

The interacting effects of the historic landscape
structure, human landscape change, and species
mobility on species extinction risk in human-altered
landscapes: an evolutionary perspective

by

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Abstract

Mobility is widely thought to be important for extinction risk in human-altered landscapes. However, there are conflicting theories and empirical findings as to whether mobile species are more or less at-risk than sedentary species. My objective was to investigate why mobility increases risk in some cases, but decreases risk in others. My first three data chapters focused on the idea that mobility-extinction risk relationships depend on interacting effects of the historic landscape structure, human landscape change, and mobility. In Chapter 2, I used simulations to demonstrate that landscape structure – particularly non-habitat (matrix) quality and disturbance frequency – can drive evolution of species behaviour at habitat boundaries, an important aspect of mobility that determines rates of movement among populations. In Chapter 3, I found empirical support for an interaction between landscape change and mobility, finding that more mobile North American bird species became less mobile over the 20th century, while less mobile species became more mobile. In Chapter 4, I simulated the interacting effects of the historic landscape, landscape change, and mobility on extinction risk. These simulations suggest that the mobility-risk relationship depends on the (1) mobility metric, because mobility increases risk when measured as emigration, but decreases risk when measured as immigration; (2) rate of landscape change, because mobility increases risk with rapid habitat loss, but decreases risk with slow habitat loss; and (3) historic landscape structure, because some structures drive evolution of species characteristics that increase

mobility and decrease risk, while other structures favor characteristics that increase both mobility and risk. The rest of my thesis focused on the idea that collinearity between habitat specialization and mobility may cause apparently conflicting mobility-risk relationships, when specialization drives risk and specialization-mobility relationships vary between species groups. I found that temperate breeding bird specialists disperse farther than generalists (Chapters 5 and 6). This was opposite to invertebrate specialization-mobility relationships, providing preliminary support for my hypothesis. My thesis contributes to our understanding of why conflicting mobility-extinction risk relationships occur. Additionally, these results have conservation implications, suggesting conservation should focus on species that frequently emigrate but cannot move long distances among habitat fragments.

Preface

Co-authorship statement

This thesis is formatted using the integrated thesis format, with each data chapter (Chapters 2 – 6) written as an independent manuscript. At the time of submission, Chapters 2, 4, and 5 were submitted to peer-reviewed journals (see **Manuscript status**, below).

Each data chapter is a co-authored work; however, I performed the majority of the work presented in this thesis. I proposed and developed all research questions and hypotheses, in cooperation with my supervisor, Dr. Lenore Fahrig. I was primarily responsible for the design of projects to address these research questions. Additionally, I (a) wrote the computer simulation models used in Chapters 2 and 4, (b) conducted all statistical analyses, and (c) wrote first drafts of each chapter (and associated manuscript). I was also responsible for finalizing the text of each chapter. The contributions of my co-authors are as follows:

(1) *Dr. Lenore Fahrig* (Carleton University) contributed to all data chapters, helping to develop research questions and hypotheses. She also provided guidance during project design, and contributed significantly to the writing of each chapter.

(2) *Dr. André Desrochers* (Université Laval) contributed to Chapter 3. He was responsible for collection of the bird primary wing projection data set used in Chapter 3, which was previously published in a peer-reviewed

journal (Desrochers 2010); however, the research question and hypothesis for this chapter were mine, and I conducted all analyses presented in this chapter. Dr. Desrochers also contributed to the writing of this chapter.

(3) *James W. Pearce-Higgins* (British Trust for Ornithology) contributed to the writing of Chapter 5. His inclusion as a co-author also reflects the contribution of the British Trust for Ornithology to this chapter, as this chapter used data from the United Kingdom Breeding Bird Survey, funded jointly by the British Trust for Ornithology, the Royal Society for the Protection of Birds, and the Joint Nature Conservation Committee.

To reference my thesis as a whole, or an unpublished chapter, I recommend the following citation:

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Chapter 1 – General introduction

Evidence of widespread population declines and species extinctions suggests that we are in the midst of a crisis of biodiversity (Dirzo et al. 2014, Pimm et al. 2014, Ceballos et al. 2015). Human activities are driving these population declines and species extinctions through land cover change, climate change, overexploitation, pollution, and facilitation of species invasions (Wilcove et al. 1998, Warren et al. 2001, Pereira et al. 2012). Of these, land cover change likely poses the greatest threat to wildlife species (Wilcove et al. 1998, Warren et al. 2001, Eglinton and Pearce-Higgins 2012, Pereira et al. 2012).

Conversion of native land cover (e.g. forest) to human-dominated land cover (e.g. human settlements) is expected to put species at risk, because it reduces habitat amounts, isolates populations, and increases the risks of movement through the non-habitat (i.e. matrix) areas of the landscape. However, not all wildlife species have been negatively affected by human landscape change: although many species are declining, some appear to be unaffected by human landscape change, and others are even increasing in the altered landscape (Stuart et al. 2004, Battersby 2005, Baillie et al. 2014). Some of these differences in the species response to landscape change may be explained by differences in the rates of landscape change these species experience; however, this does not explain why a given landscape change can cause declines in some species and increases in others (e.g. Hansen et al. 2005).

Why do species respond differently to a given landscape change? One answer to this question is that differences in species' responses to human landscape change are caused by differences in their traits, where I use the term 'trait' to refer to any feature of the species (morphological, physiological, behavioural, etc.) that affects growth, reproduction, or survival (modified from Violle et al. 2007). Empirical evidence of cross-species correlations between extinction risk and species traits supports this answer. For example, empirical studies suggest that large-bodied, habitat specialists with low fecundity and limited geographic ranges are most at-risk in human-altered landscapes (Vance et al. 2003, Sekercioğlu et al. 2004, Cardillo et al. 2005, Kotiaho et al. 2005, Jiguet et al. 2007, Davidson et al. 2009, Fritz et al. 2009).

Mobility, i.e. an organism's ability to leave its current home range or territory, is also thought to be important for extinction risk in human-altered landscapes. However, there are conflicting theories and empirical findings as to whether mobile species are more or less at-risk in human-altered landscapes than sedentary species. An organism's mobility determines its actual movements in the landscape, i.e. dispersal from its current location, which results in either mortality or settlement in a new location. The assertion that mobile species should be less at-risk in a human-altered landscape than sedentary species is largely based on the idea that greater mobility allows for greater rates of recolonization after local extinctions and rescue of small populations (Brown and Kodric-Brown 1977, Hanski 1998, Hill et al. 2002, Grimm et al. 2004, Reed 2004). Others have predicted the opposite – that mobile species should be more

at-risk in a human-altered landscape – largely because more mobile species are likely to spend more time in the human-dominated portions of the landscape, thereby suffering greater rates of mortality than sedentary species (Casagrandi and Gatto 1999, Heino and Hanski 2001, Fahrig 2001). The empirical findings on the role of mobility in species extinction risk are also mixed, with studies showing both higher risk for more mobile species (Gibbs 1998, Shahabuddin and Ponte 2005, Van Houtan et al. 2007) and lower risk for more mobile species (Jones et al. 2003, Kotiaho et al. 2005, Reinhardt et al. 2005, Sekercioğlu 2007, Jiguet et al. 2007, Mattila et al. 2008, Pöyry et al. 2009, Öckinger et al. 2010, Garrard et al. 2012). Therefore the overall objective of my thesis was to investigate the relationship between mobility and extinction risk, and use an evolutionary perspective (as described in the following paragraphs) to understand why mobility increases extinction risk in some cases, but decreases risk in others.

