differences in flight ability or average flight distances between similar species living in areas with different landscape structures.

Given the lack of correlations between scale of landscape effect and scale of dispersal or daily movement (home range and territory size) and the positive correlation between gap width and scale of effect, the latter is likely linked to some type of movement other than dispersal or regular daily movements within the breeding season. Types of movement not examined include postbreeding movement and within-season extraterritorial movement. Both could be responsible for the observed pattern.

Postbreeding movement, sometimes called postfledging movement, takes place after the breeding season and before the onset of winter or migration (Vega Rivera et al. 1999). During this period, many species experience a molt, the young of the year learn to fly and become independent, and all must spend enough time foraging to provide fat reserves for the migration to the wintering grounds or to cache food for the winter. This

period is likely crucial for overwinter survival. Populations with access to extensive habitat, i.e., large amounts of food within the range of postbreeding movement, should experience lower winter mortality and therefore maintain higher abundances than those with less habitat within this range. Thus, the scale of landscape effect might be correlated with the scale of postbreeding movement. Since the distances individuals have to travel during the postbreeding period may depend on the distances between habitat patches, I might also expect the scale of postbreeding movement to be correlated with the typical gap width. If there were correlations between landscape scale of effect and scale of postbreeding movement and between scale of postbreeding movement and typical gap width, I would expect the observed correlation between gap width and scale of effect.

Unfortunately, due to the technical challenges of documenting large- or even intermediate-scale movement in songbirds, very little reliable data on movement through the landscape are available. A number of studies have attempted to examine non-migratory movements with mark-recapture methods or radio-telemetry, and have found generally quite short movement distances (e.g., Anders et al. 1998; Vega Rivera et al. 1999; Bayne and Hobson 2001; Lang et al. 2002). Using radio-telemetry, Norris and Stutchbury (2001) recorded travel distances of up to 465 m for the Hooded Warbler (*Wilsonia citrina*), but this is still fairly small compared with many of the scales of effect found here. Mark-recapture and radio-telemetry studies are limited in the spatial extent they can cover, as most authors freely admit. The disappearance of a marked bird can either be evidence of migration, death, the movement of the individual outside of the range of the study, or the failure of equipment such as a radio-transmitter. More

technologically advanced methods or different research approaches will be necessary to properly examine movement in songbirds.

The correlation between gap width and scale of landscape effect is a configuration effect, since gap width is a component of landscape configuration. Configuration effects on songbirds and other taxa have been extensively studied (see reviews in Marzluff and Restani 1999, Stephens et al. 2003, Fahrig 2003, for example), but the general question asked is quite different from that addressed here. The typical study on configuration effects (or "fragmentation effects") asks whether configuration has a greater influence on abundance (e.g., McGarigal and McComb 1995, Betts et al. 2006) or presence/absence (e.g., Villard et al. 1999) than habitat amount (or habitat loss). The predictor is generally some element of landscape configuration and the response is an element or indicator of population health. In this study, I ask not about landscape effects themselves, but about the scales of landscape effects. Although my predictor variable is also an element of landscape configuration (gap width), my response variable is the scale of the population response, not the population response itself. This difference makes these results difficult to compare to the general landscape configuration literature.

The use of Spearman's rank correlations to identify the scale of landscape effect may seem simplistic in this age of sophisticated statistical analyses, but I found it to be the method best suited to the data. The main problem with other analyses is that the BBS data are characterised by many zeroes, so the assumption of homogeneity of variance in general linear models could not be met. I considered breaking the response (mean count / year) into categories and using ordinal logistic regressions to identify the scales of response, but I found that the assumption of proportional odds characteristic of this type

of analysis (McCullagh and Nelder 1991) was generally not met. I examined multinomial logistic regressions, which are not bound by this assumption, but because this type of analysis uses many degrees of freedom in estimating a relationship for each category of response individually (McCullagh and Nelder 1991), these analyses suffered from extremely low power. I considered using total counts rather than mean count over 10 years as the response, which would allow us to use analyses designed for count data, but owing to overdispersion, only the negative binomial model was appropriate (McCullagh and Nelder 1991). I therefore attempted multiple negative binomial regressions, to see which landcover variables would be the most important. However, using this type of analysis, models often failed to converge. An attempt to use principal components analysis to reduce the number of variables was unsuccessful; it would have taken 12 principal components to explain as little as 85 % of the variation in the data. I attempted to address this problem by limiting the number of possible predictor variables based on the available sample sizes for each species (allowing one predictor per 10 landscapes analyzed, giving 3 to 8 possible predictors per species) and on species-specific habitat associations reported in the literature (Poole and Gill 1992-2006), but these analyses also typically explained less variation in the BBS data than the simple Spearman rank correlations. In the end, Spearman's rank correlations produced the best models with the fewest assumptions.

My findings indicate that it is erroneous to assume that the scale at which songbirds respond to landscape structure can be predicted by species-specific dispersal distances, territory sizes, or home range sizes. I should instead be focussing on identifying landcover types of importance to each species and examining the scales over

which these landcover types are structured or, more specifically, the size of gaps between patches. Future research on individual movement through the landscape might provide a mechanism for the relationship between scale of landscape effect and gap width. With this knowledge, I could predict scales of landscape effect for species not examined here. In the meantime, knowledge of the scale of landscape effect should lead to the improvement of population models and the development of better conservation strategies for the 71 species examined here.

Table 4.1. Identified scales of effect, sample sizes (N), highest absolute Spearman's rank correlation coefficient (Rho), landcover variable associated with this coefficient ("landcover type of greatest importance"), mean gap width for this landcover variable, two estimates of dispersal distance [Chapter 3 (Tittler) and Poole and Gill 1992-2006 (P & G)], mean or midpoint territory and home range size, and body mass and wing length (Poole and Gill 1992-2006) for the 71 North American songbird species examined. Species are ordered as in Fig. 4.2. Gap widths were not calculated for species for which the relationship between abundance and the landcover type of greatest importance (rho) was negative (see Methods). Categories for which data are unavailable are marked NA. Values that represent midpoints are marked R, and those representing medians are marked M.

Species	Scale	N	Rho	Landcover	Gap	Dispersal	Terr.	Home	Body	Wing
	(km)			Variable	Width	Distance (km)	Size	Range	Mass	length
				(km)	(km)	Tittler	P & G	(ha)	(g)	(cm)
Northern Parula	100	33	-0.65	Pasture/hay	NA	NA	NA	NA	8.0	17.0

(*Parula americana*)

American Redstart (<i>Setophaga ruticilla</i>)	1	44	0.46	AMRE_hab ¹	1.52	NA	0.52 ^R	0.52 ^R	7.5	18.0
Common Yellowthroat (<i>Geothlypis trichas</i>)	50	70	-0.61	Shrubland	NA	NA	1.53 ^R	NA	9.5	17.0
Black-and-white Warbler (<i>Mniotilta varia</i>)	5	30	0.64	Evergreen forest	5.67	NA	3.75 ^R	NA	11.5	20.0
Ovenbird (<i>Seiurus aurocapilla</i>)	5	33	0.64	Deciduous forest	2.07	NA	1.00 ^R	1.40 ^R	22.0	23.0
Eastern Meadowlark (<i>Sturnella magna</i>)	10	52	0.56	EAME_hab ²	1.88	NA	3.65 ^R	4.88 ^R	120.0	38.0

¹ AMRE_hab = deciduous forest + mixed forest + shrubland + low-intensity residential

² EAME_hab = grassland/herbaceous + pasture/hay + row crops + small grains + fallow + urban/recreational grassland + low-intensity residential

Western Meadowlark (<i>Sturnella neglecta</i>)	5	46	0.71	WEME_hab ³	1.87	NA	0.5 ^R	7.10 ^R	10.05 ^R	102.0	41.0
Bobolink (<i>Dolichonyx oryzivorus</i>)	0.5	31	-0.57	Shrubland	NA	85	NA	0.76	NA	42.5	27.0
Yellow-headed Blackbird (<i>Xanthocephalus xanthocephalus</i>)	0.5	34	0.46	Fallow	20.08	NA	NA	0.04	NA	72.0	43.0
Yellow-breasted Chat (<i>Icteria virens</i>)	90	63	0.75	Mixed forest	7.52	40	NA	1.15	1.15	27.0	25.0
Bullock's Oriole (<i>Icterus bullockii</i>)	5	30	0.61	Row crops	14.50	NA	0.6	NA	NA	36.0	31.0
Orchard Oriole (<i>Icterus</i>)	5	47	0.39	Transitional	36.78	11	NA	NA	NA	18.0	25.0

³ WEME_hab = grassland/herbaceous + commercial, industrial, transportation + pasture/hay + row crops + small grains + fallow

spurious)

Red-winged Blackbird	1	82	0.66	RWBL_hab ⁴	1.46	85	32.1	0.20	NA	54.5	36.0
<i>(Agelaius phoeniceus)</i>											
Common Grackle	1	59	0.65	COGR_hab ⁵	1.50	NA	22.7	NA	NA	108.0	41.0
<i>(Quiscalus quiscula)</i>											
Brewer's Blackbird	1	32	0.58	Small grains	13.74	NA	NA	0.13 ^R	NA	57.0	37.0

(Euphagus

69

cyanocephalus)

Brown-headed Cowbird	1	81	0.48	Pasture/hay	4.41	NA	NA	NA	63.94	44.0	32.0
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(Molothrus ater)

⁴ RWBL_hab = water + commercial, industrial, transportation + woody wetland + emergent or herbaceous wetland + grassland/herbaceous + row crops + pasture/hay + urban/recreational grassland

⁵ COGR_hab = water + wooded wetland + emergent or herbaceous wetland + row crops + small grains + fallow + urban/recreational grassland + low-intensity residential + high-intensity residential

Savannah Sparrow (<i>Passerculus sandwichensis</i>)	0.5	43	0.57	SAVS_hab ⁶	1.97	NA	NA	0.68 ^R	NA	30.5	27.0
Song Sparrow (<i>Melospiza melodia</i>)	100	58	0.62	Urban/ recreational	48.56	45	0.2 ^R	0.30 ^R	NA	32.5	21.0
Eastern Towhee (<i>Pipilo erythrophthalmus</i>)	10	40	0.54	Transitional	30.05	15	NA	0.42	0.42	42.0	24.0
Vesper Sparrow (<i>Pooecetes gramineus</i>)	0.5	46	-0.60	Mixed forest	NA	NA	NA	4.60 ^R	NA	24.0	24.0
Grasshopper Sparrow (<i>Ammodramus savannarum</i>)	90	47	-0.68	Evergreen forest	NA	NA	NA	0.83	NA	17.0	12.0
Lark Sparrow	20	49	0.70	Grassland/	3.51	NA	NA	0.01	55.00 ^R	28.5	28.0

⁶ SAVS_hab = grassland/herbaceous + transitional + pasture/hay + row crops + small grains + fallow

<i>(Chondestes</i>	herbaceous										
<i>grammacus)</i>											
Chipping Sparrow	1	74	0.53	Deciduous	3.56	40	NA	0.60 ^R	NA	13.0	20.0
<i>(Spizella passerina)</i>				forest							
Field Sparrow (<i>Spizella</i>	100	45	-0.60	Rock	NA	NA	NA	0.76	NA	13.0	20.0
<i>pusilla)</i>											
Indigo Bunting	90	61	-0.72	Shrubland	NA	55	NA	1.15	NA	15.0	21.0
<i>(Passerina cyanea)</i>											
Blue Grosbeak	80	38	0.75	Wooded	9.50	25	NA	3.66 ^R	NA	28.5	28.0
<i>(Passerina caerulea)</i>				wetland							
Dickcissel (<i>Spiza</i>	5	36	0.62	Small grains	9.83	NA	NA	0.83 ^R	NA	26.0	25.0
<i>americana)</i>											
Summer Tanager	90	34	0.70	Transitional	28.80	NA	NA	10.00 ^R	NA	30.0	17.0
<i>(Piranga rubra)</i>											
Northern Cardinal	90	51	0.62	Wooded	7.59	70	1.9	1.41 ^R	10.00	45.0	28.0

Eastern Bluebird (<i>Sialia sialis</i>)	1	51	0.51	Pasture/hay	2.96	NA	NA	4.75 ^R	16.45	30.0	29.0
Gray Catbird (<i>Dumetella carolinensis</i>)	100	59	0.66	Urban/ recreational	48.58	15	0.4 ^M	0.31 ^R	NA	39.5	26.0
Northern Mockingbird (<i>Mimus polyglottos</i>)	90	82	0.4	High- intensity residential	55.99	45	NA	1.47 ^R	NA	51.5	33.0
Brown Thrasher (<i>Toxostoma rufum</i>)	1	55	0.54	Row crops	3.17	NA	4.9	0.82 ^R	0.97 ^R	75.0	31.0
European Starling (<i>Sturnus vulgaris</i>)	10	82	0.62	Urban/ recreational grassland	53.09	85	NA	8.0 x 10 ⁻⁵	NA	78.0	36.0
Cedar Waxwing (<i>Bombycilla cedrorum</i>)	20	40	0.56	Urban/ recreational	43.27	25	222.0	NA	NA	32.0	26.0

White-breasted	1	74	0.47	3.63	NA	NA	15.00	15.00	24.0	24.0	24.0	grassland
Nuthatch (<i>Sitta carolinensis</i>)												forest
Blue-grey Gnatcatcher	90	55	0.57	38.79	NA	NA	1.50	NA	6.0	6.0	16.0	Transitional
(<i>Polioptila caerulea</i>)												
Rock Wren (<i>Salpinctes obsoletus</i>)	0.5	31	0.47	1.76	NA	NA	1.80	NA	16.5	16.5	23.0	Shrubland
House Wren	30	62	0.40	4.50	75	NA	0.44	0.44	11.0	11.0	17.0	Row crops
(<i>Troglodytes aedon</i>)												
Marsh Wren	0.5	43	0.57	19.74	NA	2.0	0.50 ^R	NA	11.5	11.5	12.0	Emergent/
(<i>Cistothorus palustris</i>)												herbaceous
Carolina Wren	100	36	0.7	29.50	NA	NA	4.10	NA	20.0	20.0	29.0	wetland
(<i>Thryothorus</i>)												Transitional

Bank Swallow (<i>Riparia riparia</i>)	0.5	47	0.36	Small grains	14.86	NA	4.4	8.0 x 10 ⁻⁵	NA	14.5	27.0
Tree Swallow	50	52	-0.39	Mixed forest	NA	NA	NA	0.07	NA	20.5	33.0
<i>(Tachycineta bicolor)</i>											
Cliff Swallow	20	60	0.4	Fallow	30.58	NA	NA	NA	707.00	26.5	29.0
<i>(Petrochelidon pyrrhonata)</i>											
Barn Swallow	5	78	0.69	Pasture/hay	4.27	65	NA	0.01	452.00	18.5	31.0
<i>(Hirundo rustica)</i>											
Blue Jay (<i>Cyanocitta cristata</i>)	50	52	-0.51	Shrubland	NA	NA	NA	NA	3.31 ^R	85.0	37.0
American Crow	10	73	0.6	Pasture/hay	4.11	85	3.2	25.80	NA	465.0	93.0
<i>(Corvus brachyrhynchos)</i>											
Loggerhead Shrike	5	71	-0.24	Deciduous	NA	NA	12.1	14.50	14.50	42.5	30.0

Acadian Flycatcher	10	31	-0.46	Commercial/	NA	NA	NA	1.23	NA	12.5	23.0
<i>(Empidonax virescens)</i>				industrial/							
				transportation							

Table 4.2. Results of Pearson's correlation analyses between the log-transformed scale of landscape effect and dispersal distance (km) as estimated in Chapter 3 and by Poole and Gill (1992-2006) (P & G), territory size (ha), home range size (ha), wing length (cm), body mass (g) (all from Poole and Gill 1992-2006); between the phylogenetically independent contrasts (PIC) of these; and between scale of landscape effect and mean gap width (km). See Methods for an explanation of the variation in sample sizes.

Variables	Correlation Coefficient	Sample Size	P
Scale of effect – Dispersal distance (Chapter 3)	-0.205	23	0.347
Scale of effect – Dispersal distance (P & G)	-0.424	17	0.090
Scale of effect – Territory size	-0.101	55	0.463
Scale of effect – Home range	0.094	17	0.720
Scale of effect – Wing length	-0.103	70	0.397
Scale of effect – Body mass	-0.106	70	0.382
PIC scale of effect – PIC dispersal distance (Chapter 3)	-0.146	22	0.526
PIC scale of effect – PIC dispersal distance (P & G)	-0.184	16	0.495
PIC scale of effect – PIC territory size	-0.079	54	0.570
PIC scale of effect – PIC home range	-0.300	16	0.259
PIC scale of effect – PIC wing length	-0.044	69	0.720
PIC scale of effect – PIC body mass	0.023	69	0.849
Scale of effect – Gap width	0.463	56	< 0.001

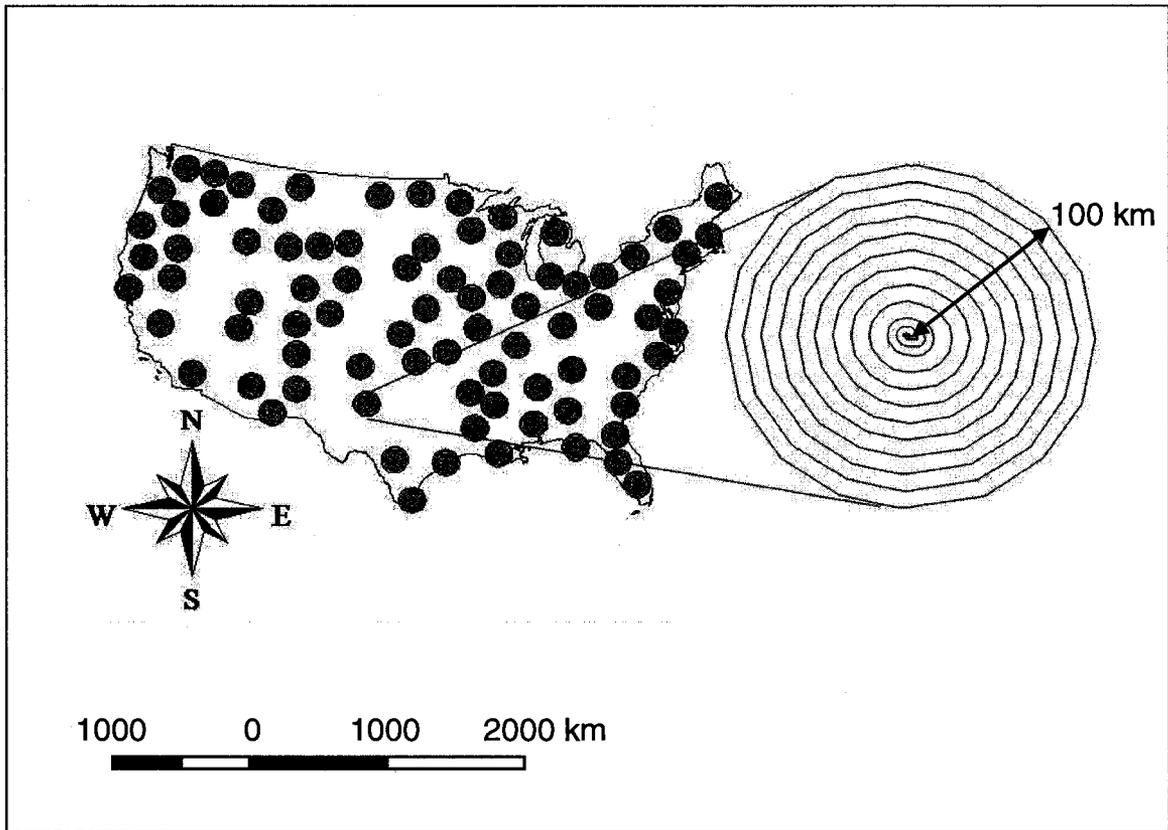


Figure 4.1. The 82 non-overlapping landscapes selected for analysis, with an inset illustrating the 13 buffers calculated around each of the corresponding 82 BBS samples. BBS samples are defined as the first 10 stops of BBS routes for which 11 years of contiguous data are available for the 1992-2002 period.