Understanding why some species have traits that reduce extinction risk in human-altered landscapes, while other species have traits that increase risk, requires an evolutionary perspective (Fahrig 2007b, Sih et al. 2011). This is because traits influence individual fitness via effects on reproduction and survival, and are thus influenced by natural selection. A species' evolutionary history affects whether it has traits that allow it to persist in a human-altered landscape. In particular, species that evolved traits that are adaptive in human-altered landscapes (e.g. cavity or cliff-nesting birds that nest on buildings; Jokimaki et al. 2014), those that evolved traits allowing for rapid evolution (e.g. short generation times; Thomas et al. 2010), and those with traits allowing for

phenotypic flexibility (Hendry et al. 2008) are likely to be at low risk in human-altered landscapes.

An evolutionary perspective also suggests that effects of species traits on extinction risk are not independent of the effects of landscape structure, and human alteration of that structure. This is because landscape structure drives evolution of species traits, through its effects on the costs and benefits associated with those traits. For example, the amount of habitat in a landscape should influence the evolution of mobility. In landscapes with less habitat the costs of mobility should be higher because individuals will spend more time in the matrix (Baker and Rao 2004, Johnson et al. 2009), driving selection for mobile species in landscapes with ample habitat and sedentary species in landscapes where habitat is rare (Bonte et al. 2006).

I propose the following framework for the interacting effects of the historic landscape structure, human landscape change, and species traits on species extinction risk (Figure 1.1). Landscape structure drives evolution of species traits, through its effects on the costs and benefits associated with those traits. Thus a species' traits depend on the landscape in which it evolved (i.e. its historic landscape). Additionally, species traits may evolve in response to human landscape change. These altered species traits then interact with the human-altered landscape structure to affect the species extinction risk, where the species risk in the altered landscape depends on its traits.

There is an inherent hierarchical structure to species traits; i.e. traits that

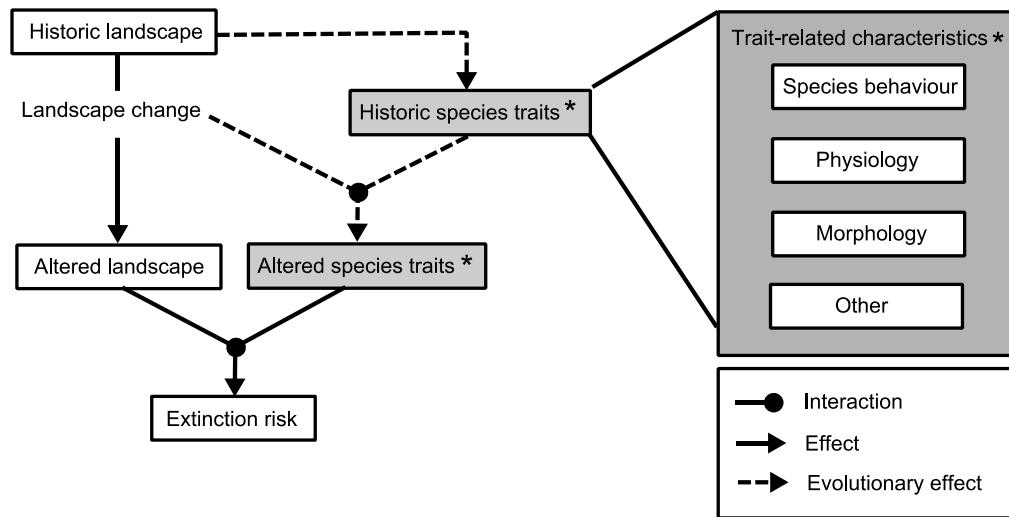


Figure 1.1. Framework for the interacting effects of the landscape structure,

human landscape change, and species traits on species extinction risk.

Landscape structure drives evolution of species traits, and the trait-related

characteristics these depend on, through the landscape's effects on the costs

and benefits associated with those traits. Therefore the historic landscape

structure affects species risk through its effects on the evolution of species traits.

Species traits may also be evolving in response to human landscape change.

These altered species traits then interact with the human-altered landscape

structure to affect the species extinction risk, where the species risk in the altered

landscape depends on its altered traits. * Note that species traits and trait-related

characteristics evolve simultaneously; thus evolution of one trait or characteristic

influence fitness directly are often the product of other species traits (Violle et al. 2007). For example, species mobility is dependent on a suite of morphological (e.g. wing shape; Dawideit et al. 2009), physiological (e.g. flight metabolic rate; Haag et al. 2005), and behavioural (e.g. probability of boundary crossing; Schtickzelle and Baguette 2003) traits. To differentiate between a given trait, and the traits that it depends on, I refer to the former as the ‘species trait’, and the latter as a ‘trait-related characteristic’ (Figure 1.1).

Studies of the interacting effects of the historic landscape structure, human landscape change, and species traits on species extinction risk are potentially vital to our efforts to protect biodiversity. First, understanding these interactions should help us to better understand why some species are on their way to extinction, while others are thriving. This in turn should help us predict which species are at greatest risk in human-altered landscapes, allowing direction of limited conservation resources to these species. Second, if we understand how the landscape structure interacts with species traits to affect species risk in human-altered landscapes, we should be able to better understand which conservation actions will be most beneficial for species. For example, we should be able to predict which groups of species will benefit from the creation of wildlife corridors. Corridors should be effective for biodiversity conservation in cases where the most mobile species are at greatest risk, because the species at greatest risk can use corridors to reduce interaction with the matrix during dispersal. However, corridors should be less effective for biodiversity conservation in cases where the most sedentary species are at

greatest risk, because the species at greatest risk will rarely use corridors.

Finally, studies of the interacting effects of the historic landscape structure, human landscape change, and species traits on species extinction risk may help to resolve conflicting theories and empirical findings as to whether a trait should increase or decrease species risk in human-altered landscapes. This is because an interaction between landscape structure and a species trait may cause the trait to increase species risk in some landscapes and decrease risk in others.

I expect that an evolutionary perspective on the interacting effects of the historic landscape structure, human landscape change, and mobility on species extinction risk can help to reconcile the conflicting theoretical and empirical findings on the role of mobility in extinction risk. Species mobility is, at least in part, determined by its evolutionary history. Empirical studies suggest that mobility has a significant heritable component in insects, reptiles, birds, and mammals (Massot et al. 2003, Pasinelli et al. 2004, Saastamoinen 2008, Doligez et al. 2009, Selonen and Hanski 2010). There is also evidence linking specific alleles to mobility-related characteristics, including flight metabolic rate (Haag et al. 2005, Niitepõld et al. 2009) and wing length (Tarka et al. 2010). Thus differences in mobility among species and populations may occur because of differences in their evolution in response to the historic landscape. There is also evidence that mobility-related characteristics can evolve within a few decades (Gilchrist et al. 2001, 2004, Phillips et al. 2006, Brown and Brown 2013), and such rapid evolution may occur when human landscape change exerts strong effects on fitness. For example, road mortality of cliff swallows (*Petrochelidon*

pyrrhonota) has been implicated in the rapid evolution of shorter wings in roadside populations, because swallows with shorter wings were less likely to be killed on roads than swallows with longer wings (Brown and Brown 2013). This suggests that a species' mobility may depend on both its historic landscape and its response to human landscape change. And if the historic landscape, landscape change, and mobility interact such that mobility increases extinction risk in some landscapes but decreases risk in others, then this could explain the conflicting findings on the role of mobility in extinction risk.