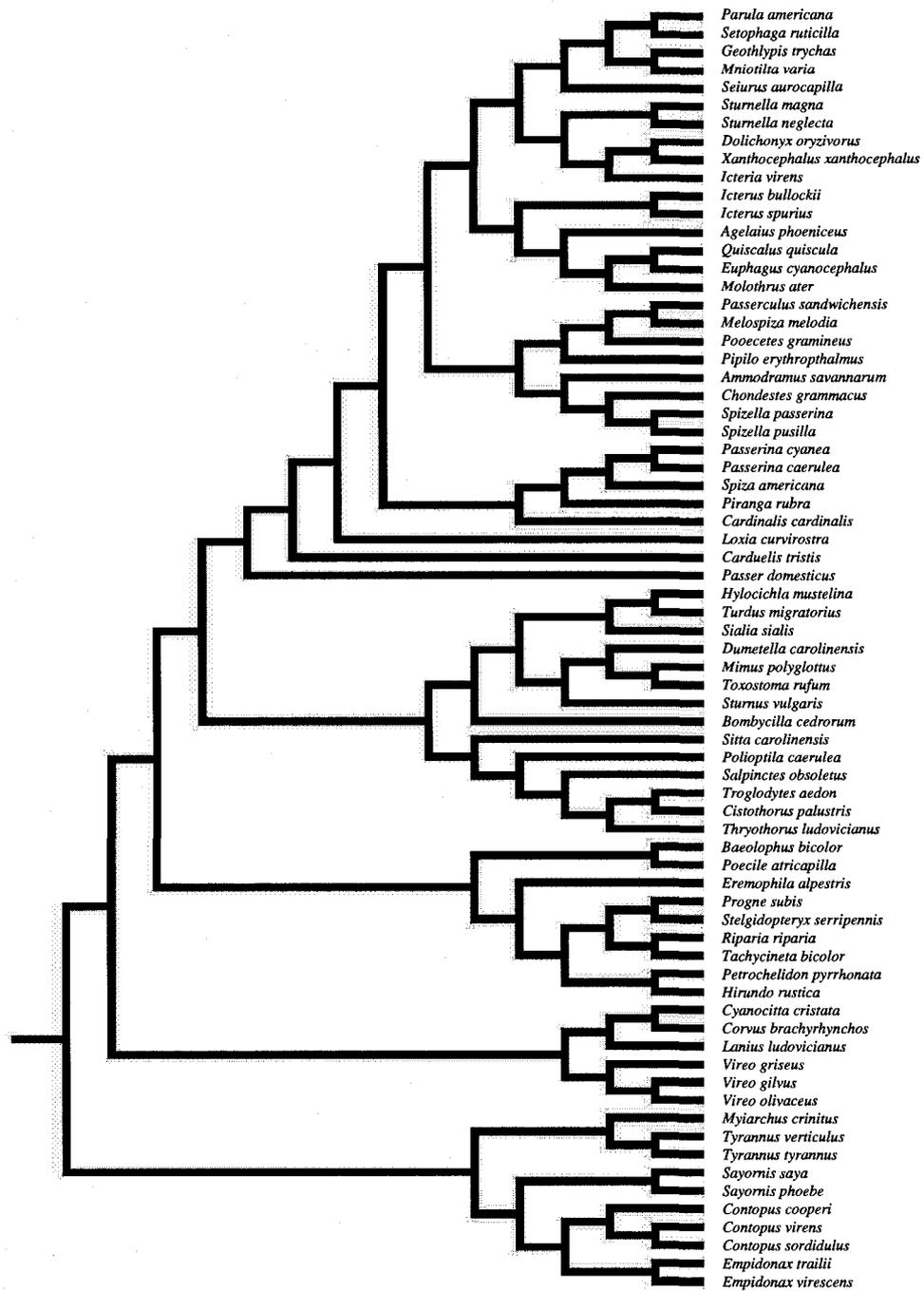


Figure 4.2. Phylogenetic tree of the 71 focal North American songbird species used to calculate phylogenetically independent contrasts for scale of landscape effect, dispersal distance, territory size, home range size, median wing length, and median body mass.

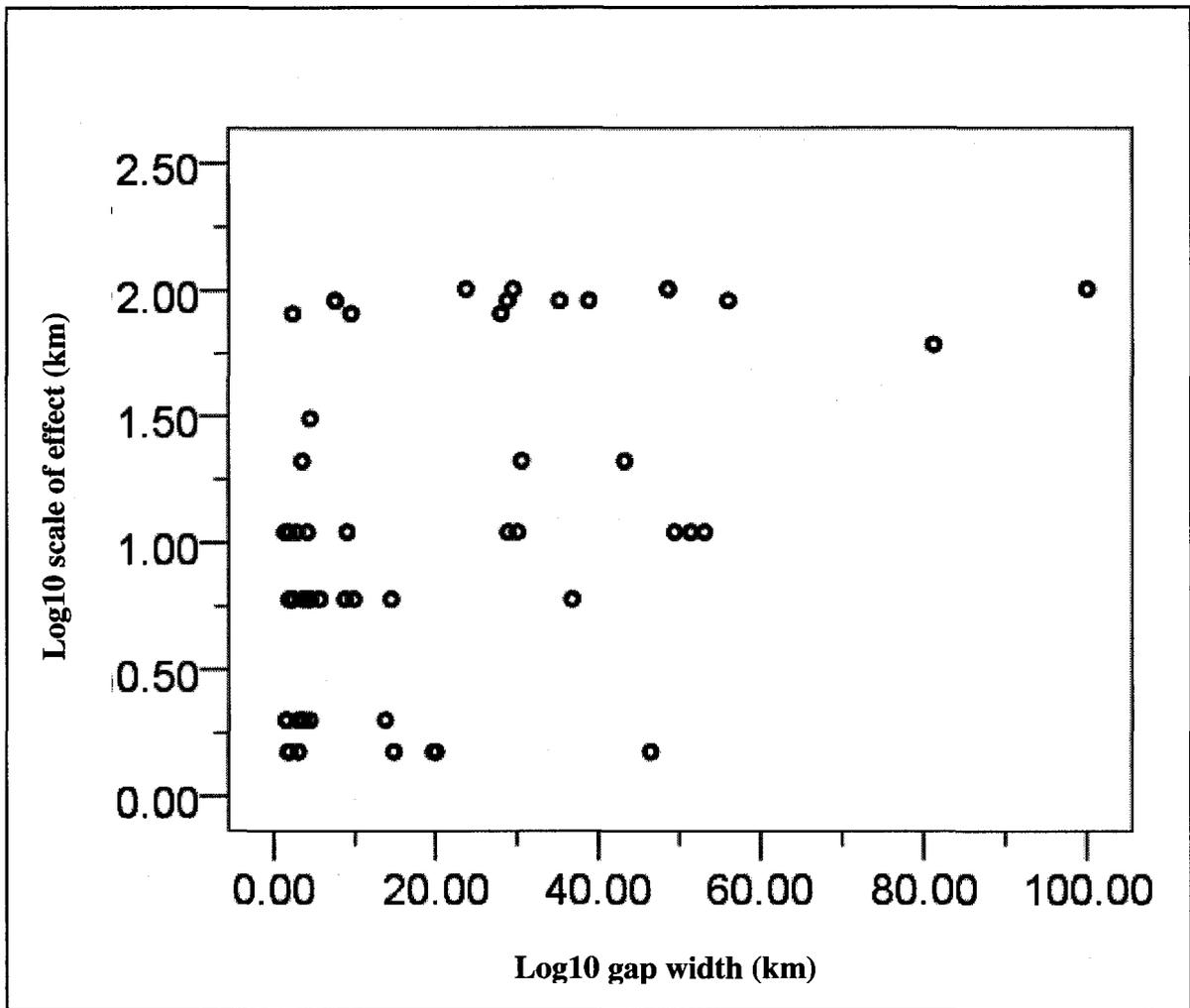


Figure 4.3. Log10 scale of landscape effect (km) vs. mean gap distance (km) for 56 species of North American songbirds. Mean gap distance was calculated as described in the Methods. Note that only species showing a positive relationship between abundance and habitat type of greatest importance were included in this analysis (see Methods).

CHAPTER 5: NO SHORTCUTS TO IDENTIFYING SONGBIRD SOURCES AND SINKS

5.1 Chapter summary:

Although it may be important for management purposes to identify sources and sinks and to understand what causes populations to become sources and sinks, it is difficult to identify source-sink populations and pairs. In this study, I asked whether there are indirect ways of identifying the source/sink status of populations. I tested for six potential correlates of source/sink status. In comparison to sink populations, sources should (1) have higher abundances, (2) have lower population variability, (3) have less negative or more positive population trends, (4) have lower rates of nest predation and brood parasitism, (5) be closer to the center of the species breeding range, (6) be in landscapes with more habitat, and (7), for edge- or area-sensitive species, be found in areas with less edge and larger habitat patches. I used putative source-sink pairs identified in Chapters 2 and 3. In both paired and unpaired analyses, I found significant differences between sources and sinks in population trend when more than 20 years of data were used to calculate the trends. Source populations tended to be increasing while sinks were declining. I found no other significant differences. These results confirm the importance of long-term data if reliable inferences are to be made on songbird population status.

5.2 Introduction:

According to Pulliam (1988), a source is an area in which a population's reproductive rate exceeds mortality, and a sink is one in which the opposite is true. To calculate source-sink status, one must therefore have data on reproduction and mortality. Source populations can maintain sink populations if the excess individuals from the

former immigrate into the latter, resulting in a net flow of individuals from the source to the sink.

Although it may be important to be able to identify population sources and their dependent sinks for management purposes, it is virtually impossible to do so in most cases because of the lack of information on survivorship (see Chapter 2). Although it is possible to identify putative sources and sinks given long-term, large-scale data using the one-year time-lagged model presented in Chapters 2 and 3, such data are often unavailable. It would therefore be useful to be able to characterize sources and sinks using a relatively easily measured parameter. Candidate parameters may include abundance, variability in abundance (Curnutt et al. 1996), and population trend (Donovan et al. 1995b).

Also for management purposes, it may be important to know what determines whether a population is likely to be a source or a sink. Maurer and Villard (1994) and Curnutt et al. (1996) suggest that sinks may be located closer to the edges of the species' breeding range than sources, implying a net flow of individuals from the centre towards the edges of species ranges. Sinks may be located in areas with higher abundances of brood parasites or nest predators than sources (Donovan et al. 1995a) resulting in elevated levels of nest predation and brood parasitism (Burke and Nol 2000), lower reproductive rates, and higher juvenile mortality. Sources may also be located in portions of the species' range with more habitat than sinks (Donovan et al. 1995a). Finally, since reproductive success of area- and edge-sensitive species is thought to be negatively affected by increased rates of nest predation and parasitism in smaller patches with more edge (e.g., Burke and Nol 2000, Johnson and Igle 2001, Fletcher and Koford 2003, Peak

et al. 2004), source populations of these species may be found in areas with larger patches and smaller edge-to-area ratios than sinks (With and King 2001).

In Chapters 2 and 3, I identified pairs of source and sink populations for several songbird species (Fig. 1). However, the question remains as to what characterizes these populations, apart from the one-year time-lagged relationships identified. Do sinks have lower abundances than sources? Do they exhibit greater variability in abundance? Are they more likely to be in decline or to be located close to the edges of the species' breeding range? Are they located in portions of the range with greater abundances of brood parasites or nest predators, or with less habitat? Are sinks of edge- and area-sensitive species found in areas with smaller habitat patches and larger edge-to-area ratios?

5.3 Methods:

I identified pairs of source-sink populations for 19 species of North American songbirds by examining one-year time-lagged correlations in abundance, as described in Chapters 2 and 3. Populations were identified as the first 10 stops of routes from the North American Breeding Bird Survey (BBS). I compared mean abundances, variability, trend, proximity to the edge of the species breeding range, amount of habitat in the surrounding area, and abundance of nest predators and parasites between sources and sinks.

I calculated mean abundance over the entire time-period for which BBS data were available for the source-sink populations in question, i.e., at least 29 years for these populations (see Chapters 2 and 3). For each population in each year, I defined abundance as the total count over the entire first ten stops of each BBS route. To compare

population variability, I calculated coefficients of variation in abundance over time for each population.

To compare trends, I performed a linear regression of mean abundance vs. time (year) for each population. I chose linear models because I was looking for overall declines or increases in population size over the long term. I considered the slope of the regression to be the trend for the population. Since the magnitude of this trend can also be expected to vary with mean abundance, I weighted the trend analyses described below by mean abundance, giving greater weight to populations with higher mean abundances.

To compare proximity to the edge of the breeding range, I calculated the Euclidian distance between the first stop of each population and the nearest edge of the breeding range of the species in question. I defined the breeding range as per Ridgely et al. (2005). I used the Nearest Features extension, v. 3.8b (Jenness 2007), in ArcView v. 3.2 for these calculations.

To examine whether sinks housed more nest predators or brood parasites than sources, I examined the abundance of Blue Jays (*Cyanocitta cristata*) and Brown-headed Cowbirds (*Molothrus ater*) over the same time period and on the same BBS 10-stops defined as populations. Brown-headed Cowbirds are the main brood parasite within the breeding range of these species (Brittingham and Temple 1983, Ridgely et al. 2005), and Blue Jays are thought to be one of the main nest predators (Wilcove 1985). Mammalian nest predators are also likely to be important (Wilcove 1985), but data on abundances of the appropriate species are not available over the temporal and spatial extent and at the resolution studied.

To examine whether sink populations are located in landscapes with less habitat than sources, I used the USGS's 30-by-30-m-resolution 1992 National Land Cover Data (NLCD) imported into Arcview version 3.2. Based on these data, I calculated the amount of habitat in a buffer corresponding in radius to the species-specific scales of landscape effect from Chapter 4. I defined habitat as the species-specific landcover type of greatest importance from Chapter 4. To avoid comparing overlapping landscapes, I limited these analyses to the species for which scale of landscape effect was at most half the distance between source and sink populations. I also limited these analyses to the species for which the relationship between abundance and the species-specific landcover type of greatest importance was positive (see Chapter 4) because I would not expect sources to be in areas with a large amount of a landcover type that had a negative effect on abundance.

For these comparisons, I used two types of analyses: paired and unpaired t-tests on pooled species, where pairings were based on the source-sink pairs identified in Chapters 2 and 3. Although paired t-test are more appropriate for my data and may be more powerful in detecting differences, I included the unpaired analyses to determine whether sources and sinks can be identified in isolation. I performed all analyses using SPSS version 13.0 (Apache Software Foundation 2004).

To test the predictions about populations of area- and edge-sensitive species differing in terms of landscape structure, I compared landscape structure among sources and sinks of the Wood Thrush (*Hylocichla mustelina*) and Red-eyed Vireo (*Vireo olivaceus*). Wood Thrushes are thought to be both edge- and area-sensitive (e.g., Peak et al. 2004). Red-eyed Vireos may be somewhat area-sensitive (Burke and Nol 2000).

Bobolinks have also been categorized as both edge-sensitive (Fletcher and Koford 2003) and area-sensitive (Johnson and Igle 2001), but I had only one source-sink pair for this species, so analyses were not possible. None of the other species for which I identified sources and sinks have been classified as area- or edge-sensitive, so they were excluded from these analyses. Using the 1992 NLCD, I identified all patches of potential habitat that overlapped the first ten stops of the routes in question. I calculated the area and perimeter of each of these patches using the Calcula Hectares extension (Villegas 2003) in ArcView. For the Red-eyed Vireo, I identified low-intensity residential, deciduous forest, mixed forest, and urban/recreational grassland as potential habitat, as defined in the literature (Cimprich et al. 2000) and in Chapter 4. For the Wood Thrush, I defined potential habitat as deciduous and mixed forest, as per Roth et al. (1996); in Chapter 4, the strongest correlation between abundance and landcover was negative, so the landcover type identified as being of greatest importance could not be considered habitat. The assumptions of parametric analyses were not met by these data, so I compared mean patch area and edge-to-area ratios among sources and sinks for these two species using Mann-Whitney U and Wilcoxon Signed Rank tests, the non-parametric equivalents of unpaired and paired t-tests, respectively.

5.4 Results:

When species were pooled, there were 200 source-sink pairs and 312 populations for unpaired analyses (some populations occurred in more than one pair). In both paired and unpaired analyses, there was a significant difference between sources and sinks in terms of population trend: on average, sources had increasing trends while sinks had decreasing trends (Tables 5.1 and 5.2). There were no significant differences between

sources and sinks in general in terms of any of the other population characteristics measured (Tables 5.1 and 5.2). Ninety-five percent confidence intervals were large for all nonsignificant results (Tables 5.1 and 5.2).

At the species level, there were 10 source-sink pairs and 18 populations for the Red-eyed Vireo, and 29 source-sink pairs and 46 populations for the Wood Thrush. There were no significant differences between sources and sinks in terms of patch area or edge-to-area ratio in either paired or unpaired analyses for the Red-eyed Vireo or the Wood Thrush (Tables 5.3 and 5.4). Again, 95% confidence intervals were large (Tables 5.3 and 5.4).

5.5 Discussion:

The finding that sources had more positive trends than sinks in both paired and unpaired analyses indicates the importance of examining long-term temporal trends in abundance to identify these populations. Owing to broad confidence intervals, it was difficult to draw any conclusions about differences between sources and sinks in terms of any of the other characteristics measured: mean abundance, temporal coefficient of variation, distance from the edge of the species' breeding range, Blue Jay and Brown-headed Cowbird abundance, amount of habitat in the landscape, or edge-to-area and patch area measures for the Red-eyed Vireo and the Wood Thrush.

Large confidence intervals indicate a lack of power and may reflect insufficient sample sizes or high variability in the data (Zar 1984). This study was carried out using the largest dataset available, both in terms of the spatial and the temporal extents covered. However, the BBS data are highly variable due to high observer errors and the short amount of time spent at each sample point, i.e., a single 3-minute point count per year per

point count station in a volunteer-based program (e.g., Sauer and Droege 1990, Sauer et al. 1994). This method of data collection undoubtedly leads to imprecise measures of abundance as many birds are likely to be missed. More precise measures of abundance should lead to increased power to detect differences between sources and sinks.

Within the source-sink model, it is not surprising that sources and sinks differ in terms of long-term population trend. While a source that produces an excess of individuals every year may be able to keep a dependent sink at equilibrium, very few populations (even sources) will produce an excess every year. If a source population increases in size, any dependent sink would also be expected to increase, although not necessarily at an equal rate. If a source population decreases in size, it produces fewer young to disperse to any dependent sinks, and the latter would therefore also be expected to decline, at a greater rate. In the case of a declining source, declines in any dependent sinks would be expected to be especially steep if dispersal were density dependent, i.e., if a smaller proportion of the population dispersed as density in the source declined.

Using trends to identify sources and sinks requires long-term data. Here, I calculated population trends over the entire time-span of the available data, i.e., over at least 29 years. Since most datasets do not span this temporal scale, in post-hoc analyses, I investigated how many years of data I would have needed to detect differences in trend between sources and sinks. To this end, I carried out the same unpaired t-test described in the Methods section on trends calculated from fewer and fewer years of data. With 22 years of data, the difference between sources and sinks was still highly significant ($F = 7.764$, $df = 1, 310$, $P = 0.006$, $R^2 = 0.025$). However, with 21 years of data, the difference was no longer significant ($F = 1.401$, $df = 1, 310$, $P = 0.237$, $R^2 = 0.005$). I conclude that

trend may be useful in differentiating between sources and sinks, but that, with the data quality available from the BBS, this trend must generally be calculated over more than 20 years.