An alternative explanation for the conflicting findings on the role of mobility in species extinction risk is that collinearity between mobility and another species trait (or traits) may obscure the true relationship between mobility and extinction risk. There are a number of reasons why certain traits tend to occur together. First, species traits may co-occur because species have limited resources, and investment of limited resources into one species trait means reduced investment into another trait (e.g. Roff et al. 1999). We may also see co-occurrence of certain species traits because these traits evolved in response to a common environmental condition; for example, high rates of herbivory can drive evolution of multiple traits involved in anti-predator defense (Coley and Barone 1996). Traits may co-occur because they depend on a common underlying morphology or physiology, such as when selection acting on a hormone-mediated trait results in changes in other traits that depend on the same hormone (McGlothlin and Ketterson 2008). Finally, collinearity between species traits may occur because traits do not evolve in isolation from one another (Figure 1.1). Thus selection for

one species trait may alter the costs and benefits associated with a second trait, influencing the selective pressure on the second trait. For example, a positive correlation between dispersal rate and fecundity may occur because the benefits of fecundity are greater for dispersers than non-dispersers, driving selection for greater fecundity in more mobile species (Hanski et al. 2006). Whatever the cause, correlations between species traits may complicate our understanding of the effects of a given species trait on the response to human landscape change, because the apparent effect of one species trait on the species extinction risk may actually be caused by another, correlated trait. If two traits are positively related in some species groups and negatively related in other species groups, this could cause contradictions in reported relationships between a given trait and the species extinction risk.

In my first three data chapters I focused on the relationships between the historic landscape structure, human landscape change, and species mobility, and how these interact to affect species extinction risk in the human-altered landscape. In my first data chapter (Chapter 2), I investigated how the historic landscape structure drives evolution of mobility-related characteristics, through the effects of landscape structure on the costs and benefits of dispersal. Previous theoretical studies suggest that a species' landscape should influence the evolution of its mobility-related behaviours (e.g. Bonte and De La Peña 2009, Poethke et al. 2011, Travis et al. 2012). However, these studies did not consider the evolution of boundary crossing, i.e. the tendency of animals to cross from habitat to matrix (Basquill and Bondrup-Nielsen 1999, Ries and Debinski 2001,

Rittenhouse and Semlitsch 2006). Therefore, in this chapter I asked the question:

How does landscape structure affect the evolution of species behaviour at habitat boundaries? To address this question, I used an individual-based, spatially explicit model to simulate the evolution of boundary crossing in response to four attributes of the landscape: habitat amount, habitat fragmentation, matrix quality, and disturbance frequency.

In Chapter 3, I investigated the interaction between landscape change and species mobility. Specifically, I asked the question: ***Do evolutionary changes in species mobility in response to human landscape alteration depend on the species' prior mobility?*** The hypothesis is that a species' prior mobility affects how its mobility evolves in response to human landscape change, because mobility should determine how strongly landscape change affects the costs versus benefits of mobility. There should be larger increases in the costs of mobility for mobile than sedentary species when habitat is lost, because mobile species interact with matrix more frequently. In contrast, the benefits of mobility should increase more for sedentary than mobile species, because sedentary species are at greater risk from inbreeding depression, competition, and predation when habitat patch sizes decline. To test this hypothesis, I used an existing data set (Desrochers 2010) to estimate the prior mobility and rate of change in mobility for 21 North American bird species, and tested for a negative, cross-species correlation between prior mobility and its rate of change.

In Chapter 4 I broadened my focus, and investigated how both the historic landscape structure and landscape change interact with species mobility, and

influence the species extinction risk in a human-altered landscape. Specifically, I asked the question: ***Why does mobility increase the risk of some species in human-altered landscapes, and decrease the risk of others?*** In this chapter, I tested the hypothesis that whether mobility increases or decreases species risk in human-altered landscapes depends on the historic landscape structures of the studied species (Fahrig 2007b). Some landscape structures should drive evolution of mobility-related characteristics that increase both mobility and risk, while others drive evolution of characteristics that increase mobility and decrease risk. I also proposed two novel, alternative hypotheses to explain these contradictory findings: (1) extinction risk increases with increasing mobility when mobility is measured as emigration, but decreases with increasing mobility when mobility is measured as immigration; and (2) the most mobile species in unaltered landscapes are least mobile in human-altered landscapes, so the relationship between mobility and extinction risk is opposite when mobility is measured in human-altered landscapes and unaltered landscapes (or in conditions similar to those in the historic landscape). To test and refine these three hypotheses, I used an individual-based, spatially explicit simulation model to simulate population dynamics, evolution of mobility-related characteristics, and species response to habitat loss.

In the remainder of my thesis I focused on collinearity between habitat specialization and mobility. Empirical studies suggest that there can be cross-species relationships between habitat specialization and mobility (e.g. Carnicer et al. 2013, Dahirel et al. 2015). If habitat specialists are the most mobile species in

some species groups, and habitat specialists are least mobile in other species groups, then this could cause contradictions in reported relationships between mobility and extinction risk. This is because, if habitat specialization increases extinction risk (Sekercioğlu et al. 2004, Kotiaho et al. 2005), then mobility may appear to decrease extinction risk in cases where habitat specialists are the least mobile species, and mobility may appear to increase extinction risk in cases where habitat specialists are the most mobile species. Empirical studies finding cross-species relationships between habitat specialization and mobility have found that habitat specialists were less mobile than habitat generalists (Bonte et al. 2003, Entling et al. 2011, Sekar 2012, Carnicer et al. 2013, Dapporto and Dennis 2013, Dahirel et al. 2015); however, these studies were limited to invertebrates. And, although theory supports this trade-off between habitat specialization and mobility, there is also support for the opposite: that habitat specialists are more mobile than habitat generalists (Kisdi 2002, Samways and Lu 2007, Venail et al. 2008, Centeno-Cuadros et al. 2011, Nagelkerke and Menken 2013).

Therefore, I wanted to evaluate the cross-species relationship between habitat specialization and a measure of species mobility (i.e. the dispersal distance) in other species groups, i.e. the temperate breeding birds of North America and the United Kingdom. Unfortunately, reliable estimates of dispersal distances were not available for many North American species. Therefore I opted to use a method to indirectly estimate dispersal distances using time-series of abundance estimates, based on the assumption that dispersal between two

locations can result in positive, one-year-lagged correlations in population abundances between those locations (Tittler et al. 2006, 2009). To justify use of this method to estimate dispersal distances, in Chapter 5 I addressed the question: ***Can one-year-lagged synchrony in abundances between locations be used to estimate typical dispersal distances?*** To answer this question, I tested how well this population synchrony dispersal index estimates mean dispersal distances for United Kingdom birds, by comparing my estimates to those from independent mark-recapture data (Paradis et al. 1998). Then in Chapter 6 I addressed my final research question: ***Is species' mobility correlated with its degree of habitat specialization?***, testing for cross-species relationships between the degree of habitat specialization, dispersal distance, and migration status for North American and United Kingdom birds.

Chapter 2 – Matrix quality and disturbance frequency drive evolution of species behaviour at habitat boundaries

2.1 Abstract

Previous theoretical studies suggest that a species' landscape should influence the evolution of its mobility-related characteristics, because landscape structure affects the costs and benefits of dispersal. However, these studies have not considered the evolution of boundary crossing, i.e. the tendency of animals to cross from habitat to non-habitat ('matrix'). It is important to understand this behaviour, because of its effects on the probability of population persistence.

Boundary-crossing behaviour drives the rate of interaction with matrix, and thus it influences the rate of dispersal among populations and the risk of dispersal mortality. I used an individual-based, spatially explicit model to simulate the evolution of boundary crossing in response to landscape structure. My simulations predict higher evolved probabilities of boundary crossing in landscapes with more habitat, less fragmented habitat, higher-quality matrix, and more frequent disturbance. Unexpectedly, my simulations also suggest that matrix quality and disturbance frequency have much stronger effects on the evolution of boundary crossing than either habitat amount or habitat fragmentation. Thus my results suggest that boundary-crossing responses are most affected by the costs of dispersal through the matrix, and the benefits of escaping local extinction events. Evolution of optimal behaviour at habitat boundaries in response to the landscape may have implications for species risk

in human-altered landscapes, because this behaviour may become sub-optimal if the landscape changes faster than the species' evolutionary response to that change. Understanding how matrix quality and habitat disturbance drive evolution of behaviour at boundaries, and how this in turn influences the extinction risk of species in human-altered landscapes, should help us identify species of conservation concern and target them for management.