This highlights the importance of collecting long-term as well as large-scale data on songbird abundances. Because of the large scales over which source-sink dynamics occur, both are necessary if sources and their dependent sinks are to be identified based on the one-year time-lagged model presented in Chapters 2 and 3. Long-term, large-scale monitoring programs such as the BBS should therefore be continued and expanded. However, lacking large-scale data, long-term data are still useful in identifying sources and sinks independently based on trend. This highlights the importance of even those long-term monitoring programs that do not cover large spatial extents. Since source-sink dynamics are of particular interest in predicting the effects of management, priority should be given to establishing long-term monitoring programs in areas where management is likely to change the existing landscape. Examples of such programs include urban monitoring programs such as the Ottawa Breeding Bird Count (Smith 2008) and the Tucson Bird Count (Turner 2003).

It might be possible to differentiate between sources and sinks on the basis of trends with less than 22 years of data if there were less variation in these data. Such data could result from a more intensive sampling protocol, involving more than the one 3-minute point count annually required by the BBS. Most smaller-scale studies involve 3 or 4 point counts per year (e.g., Tittler et al. 2001). Although such an increase would be difficult considering the fact that the BBS data are collected by volunteers, it would undoubtedly improve the quality and accuracy of the data. Other types of data might also

be useful: trends could be estimated based on nest monitoring data such as that collected by the Breeding Bird Research and Monitoring Database (BBIRD) (Martin et al. 1997) and on data from constant-effort breeding-season mist-netting like that collected by the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante et al. 2007).

The results of this study indicate that songbird source and sink populations differ in terms of long-term population trend. This information may help managers to identify potential sources and sinks and take appropriate conservation measures, but it also highlights the need for long-term monitoring programs, particularly in areas of management concern.

Table 5.1. Results of unpaired t-tests examining differences between sources and sinks in abundance (Abund.), variability (CV), trend, Brown-headed Cowbird abundance (BHCO), Blue Jay abundance (BLJA), distance from the edge of the species' breeding range, and amount of habitat in the landscape. SE is the standard error of the mean, and N is the number of populations of each type examined. CI is the 95% confidence interval of the difference between means. Results of significant analyses ($P \leq 0.05$) are presented in bold.

Predictor	Source Mean \pm SE (N)	Sink Mean \pm SE (N)	R ²	t	P	CI
Abund.	6.7 \pm 0.45 (162)	6.5 \pm 0.53 (148)	<0.001	0.257	0.798	-1.177 – 1.530
CV	0.9 \pm 0.04 (162)	0.8 \pm 0.04 (148)	0.001	0.483	0.630	-0.090 – 0.152
Trend	0.01 \pm 0.02 (162)	-0.01 \pm 0.03 (148)	0.037	3.463	0.001	
BHCO	1.44 \pm 0.090 (162)	1.47 \pm 0.100 (148)	<0.001	0.164	0.871	-0.286 – 0.242
BLJA	1.97 \pm 0.116 (162)	1.89 \pm 0.103 (148)	0.001	0.519	0.604	-0.226 – 0.388
Distance	198.4 \pm 20.62 (162)	217.2 \pm 22.38 (148)	0.001	0.619	0.536	-78.580 – 40.965
Habitat	45.6 \pm 19.08 (66)	21.0 \pm 2.19 (62)	0.012	1.237	0.218	-14.752 – 63.916

Table 5.2. Results of paired t-tests examining differences between sources and their associated sinks in terms of abundance (Abund.), variability (CV), trend, Brown-headed Cowbird abundance (BHCO), Blue Jay abundance (BLJA), distance from the edge of the species breeding range, and amount of habitat in the landscape. SE is the standard error of the mean difference between sources and their associated sinks, and N is the number of pairs examined. R is the Pearson's correlation coefficient. CI is the 95% confidence interval of the mean difference between paired sources and sinks. Results of significant analyses ($P \leq 0.05$) are presented in bold.

Predictor	Mean Difference (Source-Sink) \pm SE (N)	R ²	t	P	CI
Abund.	0.08 \pm 0.45 (200)	0.150	0.184	0.854	-0.813 – 0.980
CV	0.005 \pm 0.04 (200)	0.171	0.128	0.898	-0.080 – 0.089
Trend	0.03 \pm 0.02 (200)	0.181	3.550	<0.0001	
BHCO	-0.02 \pm 0.10 (200)	0.144	-0.190	0.850	-0.213 – 0.175
BLJA	0.06 \pm 0.11 (200)	0.110	0.509	0.612	-0.162 – 0.274
Distance	0.60 \pm 2.81 (200)	0.098	-0.213	0.832	-6.137 – 4.942
Habitat	38.07 \pm 28.61 (85)	0.127	1.275	0.204	-94.973 – 18.826

Table 5.3. Results of Mann-Whitney U tests examining differences between sources and sinks in mean patch area (ha) and edge-to-area ratio (km/ha) for the Red-eyed Vireo (*Vireo olivaceus*) and the Wood Thrush (*Hylocichla mustelina*). SE is the standard error of the mean, and N is the number of populations of each type examined.

Species	Predictor	Source Mean \pm SE (N)	Sink Mean \pm SE (N)	U	P	CI
Red-eyed Vireo	Patch Area	39.20 \pm 19.834 (10)	69.06 \pm 40.550 (8)	32.0	0.470	-119.588 - 59.932
Red-eyed Vireo	Edge : Area	1.16 \pm 0.020 (10)	1.13 \pm 0.041 (8)	30.0	0.374	-0.065 - 0.116
Wood Thrush	Patch Area	27.02 \pm 8.007 (25)	33.92 \pm 17.224 (21)	259.0	0.938	-43.213 - 29.421
Wood Thrush	Edge : Area	1.19 \pm 0.015 (25)	1.20 \pm 0.025 (21)	251.0	0.833	-0.063 - 0.051

Table 5.4. Results of Wilcoxon Signed Rank tests examining differences between sources and their associated sinks in terms of patch area (ha) and edge-to-area ratio (km/ha) for the Red-eyed Vireo (*Vireo olivaceus*) and the Wood Thrush (*Hylocichla mustelina*). SE is the standard error of the mean difference between sources and their associated sinks, and N is the number of pairs examined. CI is the 95% confidence interval of the mean difference between paired sources and sinks.

Species	Predictor	Mean Difference (Source-Sink) ± SE (N)	Z	P	CI
Red-eyed Vireo	Patch Area	-16.29 ± 15.591 (10)	-0.764	0.445	-18.978 – 51.561
Red-eyed Vireo	Edge:Area	-0.02 ± 0.048 (10)	-1.274	0.203	-0.131 – 0.087
Wood Thrush	Patch Area	0.036 ± 12.116 (29)	-0.205	0.837	-24.783 – 24.854
Wood Thrush	Edge:Area	0.01 ± 0.026 (29)	-0.638	0.524	-0.043 – 0.062

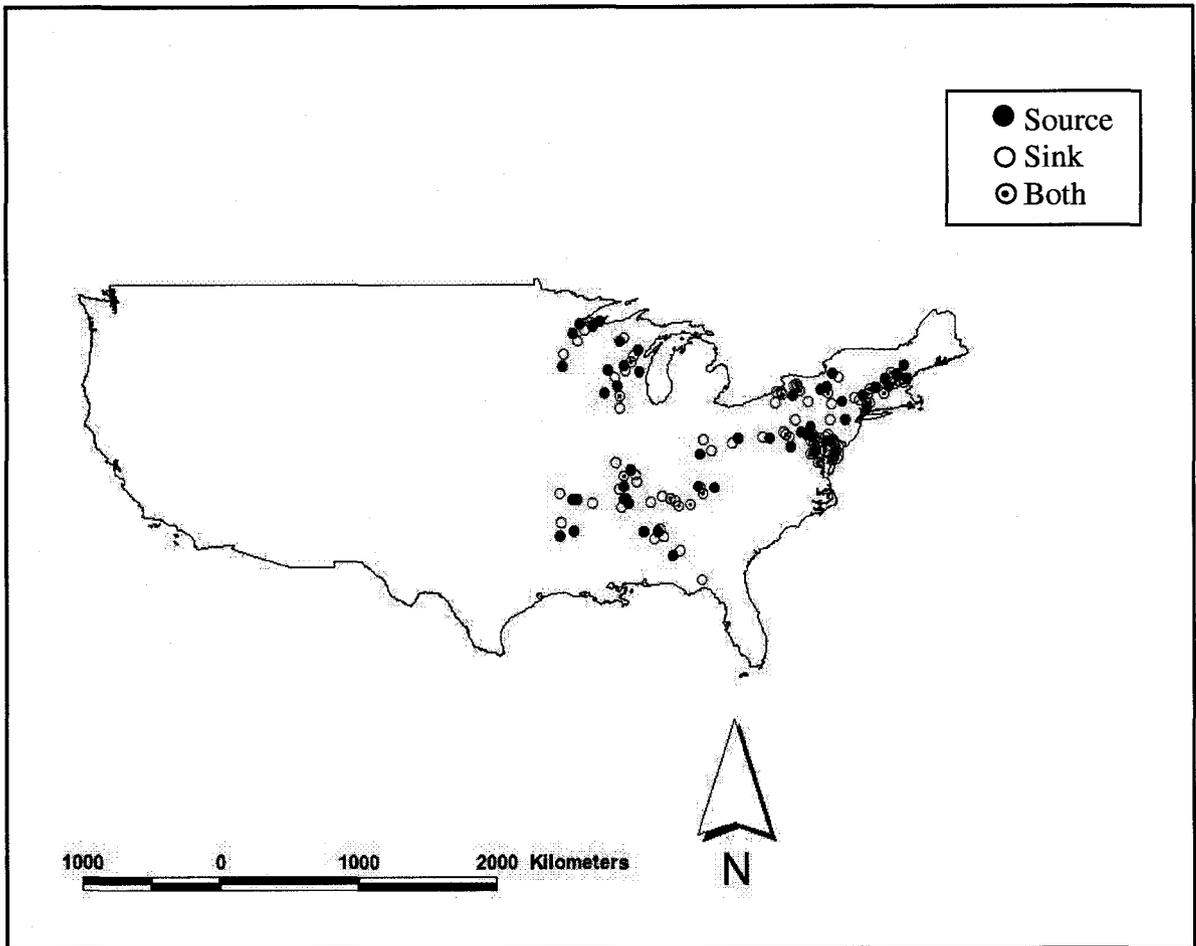


Figure 5.1. Songbird sources and sinks identified based on the one-year time-lagged model presented in Chapters 2 and 3. Species are pooled.