2.2 Introduction

Dispersal among habitat patches has both costs and benefits, and the effects of these on fitness should drive evolution of mobility-related characteristics that minimize the cost:benefit ratio (Bowler and Benton 2005). The primary cost is the risk of mortality in the matrix, i.e. the non-habitat parts of the landscape (McLoughlin et al. 2005, Johnson et al. 2009). And, even if the individual survives, the energy expended during dispersal may compromise its fitness (Baker and Rao 2004). The primary benefits of dispersal are that it allows individuals to track available resources and escape declining local conditions (Tellería and Pérez-Tris 2003). Dispersal also allows individuals to avoid competition, inbreeding, and predation (Bollinger et al. 1993, Cronin et al. 2004, Moore et al. 2006).

A species' landscape should influence the evolution of mobility-related characteristics, because it influences the costs and benefits of dispersal. For example, the costs of dispersal should be higher in landscapes with less habitat, because individuals will spend more time in the matrix (Schtickzelle and Baguette

2003, Johnson et al. 2009). The benefits of dispersal should be higher in landscapes where disturbances are frequent, because dispersal allows individuals to escape declining local conditions (Friedenberg 2003). Thus, differences in mobility-related characteristics among species and populations are likely at least partly explained by differences in their landscapes (e.g. Merckx et al. 2003).

Previous studies support this idea. For example, models predict higher dispersal rates in landscapes with more habitat, less fragmented habitat, more dynamic habitat, and higher-quality matrix (Travis and Dytham 1999, Heino and Hanski 2001, Poethke and Hovestadt 2002, Bonte and De La Peña 2009, Poethke et al. 2011). In addition, movement pathways are predicted to be straighter in landscapes with less habitat, less fragmented habitat, and lower-quality matrix (Zollner and Lima 1999, Bartoń et al. 2009, Travis et al. 2012).

Previous studies of the evolution of mobility-related characteristics have not considered evolution of the tendency to cross habitat boundaries when they are encountered. When a dispersing individual encounters a habitat boundary, does it turn back into habitat, or cross into the matrix (Figure 2.1)? Responses to habitat-matrix boundaries have been observed in insects, amphibians, mammals, and birds (Basquill and Bondrup-Nielsen 1999, Rodríguez et al. 2001, Merckx et al. 2003, Schtickzelle and Baguette 2003, Rittenhouse and Semlitsch 2006). The boundary-crossing response is important for population persistence, particularly in a human-altered landscape, because it drives rates of interaction with human-dominated areas of the landscape.

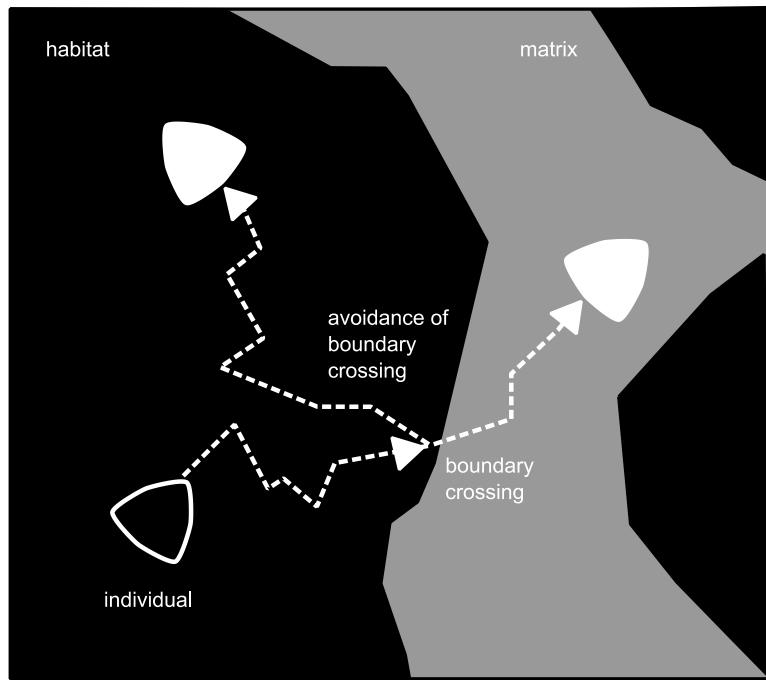


Figure 2.1. When an individual encounters a boundary between habitat and non-habitat (i.e. matrix), it may turn back into the habitat (i.e. avoidance of boundary crossing), or it may cross the boundary and enter the matrix (i.e. boundary crossing).

I predict that the optimal probability of boundary crossing should be higher in landscapes with more habitat that is less fragmented. This is because the time spent in the matrix should be lower and the chance of finding new habitat should be higher than in landscapes with less habitat that is more fragmented. In addition, boundary crossing should be higher when the matrix quality is higher, as the risk of movement into matrix is reduced. I also predict that the optimal probability of boundary crossing should be higher in landscapes that are more dynamic, e.g. where disturbances are more frequent, as the benefit of dispersal is higher in such landscapes.

Here I evaluated these predictions by simulating the evolution of the boundary-crossing response in landscapes that differ in habitat amount, habitat fragmentation, matrix quality, and disturbance frequency.

2.3 Methods

2.3.1 Overview

My modelling framework was based on previously published individual-based, spatially explicit models of the evolution of dispersal probability in response to landscape structure (Travis and Dytham 1998, 1999). I simulated population dynamics and the evolution of the boundary-crossing response in landscapes that varied in habitat amount, habitat fragmentation, matrix quality, and disturbance frequency. Evolution of the boundary-crossing response occurred because the probability of an individual crossing from habitat to matrix when it encountered a habitat boundary, i.e. its probability of boundary crossing,

was simulated as a heritable trait. I measured the boundary-crossing response as both the evolved population mean of the boundary-crossing trait value, and the actual per capita rate of boundary crossing during the simulation, i.e. the proportion of the population that crossed from habitat to matrix. To evaluate my predictions, I related each of these measures to habitat amount, fragmentation, matrix quality, and disturbance frequency.

Because mobility-related characteristics co-evolve in response to landscape structure, in addition to the boundary-crossing response I included evolution of three other characteristics as independent, heritable traits: (1) dispersal probability, or the probability that an individual disperses, (2) path straightness in matrix, and (3) path straightness in habitat. I interpreted effects of these additional characteristics on the evolution of boundary crossing as indirect effects of the landscape structure on the evolution of boundary crossing. For example, if evolved dispersal paths are straighter in certain landscapes, and path straightness influences the evolved boundary-crossing response, then the optimal boundary-crossing response is indirectly affected by landscape structure.

2.3.2 *Model description*

I constructed the model in NetLogo (Wilensky 1999). Each generation involved (1) habitat disturbance, resulting in some local population extinctions, (2) density-dependent reproduction, including transfer of genetic information, followed by (3) dispersal, i.e. movement of individuals from their birth place, resulting in either dispersal mortality or settlement in a new location (Figure 2.2).

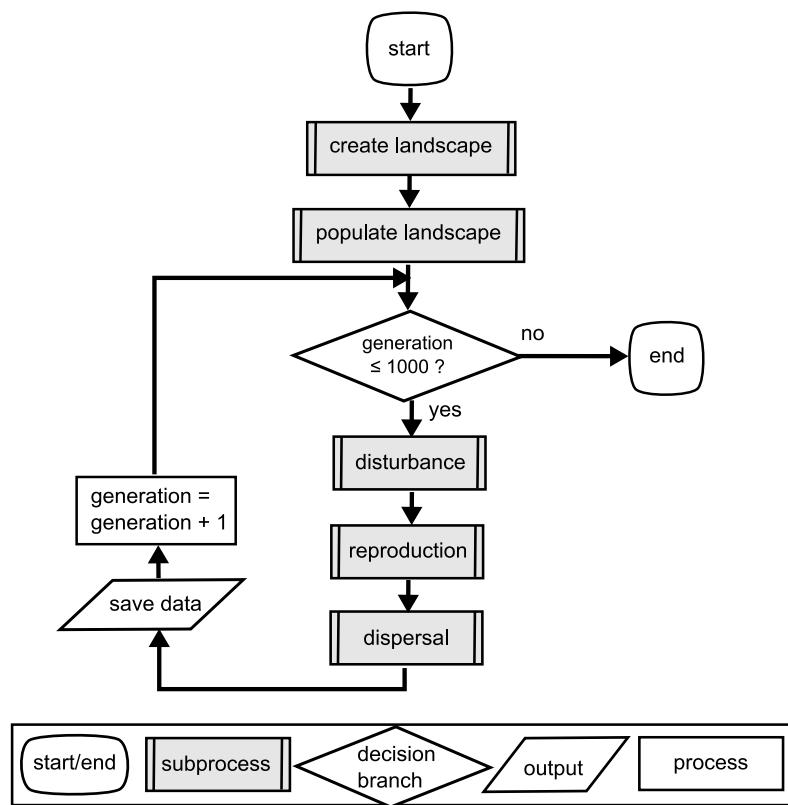


Figure 2.2. Flow chart of the simulation model. See Appendix A for flow charts for each of the five subprocesses.

See Appendix A for additional flow charts and Appendix B for model parameters.

2.3.2.1 *Create landscape*

Each simulation began by creating a square 127×127 (16,129) grid of cells, with each cell assigned as habitat or matrix. The differences between habitat and matrix were that reproduction could only occur in habitat cells, and dispersal mortality was lower in habitat than in matrix. To determine which cells were habitat and which were matrix, I used a midpoint displacement algorithm to generate a fractal surface (Saupe 1988). Fragmentation, independent of habitat amount was controlled by the Hurst exponent (H), which determines the autocorrelation in a fractal surface. I superimposed the fractal surface on the landscape, and assigned the required proportion of cells (based on habitat amount) with the highest fractal values as habitat; remaining cells were matrix (Figure 2.3). Matrix quality was assigned as the probability of dispersal mortality in matrix cells. I then identified habitat patches (for the disturbance algorithm; see below) as groups of contiguous habitat cells, based on a Moore neighborhood rule.

2.3.2.2 *Populate landscape*

For each simulation run I seeded the landscape with one individual per habitat cell. Each individual was assigned a random value for its initial probability

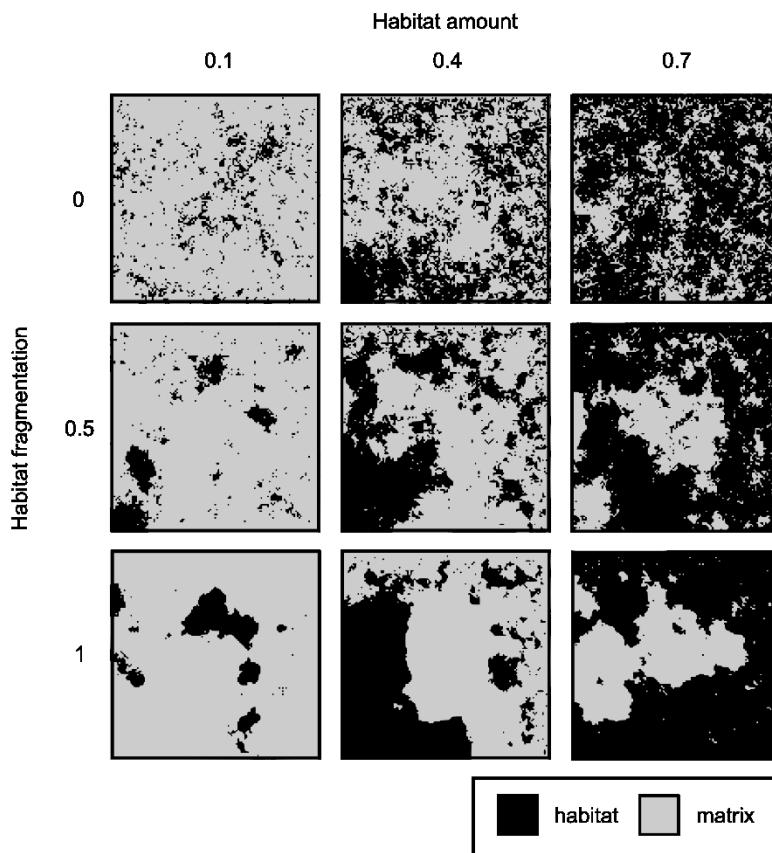


Figure 2.3. Examples of the artificial landscapes created through the midpoint displacement algorithm (Saupe 1988). Habitat amount was the proportion of the landscape in habitat. Habitat fragmentation was determined by the Hurst exponent, which controls the autocorrelation in a fractal surface created by the midpoint displacement algorithm, and sets the level of patchiness for a given habitat amount. I simulated population dynamics and the evolution of the boundary-crossing response in 1000 different landscapes, with habitat amounts ranging from 0.1 to 0.7, and habitat fragmentation ranging from 0 to 1.

of boundary crossing, dispersal probability, path straightness in matrix, and path straightness in habitat.

2.3.2.3 Habitat disturbance

Disturbance caused death of all individuals in a habitat patch. To spread disturbances over time, at the beginning of a run I assigned each patch a number of generations until disturbance. This disturbance interval was randomly drawn from a Poisson distribution, with a mean equal to the disturbance frequency. When a habitat patch reached its disturbance interval it was disturbed, after which a new disturbance interval was selected from the Poisson distribution.

2.3.2.4 Reproduction and genetic transfer

I modelled an asexual, haploid species with non-overlapping generations. The number of offspring produced by each adult in a habitat cell was randomly drawn from a Poisson distribution, where the mean for cell i in generation t was:

$$\mu_{i,t} = \lambda / (1 + a \times N_{i,t}) \quad \text{equation 2.1}$$

where $a = (\lambda - 1)/k$, λ = intrinsic growth rate, k = cell carrying capacity, and $N_{i,t}$ = number of adults in cell i at generation t (Hassell 1975). This density-dependent reproduction introduces within-cell competition.

Offspring inherited the parental genotype for the four mobility-related characteristics, subject to possible mutation of the gene controlling each.

Mutation randomly increased or decreased the value of the characteristic by 0.01.

2.3.2.5 Dispersal

Each juvenile dispersed or not, depending on its genetically-determined dispersal probability. A dispersing individual kept moving until it either found a new habitat cell, or died. Dispersal could be within or between habitat patches and was modelled as a series of movement steps of one cell-length each. The change in direction between consecutive steps was randomly drawn from a wrapped Cauchy distribution with a mean of zero and a concentration parameter (ρ) which varied from 0 (uncorrelated) to 1 (straight line). The ρ was genetically determined for each individual, with different values for habitat and matrix. If a movement step would result in the individual crossing from habitat to matrix, its decision to cross or not depended on its genetically-determined probability of boundary crossing. If the individual decided not to cross, it would either move in a randomly selected direction within the habitat or, if no such option existed, it remained in its current location. If a movement step would take an individual outside the landscape, a new direction was randomly selected that would keep the individual within the landscape. Dispersal mortality was applied after each movement step. If the individual moved between a habitat cell and a matrix cell, the probability of mortality was the average of the two. After each movement

step, if the individual was in a habitat cell with fewer than k individuals, it settled; otherwise it took another movement step.