Chapter 6: General Conclusions

The main findings of this thesis are that (1) consistent source-sink dynamics do occur among songbird populations, and they take place over relatively large spatial scales, (2) songbirds disperse over much larger distances than previously thought, and (3) the scale over which landscape structure affects songbird populations is also often quite large, i.e., tens of kilometers for many species. This scale of effect is not correlated with species-specific dispersal distances, home range sizes, or territory sizes, but is correlated with mean gap width, a measure of landscape structure. Species whose habitat tends to be more aggregated (small gap widths) are generally affected by the landscape at smaller scales than those whose habitat tends to be less aggregated (large gap widths).

The finding that songbirds disperse over much larger distances than previously thought has far-reaching implications. For one, it might explain the rapid spread of invasive songbird species like the European Starling (Cabe 1993, Gammon and Maurer 2002), the House Sparrow (Lowther and Cink 2006), and the House Finch (*Carpodacus mexicanus*) (Gammon and Maurer 2002). This finding may also be useful in predicting responses to climate change and large-scale changes in land use. Because of their long-distance dispersal abilities, provided appropriate habitat still exists, songbirds should be more resilient than other taxa to these large-scale changes; large dispersal distances facilitate range shifts (Thomas and Lennon 1999) and the exchange of genes that might help species adapt to change across large areas (Pulido and Berthold 2004). Given that the scales over which songbirds seem to disperse are much larger than those previously reported, they may be even more resilient than previously thought.

The findings of Chapters 2 and 3 also indicate that the distribution of dispersal distances may not correspond to those commonly proposed in the literature. 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 (e.g., Howe and Westley 1986, Okubo and Levin 1989) or from insects (e.g., Taylor 1978). The two species [Eastern Towhee (*Pipilo erythrophthalmus*) and Gray Catbird (*Dumetella carolinensis*)] with significant time-lagged correlation distances at the smallest distance class examined (10-20 km) 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, the implied distribution of dispersal distances either has two peaks (one at less than the 10 km studied here and one at the larger dispersal distance found in Chapter 2 and 3), or only the one identified in Chapter 2 or 3. This suggests that although many young may still settle less than 10 km from their natal sites, many of those who do not travel quite far, possibly flying a certain distance before beginning to look for breeding sites. This should not come as too much of a surprise considering the typically low juvenile recapture rates of mark-recapture studies. However, most spatially explicit population models incorporating dispersal assume that individuals settle in the closest available habitat (e.g., Hanski 1994, Vos et al. 2001; but see Lande 1987, Fahrig 1992, With and

King 1999, King and With 2002). My findings may thus bring into question the predictions of these models as they pertain to most songbirds.

The evidence in favour of large-scale source-sink dynamics among many songbird species also has far reaching implications, especially for conservation. It indicates that source-sink status should be considered in management planning, and reinforces the idea that planning should occur over large spatial scales, at least over the scales over which source-sink dynamics occur. Since population trend is an indicator of source-sink status (Chapter 5), if long-term data are available, any population with an increasing long-term trend should be considered to be a potential source, the management of which could affect other populations as far away as the typical dispersal distance. When long-term data are lacking, to err on the side of caution, all populations should be considered to be potential sources, the management of which could have similar effects.

Imagine the example of an urban expansion project. In the process of carrying out an environmental assessment, authorities want to predict the long-term implications of developing a woodlot that currently provides good habitat for the Eastern Towhee, which is declining across its range (Greenlaw 1996). If there is the slightest possibility that the woodlot currently provides source habitat for this species, assessment of the long-term impact of developing the woodlot must include the potential extinction of any other populations 10-20 km away (see Chapter 3), even if the habitat occupied by these relatively distant populations is not itself slated for development.

The finding that populations of many songbird species respond to the landscape at relatively large scales has implications for research in landscape ecology, and also for conservation. It is especially applicable to focal patch studies, which consider the effects

of landscapes within a specific radius on populations at their centre (Brennan et al. 2002). For example, imagine a researcher wants to know the effect of landscape structure on populations of the Loggerhead Shrike (*Lanius ludovicianus*), a declining songbird that resides largely in pasture-land (Yosef 1996). As suggested by Brennan et al. (2002), to address this question, it would be appropriate to examine the relationship between abundance in focal patches, in this case patches of pasture-land, and landcover within the landscape surrounding these patches. For this species, the appropriate scale of effect is 5 km (Chapter 4), so the effect of landscape structure should be examined within a 5-km radius of each patch of habitat, regardless of the dispersal distance of this species.

If the scales of effect found here are relevant across the ranges of the species examined, the results of many landscape studies may be brought into question. For example, many studies claim to compare the effects of patch- and landscape-level characteristics on songbird abundances using different scales than those found here to be the most relevant. Examples of such studies include Lee et al. (2002), Crozier and Niemi (2003), and Koper and Schmiegelow (2006). Koper and Schmiegelow's results are particularly interesting within the context of my research. They studied landscape effects on 11 songbird species within 5-km-radius landscapes, and found landscape effects at this scale to be important for only one species, the Western Meadowlark (*Sturnella neglecta*). Of the 7 songbird species included in their study for which I have scales of landscape effect (Chapter 4), this is the only one whose scale of effect is 5 km. Hence, the conclusion that patch-scale characteristics are more important than landscape characteristics in explaining patterns of abundance (e.g., Lee et al. 2002, Crozier and

Niemi 2003) might be found to be erroneous if studies were carried out at different landscape scales.

If my finding of very different scales of effect for species that often inhabit the same habitat are correct, it might also be appropriate to carry out landscape studies that examine more than one species at more than one scale. The tendency is to group species together as grassland, forest, etc., and to study these groups of species at one landscape scale. For example, Lee et al. (2002) studied the effect of a 2 km² landscape on three species of “area-sensitive forest birds”; the Ovenbird (*Seiurus aurocapilla*), Red-eyed Vireo (*Vireo olivaceus*), and Wood Thrush (*Hylocichla mustelina*). My results indicate that, although these species may occur in sympatry, the landcover types of greatest importance to each differ, and the scales of landscape effect also differ substantially (Chapter 4). Although they did not examine such large landscapes, Cunningham and Johnson (2006) found similar differences between species in scales of landscape effect. Landscape studies should consider landscapes of different scales for different species.

The results on scale of landscape effect may be the most intriguing of this thesis in terms of future research. My thesis has led to the identification of scale of landscape effect for many species of North American songbirds, but the relationship between this and gap width is not strong enough to be the basis for prediction of scale of effect for other species and taxa. Although studies on several different taxa have indicated individual differences in movement depending on the structure of the landscape within species (see Chapter 4), as far as I know, this is the first study to explore such relationships across species. Despite the lack of a correlation between scale of landscape effect and any of the scales of movement investigated here (dispersal, territory size, and

home range size), the correlation between landscape structure and scale of effect still indicates a relationship between the latter and some aspect of individual movement, perhaps postbreeding movement or breeding-season forays. As discussed in Chapter 4, more detailed study of these types of movement might provide a mechanism for this relationship. If this were the case, we could use knowledge about the scale of these movements to predict the scale of landscape effect in species not examined here. This would be especially useful when landcover data are not readily available.

Given the satellite technology of the day, it is likely possible to collect an infinite amount of detailed data on songbird movements, but the price tag might be exorbitant. Instead, to build more specific predictions about the relationship between landscape scale of effect, gap width, and movement, it might be useful to start with taxa that function on finer spatial scales, such as beetles (Holland et al. 2004), Lepidoptera (e.g., Szymanski et al. 2004), or other insects. Because of the smaller scales of movement among these taxa, mark-recapture studies are often more successful in recapturing large proportions of the population (e.g., Heller and von Helverson 1990). This smaller scale of movement also means that researchers can effectively make use of tracking technologies with relatively small ranges, such as harmonic direction finding (e.g., Roland et al. 1996) and harmonic radar (e.g., Osborne et al. 1999).

Considering the potential importance of source-sink dynamics in predicting the effects of landscape change and management, I also recommend that more resources be put into the continuation, development, and expansion of long-term, large-scale, systematic monitoring programs like the North American Breeding Bird Survey. It is through these programs that sufficient data are generated to calculate long-term trends,

useful in the identification of source and sink populations, as found in Chapter 5. Expanding these programs would also allow for the further development and application of the time-lagged model used throughout this thesis to identify source-sink pairs and the scales over which source-sink dynamics might occur. In songbirds, it would be interesting to determine whether even larger-scale patterns in source-sink dynamics can be detected by extending the time-lag to two or more years. Given the extensive dispersal range revealed by this thesis, multi-year time-lagged correlations might allow for the investigation of range-wide source-sink dynamics in species with limited distributions.

Since issues of dispersal and source-sink dynamics are not exclusive to songbirds (e.g., Thomas et al. 1996, Schick and Lindley 2007), I also recommend the development and expansion of systematic long-term, large-scale monitoring programs on other taxa. Countless others have called for the same thing (e.g., Noss and Cooperrider 1994), and there has been a general expansion in the number of established long-term monitoring programs over the past few decades. Examples of existing programs that could be further expanded and developed include the Marsh Monitoring program in the Great Lakes region, which collects data on amphibians as well as birds, the Wisconsin Frog and Toad Monitoring Program, the Netherlands National Amphibian Monitoring Program, the Dutch Reptile Monitoring Program, and the Ohio Lepidopterists Long-term Monitoring of Butterflies.

Some existing monitoring programs could already support a time-lagged correlation study like the one presented here. The most obvious of these is the U.K. Butterfly Monitoring Scheme, which has been systematically collecting data on Lepidoptera in Great Britain since 1976 (Pollard and Yates 1995). Although the details

of the time-lagged model would have to be adapted to butterflies (the appropriate time-lag would likely be shorter than one year, for example), analysis of these data could be useful in examining source-sink dynamics among butterflies and in investigating whether the findings of the present study can be generalized to other taxa.