2.3.3 Testing the hypotheses

I simulated population dynamics and evolution of mobility-related characteristics in 1000 different landscapes. I measured the evolved boundary-crossing behaviour after 1000 generations in two ways: (1) the evolved population mean boundary-crossing trait value and (2) the actual per capita rate of boundary crossing, i.e. the proportion of the population that crossed from habitat to matrix. To evaluate my predictions for the effects of landscape structure on the evolved boundary-crossing response, I related each of these two measures to each landscape attribute: habitat amount, habitat fragmentation, matrix quality, and disturbance frequency. Relationships were modelled by multiple linear regression, using square-root-transformed measures of boundary crossing and standardized landscape attribute values. I included quadratic terms for each predictor, to account for non-linear relationships. I used the percent sum of squares (%SS) from an analysis of variance as a measure of variation explained by each landscape attribute, measured as

$$\%SS = 100 \times SS_p / SS_t \quad \text{equation 2.2}$$

where SS_p = sum of squared variation explained by a given attribute, and SS_t =

total sum of squared variation around the grand mean (Jackson and Fahrig 2012).

To assess how my model compared to previously published simulation models (see Introduction), I also modelled the landscape effects on the remaining three mobility-related characteristics: (a) dispersal probability, (b) path straightness in matrix, and (c) path straightness in habitat after the 1000th generation, as described above.

Statistical models were run in R (R Core Team 2014).

2.4 Results

The simulation results supported my predictions for the effects of landscape structure on the evolved boundary-crossing trait. The mean probability of boundary crossing increased in landscapes with more habitat and less fragmented habitat (Figure 2.4a-b). Species evolved higher probabilities of boundary crossing in landscapes with higher-quality matrix and more frequent habitat disturbance (Figure 2.4c-d). The evolution of boundary crossing was largely driven by matrix quality and habitat disturbance: the %SS for matrix quality was more than three times the %SS for either habitat amount or fragmentation, and the %SS for disturbance frequency was more than six times the %SS for either habitat amount or fragmentation (Table 2.1).

The relationships between the actual per capita rate of boundary crossing and landscape attributes generally mirrored the relationships between the

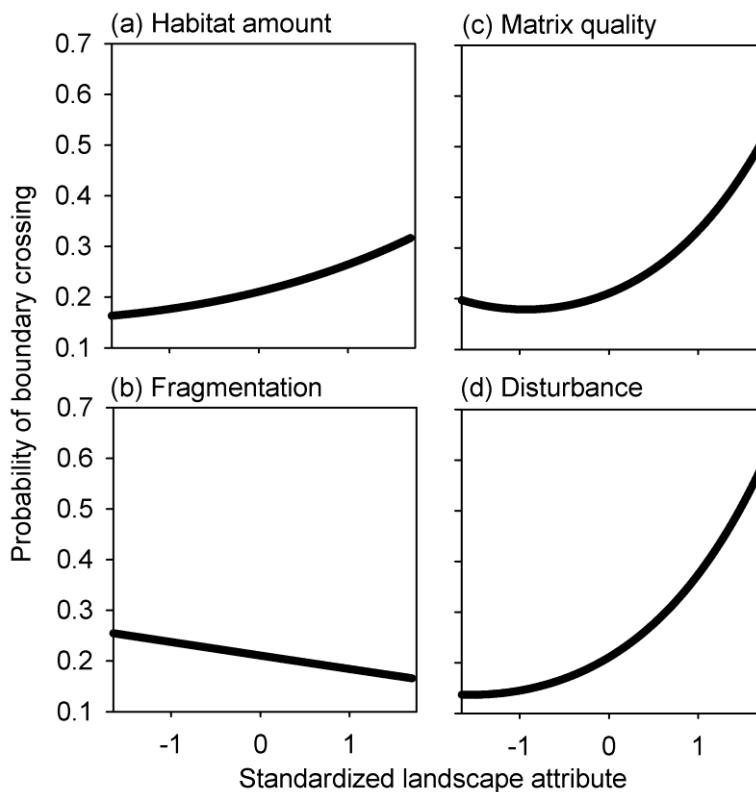


Figure 2.4. Effects of (a) habitat amount, (b) habitat fragmentation, (c) matrix quality, and (d) disturbance frequency on the evolved mean boundary-crossing trait (probability of boundary crossing), when holding all other landscape attributes at their mean values. Standardized landscape attribute values were scaled such that larger values indicate more habitat, more fragmented habitat, higher matrix quality, and more frequent disturbance. Relationships were modelled by multiple linear regression, using square-root-transformed probabilities of boundary crossing (back-transformed prior to plotting), for the 1000 simulation runs.

Table 2.1. Percent sum of squares (%SS), for a multiple linear regression model of the relationship between each of the two measures of the boundary-crossing response (i.e. evolved mean boundary-crossing trait value and the actual per capita rate of boundary crossing, after 1000 generations) and the four landscape attributes. Relationships were modelled using square-root-transformed measures of the boundary-crossing response. I included quadratic terms for each predictor, to account for non-linear relationships. %SS combines the variance explained by both the linear and quadratic terms.

Attribute	Boundary-crossing trait	Rate of boundary crossing
Habitat amount	6.80	0.56
Habitat fragmentation	2.62	10.72
Matrix quality	22.66	21.18
Disturbance frequency	42.03	41.65
Residual	25.89	25.89

evolved boundary-crossing trait and landscape structure discussed above (Figure 2.5). Matrix quality and disturbance frequency explained more of the variation in the rate of boundary crossing after 1000 generations than either habitat amount or fragmentation (Table 2.1), with increasing rates of boundary crossing in landscapes with higher matrix quality and more frequent disturbance. The one exception was that the evolved probability of boundary crossing decreased with habitat fragmentation (Figure 2.4b), while the actual per capita rate of boundary crossing increased with habitat fragmentation (Figure 2.5b).

2.5 Discussion

My simulation results support the hypothesis that boundary-crossing behaviour evolves in response to landscape structure. To my knowledge, this is the first theoretical study to examine the effects of landscape structure on the evolution of behaviour at habitat boundaries. The boundary-crossing response is important for population persistence, because it influences the rates of movement among habitat patches. It may be particularly important in human-altered landscapes, where populations may only persist if individuals can move among habitat remnants within a human-dominated matrix (Brown and Kodric-Brown 1977, Hanski et al. 1995).

Species evolved to cross boundaries more readily in landscapes with more frequent disturbance. More frequent disturbance increases the benefits of dispersal relative to its costs, because boundary crossing allows individuals to escape declining local conditions and access unexploited habitat. While

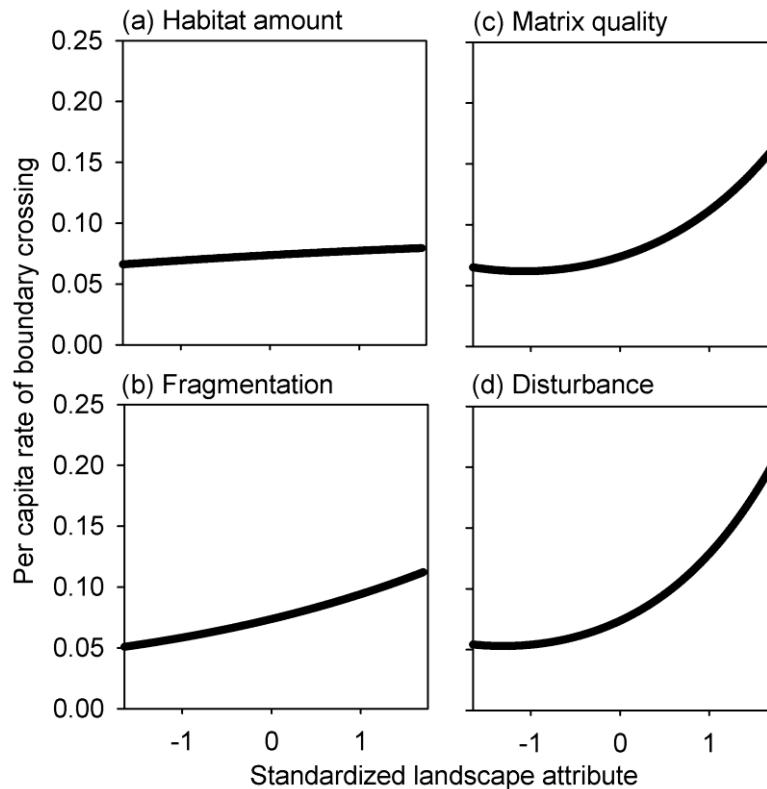


Figure 2.5. Effects of (a) habitat amount, (b) habitat fragmentation, (c) matrix quality, and (d) disturbance frequency on the actual per capita rate of boundary crossing, when holding all other landscape attributes at their mean values.

Standardized landscape attribute values were scaled such that larger values indicate more habitat, more fragmented habitat, higher matrix quality, and more frequent disturbance. Relationships were modelled by multiple linear regression, using square-root-transformed rates of boundary crossing (back-transformed prior to plotting), for the 1000 simulation runs.

previously hypothesized (Fahrig 2007b), the effect of disturbance on evolution of behaviour at boundaries has not, to my knowledge, been studied before.

Species evolved to avoid crossing from habitat to matrix in landscapes with lower-quality matrix, allowing individuals to avoid the higher costs of dispersal in a lower-quality matrix. As with disturbance frequency, the effects of matrix quality on the evolution of behaviour at boundaries have not been explicitly studied before. However, the relationship I found is consistent with studies finding fewer boundary crossings into lower-quality matrix than into higher-quality matrix (Haynes and Cronin 2003, Stevens et al. 2006).

Species evolved higher probabilities of boundary crossing in landscapes with more habitat and less fragmented habitat, as observed in empirical studies (Merckx et al. 2003, Schtickzelle and Baguette 2003). This appears to be because species in landscapes with more habitat and less fragmented habitat encounter matrix less frequently. If interaction with matrix is rare, individuals will rarely experience the costs of dispersal through matrix, resulting in weaker selection for avoidance of boundary crossing. Additionally, there is a higher chance of successful dispersal through the matrix when there is more habitat in the landscape, because habitat patches are less isolated, further reducing the costs of dispersal.

Although landscape structure generally had the same effects on the evolved boundary-crossing trait and the actual per capita rates of boundary crossing, I did find one exception: the evolved probability of boundary crossing decreased with habitat fragmentation, while the per capita rate of boundary-

crossing increased with habitat fragmentation. This is because the actual per capita rate of boundary crossing results from the combined effects of the evolved boundary-crossing trait and the frequency of encounters with boundaries.

Individuals in landscapes with more fragmented habitat encountered habitat boundaries more frequently than individuals in landscapes with less fragmented habitat. This resulted in more actual boundary-crossing events in fragmented landscapes, even though the probability of crossing per boundary interaction was lower.

Surprisingly, my simulations suggest that habitat amount and habitat fragmentation have weaker effects on the evolution of boundary crossing than matrix quality or disturbance frequency. This was surprising because most empirical studies of the relationships between landscape structure and mobility-related characteristics have focused on habitat amount and fragmentation (e.g. Merckx et al. 2003, Schtickzelle and Baguette 2003, Bonte et al. 2006, Ahlroth et al. 2010). Instead, my simulations suggest that boundary-crossing responses are most affected by the costs of dispersal through the matrix, and the benefit of escaping local extinction events. This suggests that we should shift focus to the roles of matrix quality and disturbance, because these have potentially larger effects on the costs and benefits of boundary crossing than either habitat amount or fragmentation. It also suggests we should be cautious in attributing differences in evolved boundary responses between landscapes to habitat amount or fragmentation when these landscape attributes are correlated with either matrix quality or disturbance. For example, differences in the evolved boundary-

crossing behaviour of speckled wood butterflies (*Pararge aegeria*) between a woodland landscape and a high-intensity agricultural landscape may be driven by differences in matrix quality between these two landscapes, rather than differences in the availability of forested areas (Merckx et al. 2003).

2.5.1 Model evaluation

My model extensions, to include behaviour at habitat boundaries, did not contradict previous theoretical findings on the evolution of other mobility-related characteristics. In particular, my predictions for evolution of dispersal probability were consistent with previous studies, predicting higher dispersal probabilities in landscapes with more habitat, less fragmented habitat, higher-quality matrix, and more frequent disturbance (Appendix C; Travis and Dytham 1999, Heino and Hanski 2001, Poethke and Hovestadt 2002, Bonte and De La Peña 2009, Poethke et al. 2011). However, landscape effects on the evolution of the dispersal probability were weaker than expected from previous studies, likely because evolution of boundary crossing behaviour offset the costs of dispersal, reducing the landscape effects on dispersal probability. Also consistent with previous studies, I found selection for straighter dispersal paths in matrix when there was less habitat, less fragmented habitat, and lower-quality matrix (Appendix C; Zollner and Lima 1999, Bartonó et al. 2009, Travis et al. 2012).

2.5.2 Conclusions

Overall, my simulations suggest that landscape structure influences evolution of behaviour at habitat boundaries. In particular, I found strong effects of matrix quality and disturbance frequency on the optimal probability of boundary crossing. To date, the few empirical studies of the evolution of boundary crossing in response to landscape structure have focused on the effects of habitat amount and fragmentation (Merckx et al. 2003, Schtickzelle and Baguette 2003). My simulations suggest that future research should shift focus to the roles of matrix quality and disturbance in the evolution of this mobility-related characteristic.

My results have implications for species risk in human-altered landscapes. Evolved boundary-crossing behaviour may become sub-optimal if the landscape changes faster than the species' evolutionary response to that change (Fahrig 2007b). For example, species with low probabilities of boundary crossing may be particularly prone to extinction from habitat loss, because they are less able to recolonize local extinctions or rescue small populations when habitat is lost. Understanding how matrix quality and habitat disturbance drive evolution of a species' behaviour at boundaries, and how this in turn influences the extinction risk of species in human-altered landscapes, should help us identify species of conservation concern and target them for management.

Chapter 3 – Homogenization of species mobility in a human-altered landscape: mobility increases in sedentary species but decreases in mobile species

3.1 Abstract

How species mobility evolves in response to human landscape change depends on how that alteration changes the costs and benefits of mobility. I propose a novel hypothesis: that a species' prior mobility affects how its mobility evolves in response to human landscape change. There should be larger increases in the costs of mobility for mobile than sedentary species, because mobile species interact with non-habitat more frequently. In contrast, the benefits of mobility should increase more for sedentary species, because sedentary species are at greater risk from inbreeding depression, competition, and predation. Therefore I predict that less mobile species become more mobile in a human-altered landscape, while more mobile species become less mobile. I tested this prediction using the primary wing projection to estimate the prior mobility and rate of change in mobility for 21 North American bird species. I found a strong, negative correlation between these two measurements, as predicted. My result provides the first evidence that human landscape alteration is homogenizing bird communities by driving selection for intermediate mobility across species. It also implies that more mobile species are more at-risk from human landscape change, because the costs of mobility increase more for

mobile than sedentary species. Therefore mobile species should be prioritized for conservation action.

3.2 Introduction

A species' mobility may evolve in response to human alteration of the landscape, due to changes in the cost:benefit ratio of mobility. The main costs of mobility are the risk of mortality in the non-habitat ('matrix') parts of the landscape and energy expenditure during movement, which may in turn reduce reproductive success (Baker and Rao 2004, Johnson et al. 2009). The main benefits of mobility are that it allows individuals to track available resources, escape declining local conditions, and avoid inbreeding, competition, and predation (Bollinger et al. 1993, Tellería and Pérez-Tris 2003, Cronin et al. 2004, Moore et al. 2006). Species mobility should decline when human landscape change increases the costs of mobility more than its benefits, and mobility should increase when landscape change increases the benefits of mobility more than its costs.