Note that all analyses performed in this study were correlational; no experimental manipulation was performed and, therefore, causation cannot necessarily be inferred. In Chapters 2 and 3, I cannot claim that temporal fluctuations in one area necessarily caused temporal fluctuations in linked populations with a one-year time-lag. It is possible that fluctuations in paired samples were entirely caused by something else, and therefore correlated simply because of this common cause. However, as described in Section 3.5, it is difficult to imagine what would cause such correlations with the one-year time-lag observed here, once I had controlled for within-year correlations. In Chapter 4, I cannot claim that abundances were necessarily a result of the amount of the habitat type of greatest importance in the landscape. There are undoubtedly many other things that contribute to abundance. Furthermore, the habitat type identified as that of greatest importance may simply be correlated with some type or combination of habitat not well represented by the NLCD. This is not as likely to be the case for the majority of species, abundances of which were most highly correlated with at least one landcover type identified as habitat in the literature. However, it may be the case for the few species for which abundances were most highly correlated with a landcover type not identified as habitat in the literature.

This thesis has been about results, but it has also been about ideas. It is largely based on the novel idea that one-year time-lagged correlations provide an indication of

typical dispersal distances and source-sink dynamics in songbirds. The relative simplicity of this approach should render it easily adaptable to other taxa, perhaps with adjustments to the length of the appropriate time-lag, as noted above. I hope this idea will be used and tested in the future to explore dispersal and source-sink dynamics in birds and other taxa.

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Appendix 1. Landcover variables used to identify species-specific scales of effect. More information on the first 20 of these classifications can be found in USGS 2007.

h2o = percent water

lires = percent low-intensity residential

hires = percent high-intensity residential

comint = percent commercial, industrial, and transportation

rock = percent bare rock

quarmin = percent quarries and mines

transit = percent transitional (clearcuts, etc.)

decfor = percent deciduous forest

evfor = percent evergreen forest

mixfor = percent mixed forest

shrub = percent shrubland

orchvin = percent orchards and vineyards

graherb = percent grassland and herbaceous cover

pasthay = percent pasture and hay

rowcr = percent row crop

smgrain = percent small grain

fallow = percent fallow

urg = percent urban and recreational grassland

wowet = percent wooded wetland

ehwet = percent emergent and herbaceous wetland

allh2o = percent water + percent woody wetland + percent emergent or herbaceous wetland

allwet = percent woody wetland + percent emergent or herbaceous wetland

allfor = percent deciduous forest + percent evergreen forest + percent mixed forest

dmfor = percent deciduous forest + percent mixed forest

cmfor = percent evergreen forest + percent mixed forest

allurb = percent low-intensity residential + percent high-intensity residential + percent urban and recreational grassland

allres = percent low-intensity residential + percent high-intensity residential

allurb = percent high-intensity residential + percent low-intensity residential + percent urban and recreational grassland

allurb2 = percent high-intensity residential + percent low-intensity residential + percent urban and recreational grassland + percent commercial, industrial, and transportation

allag = percent fallow + percent small grain + percent row crops + percent orchards and vineyards + percent pasture and hay

allcrop = percent small grain + percent row crops

allgrass = percent urban and recreational grassland + percent grasslands and herbaceous cover + percent pasture and hay

allpercent bare rock = percent bare rock + percent quarries and mines

AMRE_hab = percent deciduous forest + percent mixed forest + percent shrubland + percent low-intensity residential

COGR_hab = percent water + percent woody wetland + percent emergent or herbaceous wetland + percent row crops + percent small grain + percent fallow + percent urban and

recreational grassland + percent low-intensity residential + percent high-intensity residential

EAME_hab = percent grassland and herbaceous cover + percent pasture and hay + percent row crop + percent small grain + percent fallow + percent urban and recreational grassland + percent low-intensity residential

HOSP_hab = percent orchards and vineyards + percent pasture and hay + percent row crops + percent small grain + percent fallow

REVI_hab = percent low-intensity residential + percent deciduous forest + percent mixed forest + percent urban and recreational grassland

RWBL_hab = percent water + percent commercial, industrial, and transportation + percent woody wetland + percent emergent or herbaceous wetland + percent grasslands and herbaceous cover + percent row crops + percent pasture and hay + percent urban and recreational grassland

SAPH_hab = percent grasslands and herbaceous cover + percent fallow + percent shrubland

SAVS_hab = percent grasslands and herbaceous cover + percent transitional + percent pasture and hay + percent row crops + percent small grain + percent fallow

WEME_hab = percent grasslands and herbaceous cover + percent commercial, industrial, and transportation + percent pasture and hay + percent row crops + percent small grain + percent fallow

Appendix 2. Range, mean, and standard error of landcover variables over all 82

landscapes for the different buffer sizes used in Chapter 4. For full names and definitions of landcover variables, see Appendix 1.

Buffer Radius (km)	Landcover Variable	Range	Mean	Standard
				Error
0.5	comint	0.00-14.76	1.311	0.3023
0.5	confor	0.00-73.49	10.979	1.9887
0.5	decfor	0.00-86.23	10.852	1.7867
0.5	ehwet	0.00-22.06	1.653	0.4456
0.5	fallow	0.00-61.62	1.501	0.8611
0.5	graherb	0.00-72.53	11.593	1.9967
0.5	h2o	0.00-20.16	0.809	0.2932
0.5	hires	0.00-15.19	0.376	0.2026
0.5	ice	0.00-0.00	0	0
0.5	lires	0.00-21.25	1.808	0.4507
0.5	mixfor	0.00-36.76	4.756	1.0081
0.5	orchvin	0.00-44.61	1.122	0.6127
0.5	pasthay	0.00-64.3	12.894	1.8092
0.5	quarmin	0.00-4.29	0.055	0.0523
0.5	rock	0.00-27.91	0.548	0.3461
0.5	rowcr	0.00-91.21	18.666	2.973
0.5	shrub	0.00-99.96	12.311	2.7355
0.5	smgrain	0.00-52.95	4.126	1.1603

0.5	transit	0.00-7.36	0.402	0.149
0.5	urg	0.00-19.3	0.738	0.3181
0.5	wowet	0.00-89.06	3.5	1.1773
1	comint	0.00-4.85	0.638	0.1177
1	confor	0.00-87.14	13.354	2.2916
1	decfor	0.00-85.98	12.436	1.9597
1	ehwet	0.00-35.65	2.004	0.5777
1	fallow	0.00-60.49	1.605	0.8532
1	graherb	0.00-71.27	10.705	1.9658
1	h2o	0.00-41.55	1.98	0.6706
1	hires	0.00-8.10	0.285	0.1403
1	ice	0.00-0.00	0.000	0.000
1	lires	0.00-13.78	1.29	0.3182
1	mixfor	0.00-42.31	4.918	1.0051
1	orchvin	0.00-39.14	0.956	0.5243
1	pasthay	0.00-63.17	10.612	1.4943
1	quarmin	0.00-3.39	0.054	0.0419
1	rock	0.00-34.5	0.608	0.4245
1	rowcr	0.00-94.56	18.232	2.957
1	shrub	0.00-97.39	11.999	2.6992
1	smgrain	0.00-60.62	4.228	1.201
1	transit	0.00-5.03	0.29	0.0846
1	urg	0.00-5.9	0.421	0.1332

1	wowet	0.00-29.59	3.384	0.7094
5	comint	0.00-4.21	0.525	0.0911
5	confor	0.00-86.58	14.355	2.4184
5	decfor	0.00-72.15	12.187	1.8861
5	ehwet	0.00-39.73	2.170	0.6802
5	fallow	0.00-55.49	1.469	0.7778
5	graherb	0.00-68.14	10.822	1.9411
5	h2o	0.00-46.98	2.651	0.7946
5	hires	0.00-2.52	0.172	0.0482
5	ice	0.00-0.00	0.000	0.000
5	lires	0.00-12.5	1.073	0.2602
5	mixfor	0.00-40.03	4.969	0.975
5	orchvin	0.00-34.23	0.873	0.473
5	pasthay	0.00-65.34	9.334	1.3698
5	quarmin	0.00-0.57	0.032	0.0114
5	rock	0.00-41.91	0.778	0.5121
5	rower	0.00-91.46	17.678	2.8771
5	shrub	0.00-96.51	12.312	2.7198
5	smgrain	0.00-68.79	3.731	1.1567
5	transit	0.00-6.32	0.487	0.1436
5	urg	0.00-6.90	0.354	0.1262
5	wowet	0.00-27.96	4.031	0.7584
10	comint	0.00-4.73	0.539	0.0908

10	confor	0.00-88.02	14.794	2.3707
10	decfor	0.00-68.18	12.016	1.8411
10	ehwet	0.00-49.05	2.510	0.8114
10	fallow	0.00-52.01	1.311	0.7302
10	graherb	0.00-67.20	11.032	1.9351
10	h2o	0.00-53.36	3.052	0.8494
10	hires	0.00-2.32	0.172	0.0426
10	ice	0.00-0.00	0.000	0.0000
10	lires	0.00-14.85	1.086	0.2681
10	mixfor	0.00-40.86	4.831	0.9588
10	orchvin	0.00-30.45	0.758	0.4194
10	pasthay	0.00-61.43	9.282	1.3344
10	quarmin	0.00-1.08	0.04	0.015
10	rock	0.00-41.73	0.901	0.5149
10	rowcr	0.00-92.4	16.96	2.7518
10	shrub	0.00-93.42	12.534	2.6385
10	smgrain	0.00-63.04	3.349	1.0449
10	transit	0.00-7.94	0.554	0.1521
10	urg	0.00-5.41	0.27	0.0799
10	wowet	0.00-25.63	4.009	0.7552
20	comint	0.00-6.25	0.58	0.1023
20	confor	0.00-87.98	15.432	2.2897
20	decfor	0.00-64.42	11.69	1.7423

20	ehwet	0.00-61.23	2.425	0.8336
20	fallow	0.00-38.31	0.987	0.5461
20	graherb	0.00-65.32	11.108	1.8717
20	h2o	0.00-60.02	4.147	1.0081
20	hires	0.00-3.09	0.209	0.0558
20	ice	0.00-0.12	0.003	0.0018
20	lires	0.00-16.08	1.099	0.2815
20	mixfor	0.00-41.47	4.777	0.9321
20	orchvin	0.00-27.25	0.626	0.3627
20	pasthay	0.00-55.09	9.123	1.2534
20	quarmin	0.00-2.3	0.086	0.0342
20	rock	0.00-34.55	0.856	0.4296
20	rowcr	0.00-90.88	15.99	2.5264
20	shrub	0.00-92.2	12.725	2.5679
20	smgrain	0.00-55.56	3.115	0.9481
20	transit	0.00-8.98	0.672	0.1624
20	urg	0.00-3.20	0.265	0.0557
20	wowet	0.00-26.47	4.082	0.7429
30	comint	0.00-5.04	0.617	0.0987
30	confor	0.00-84.89	15.629	2.1881
30	decfor	0.00-67.89	11.682	1.7379
30	ehwet	0.00-60.10	2.210	0.7821
30	fallow	0.00-26.82	0.810	0.4156

30	graherb	0.00-59.37	11.190	1.8319
30	h2o	0.00-62.07	4.677	1.1374
30	hires	0.00-2.86	0.230	0.0545
30	ice	0.00-0.46	0.007	0.0057
30	lires	0.00-16.23	1.150	0.2638
30	mixfor	0.00-38.97	4.755	0.8915
30	orchvin	0.00-25.39	0.584	0.3317
30	pasthay	0.00-54.87	9.202	1.2115
30	quarmin	0.00-1.35	0.080	0.0229
30	rock	0.00-23.83	0.772	0.3093
30	rowcr	0.00-88.00	15.758	2.4717
30	shrub	0.00-86.23	12.717	2.4891
30	smgrain	0.00-52.61	2.850	0.8715
30	transit	0.00-8.53	0.694	0.1539
30	urg	0.00-2.20	0.255	0.0434
30	wowet	0.00-24.75	4.132	0.7375
40	comint	0.00-4.04	0.622	0.0856
40	confor	0.00-84.68	15.412	2.0777
40	decfor	0.00-68.39	11.732	1.736
40	ehwet	0.00-56.21	2.121	0.7317
40	fallow	0.00-20.18	0.736	0.3485
40	graherb	0.00-56.06	11.129	1.7734
40	h2o	0.00-63.91	5.138	1.2351

40	hires	0.00-3.18	0.251	0.0576
40	ice	0.00-0.75	0.011	0.0093
40	lires	0.00-14.13	1.240	0.259
40	mixfor	0.00-36.68	4.765	0.8681
40	orchvin	0.00-22.39	0.562	0.2998
40	pasthay	0.01-51.52	9.160	1.1682
40	quarmin	0.00-1.06	0.075	0.0173
40	rock	0.00-17.94	0.755	0.2537
40	rowcr	0.00-87.26	15.497	2.4587
40	shrub	0.00-85.48	12.935	2.4719
40	smgrain	0.00-50.73	2.751	0.8487
40	transit	0.00-7.49	0.696	0.1424
40	urg	0.00-1.79	0.246	0.0388
40	wowet	0.00-26.22	4.162	0.7308
50	comint	0.00-3.58	0.640	0.0795
50	confor	0.00-82.1	15.144	1.9908
50	decfor	0.00-67.38	11.715	1.7085
50	ehwet	0.00-48.86	2.015	0.6465
50	fallow	0.00-18.18	0.703	0.3193
50	gra herb	0.00-57.28	11.112	1.7423
50	h2o	0.00-64.57	5.483	1.2879
50	hires	0.00-3.76	0.272	0.0588
50	ice	0.00-0.96	0.015	0.0119

50	lires	0.00-13.66	1.313	0.2598
50	mixfor	0.00-35.43	4.789	0.857
50	orchvin	0.00-19.28	0.488	0.2565
50	pasthay	0.01-49.62	9.174	1.1587
50	quarmin	0.00-1.08	0.079	0.0173
50	rock	0.00-14.87	0.892	0.2695
50	rower	0.00-83.25	15.087	2.4298
50	shrub	0.00-85.75	13.221	2.4963
50	smgrain	0.00-49.9	2.709	0.8373
50	transit	0.00-7.11	0.705	0.1417
50	urg	0.00-1.90	0.261	0.0396
50	wowet	0.00-26.59	4.178	0.7417
60	comint	0.03-3.49	0.67	0.0786
60	confor	0.00-79.67	14.913	1.9229
60	decfor	0.00-65.13	11.756	1.6846
60	ehwet	0.00-44.86	1.927	0.6013
60	fallow	0.00-17.12	0.681	0.3003
60	graherb	0.00-60.85	11.15	1.7363
60	h2o	0.01-64.88	5.905	1.3379
60	hires	0.00-3.45	0.305	0.0586
60	ice	0.00-0.85	0.016	0.0108
60	lires	0.00-12.36	1.361	0.2503
60	mixfor	0.00-34.35	4.816	0.8496

60	orchvin	0.00-17.38	0.448	0.2315
60	pasthay	0.04-49.03	9.189	1.1435
60	quarmin	0.00-1.10	0.086	0.017
60	rock	0.00-17.05	0.982	0.2969
60	rowcr	0.00-81.37	14.674	2.3769
60	shrub	0.00-82.5	13.305	2.493
60	smgrain	0.00-48.08	2.699	0.8184
60	transit	0.00-6.89	0.719	0.142
60	urg	0.00-2.38	0.270	0.043
60	wowet	0.00-28.49	4.127	0.7356
70	comint	0.03-3.18	0.678	0.0786
70	confor	0.00-77.59	14.732	1.875
70	decfor	0.00-62.16	11.795	1.6718
70	ehwet	0.00-41.64	1.861	0.5708
70	fallow	0.00-16.59	0.688	0.2989
70	graherb	0.00-61.86	11.226	1.7374
70	h2o	0.07-65.50	6.332	1.3965
70	hires	0.00-3.40	0.324	0.0628
70	ice	0.00-0.67	0.019	0.0098
70	lires	0.01-10.96	1.351	0.2416
70	mixfor	0.00-33.20	4.814	0.8386
70	orchvin	0.00-15.58	0.409	0.2088
70	pasthay	0.11-47.49	9.155	1.1245

70	quarmin	0.00-0.90	0.088	0.0148
70	rock	0.00-20.50	1.029	0.3167
70	rowcr	0.00-80.16	14.391	2.326
70	shrub	0.00-81.48	13.291	2.4726
70	smgrain	0.00-45.77	2.723	0.8029
70	transit	0.00-6.72	0.741	0.144
70	urg	0.00-2.47	0.273	0.0436
70	wowet	0.00-29.32	4.082	0.7293
80	comint	0.03-2.91	0.659	0.0725
80	confor	0.00-75.40	14.626	1.8364
80	decfor	0.00-59.18	11.775	1.6481
80	ehwet	0.00-38.03	1.822	0.545
80	fallow	0.00-16.39	0.711	0.3022
80	graherb	0.00-62.35	11.217	1.73
80	h2o	0.05-65.80	6.875	1.4482
80	hires	0.00-3.27	0.316	0.0606
80	ice	0.00-0.56	0.022	0.0105
80	lires	0.01-9.62	1.296	0.2261
80	mixfor	0.00-32.02	4.782	0.8251
80	orchvin	0.00-13.97	0.382	0.1903
80	pasthay	0.09-46.28	9.172	1.1048
80	quarmin	0.00-0.83	0.085	0.0145
80	rock	0.00-22.26	1.05	0.33

80	rowcr	0.00-78.63	14.193	2.2698
80	shrub	0.00-78.7	13.153	2.4195
80	smgrain	0.00-41.87	2.794	0.7818
80	transit	0.00-6.38	0.759	0.1472
80	urg	0.00-2.38	0.267	0.0416
80	wowet	0.00-29.97	4.040	0.7243
90	comint	0.03-2.61	0.636	0.0663
90	confor	0.00-74.78	14.57	1.8241
90	decfor	0.00-58.78	11.763	1.6263
90	ehwet	0.00-33.72	1.748	0.5049
90	fallow	0.00-15.98	0.722	0.2953
90	graherb	0.00-63.32	11.205	1.74
90	h2o	0.05-65.82	7.398	1.4926
90	hires	0.00-3.13	0.297	0.0563
90	ice	0.00-0.56	0.021	0.01
90	lires	0.01-8.81	1.255	0.2117
90	mixfor	0.00-31	4.754	0.8099
90	orchvin	0.00-12.77	0.360	0.1768
90	pasthay	0.09-45.05	9.187	1.0835
90	quarmin	0.00-0.83	0.083	0.0139
90	rock	0.00-22.9	1.051	0.3333
90	rowcr	0.00-76.4	14.063	2.2152
90	shrub	0.00-75.22	12.988	2.367

90	smgrain	0.00-39.39	2.896	0.766
90	transit	0.00-6.13	0.769	0.1466
90	urg	0.00-2.22	0.261	0.0393
90	wowet	0.00-30.44	3.970	0.7139
100	comint	0.03-2.42	0.620	0.0611
100	confor	0.00-74.94	14.495	1.8061
100	decfor	0.00-58.29	11.778	1.6022
100	ehwet	0.00-30.21	1.664	0.4638
100	fallow	0.00-15.26	0.718	0.2851
100	graherb	0.00-64.76	11.191	1.7535
100	h2o	0.05-65.91	7.841	1.5301
100	hires	0.00-2.98	0.289	0.0527
100	ice	0.00-0.56	0.023	0.0105
100	lires	0.01-8.85	1.231	0.2025
100	mixfor	0.00-30.17	4.745	0.7941
100	orchvin	0.00-11.52	0.340	0.1624
100	pasthay	0.1-44.16	9.210	1.0634
100	quarmin	0.00-0.73	0.079	0.0122
100	rock	0.00-21.73	1.053	0.3237
100	rowcr	0.00-75.2	13.978	2.1674
100	shrub	0.00-73.53	12.846	2.3284
100	smgrain	0.00-36.72	2.964	0.7487
100	transit	0.00-5.96	0.778	0.146

100	urg	0.00-2.12	0.258	0.0375
100	wowet	0.00-31.04	3.900	0.7015