A given landscape change may increase both the costs and benefits of mobility. For example, habitat loss increases the costs of mobility, because it increases the distances between habitat patches and decreases habitat patch sizes, leading to more frequent interaction with the matrix (Hill et al. 1996, Baker and Rao 2004, Johnson et al. 2009). Habitat loss also increases the benefits of mobility, because species need to move farther to locate resources when habitat fragments are farther apart, and because risks of inbreeding and competition

increase when habitat patches are smaller and more isolated (Matthysen et al. 1995, Ramsay et al. 1997, Saccheri et al. 1998). This suggests that how species mobility changes in response to habitat loss depends on whether habitat loss increases the costs of mobility more than its benefits.

I hypothesize that a species' prior mobility affects how its mobility changes in response to human landscape change, because its prior mobility determines whether landscape change increases the costs of mobility more than its benefits (Figure 3.1). I expect larger increases in the costs of mobility for mobile than sedentary species when habitat is lost, because mobile species interact with matrix more frequently than sedentary species; if interaction with matrix is rare, individuals will rarely experience the costs of movement through matrix. This is consistent with a previous study, which found that the negative effects of patch isolation increased with species mobility (Öckinger et al. 2009). In contrast, I expect larger increases in the benefits of mobility for sedentary than mobile species. This is because the negative effects of small habitat patches decrease with mobility (Öckinger et al. 2009). Sedentary species are likely more sensitive to declining patch areas than mobile species, because they are at greater risk from inbreeding depression, competition, and predation when patch sizes decline, and cannot supplement their limited local resources by movement among habitat fragments. Thus habitat loss should increase the benefits of mobility more than its costs when mobility is low, driving selection for greater mobility (species A, Figure 3.1). In contrast, habitat loss should drive selection for lower mobility when mobility is high (species B, Figure 3.1). Therefore I predict

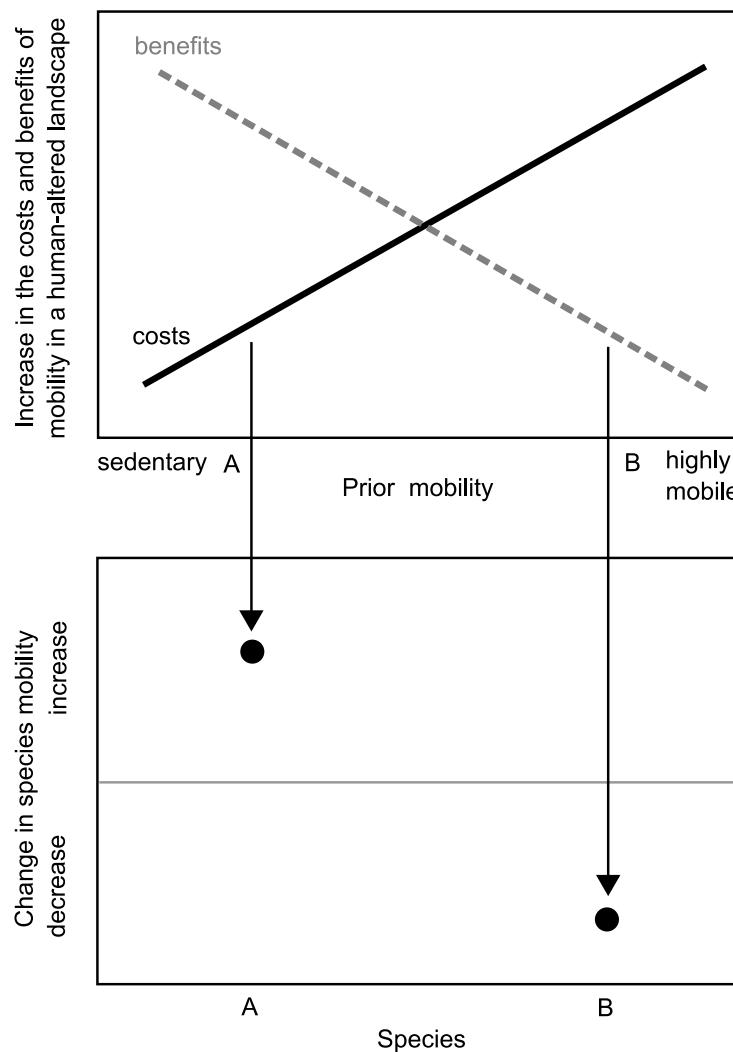


Figure 3.1. Less mobile species become more mobile in a human-altered landscape, while more mobile species become less mobile. For a sedentary species (A), the benefits of mobility increase more than its costs, driving selection for greater mobility. In contrast, for a highly mobile species (B), the costs of mobility increase more than its benefits, driving selection for reduced mobility.

that less mobile species will become more mobile in a human-altered landscape, while more mobile species become less mobile.

I tested this prediction using an existing data set (Desrochers 2010) to estimate the prior mobility and rate of change in mobility for 21 North American bird species.

3.3 Methods

My estimates of prior mobility and rate of change in mobility were derived from data in Desrochers (2010). Desrochers (2010) used the primary wing projection as an index of species mobility. The primary wing projection was measured as

$$100([w - a] / w) \quad \text{equation 3.1}$$

where a = distance from the carpal joint of the wing to the distal end of the outermost secondary feather, and w = distance from the carpal joint of the wing to the wing tip. The primary wing projection is a measure of wing pointedness. More pointed wings are associated with greater mobility (Dawideit et al. 2009), likely because they result in more energy-efficient sustained flight (Bowlin and Wikelski 2008). Previous study suggests wing shape is heritable, and can evolve rapidly within species (Akesson et al. 2007, Tarka et al. 2010, Brown and Brown 2013).

Desrochers (2010) measured the primary wing projection of museum specimens collected between 1900 and 2008, and used these measurements to estimate the primary wing projection of 21 bird species in a baseline year (i.e. 1950), and the rate of change in primary wing projection per 100 years. To obtain the prior estimate of relative mobility for each species, I predicted the primary wing projection in 1900, i.e. the first year of data collection, as

$$b - 0.5c \quad \text{equation 3.2}$$

where b = primary projection in 1950 and c = rate of change in primary projection per 100 years. Note that for *Sitta canadensis* Desrochers (2010) made separate measurements for boreal and temperate populations; I used only the boreal data for this species, because my conclusions did not depend on whether I used the boreal or temperate population.

To test my prediction that less mobile species become more mobile and more mobile species become less mobile in a human-altered landscape, I tested for a negative correlation between the prior primary wing projection and the rate of change in primary projection. To account for non-independence of observations caused by phylogenetic relatedness, I used phylogenetically independent contrasts in my correlation test (Felsenstein 1985). There is uncertainty in the phylogenetic relationships among species. To account for this uncertainty I used a random sample of 5000 possible phylogenetic trees for my species, chosen from the pseudoposterior distribution of trees with a Hackett

backbone (Jetz et al. 2012), and repeated the correlation test 5000 times, each time using a different phylogeny. To determine the support for a relationship between the prior primary projection and the rate of change in primary projection, I calculated the median correlation and p-value from the 5000 analyses.

Data analysis was conducted in R (R Core Team 2014), using the ‘ape’ (Paradis et al. 2004) and ‘picante’ (Kembel et al. 2014) packages.

3.4 Results

The primary wing projections of 11 species increased over time, while the primary wing projections of the remaining 10 species decreased over time. Prior primary projections ranged from 10.15 (for *Ammodramus henslowii*) to 33.24 (for *Dendroica cerulea*).

Less mobile species became more mobile over time, while more mobile species became less mobile, as predicted. I found a strong, negative correlation between the prior primary wing projection and the rate of change in primary projection (Figure 3.2, $r = -0.74$, $p < 0.001$).

3.5 Discussion

My results support the prediction that less mobile bird species have become more mobile, while more mobile species have become less mobile. I infer that habitat loss and the increasing intensity of human land uses over the past century had different effects on mobile and sedentary species, because human landscape change decreased the cost:benefit ratio of mobility for

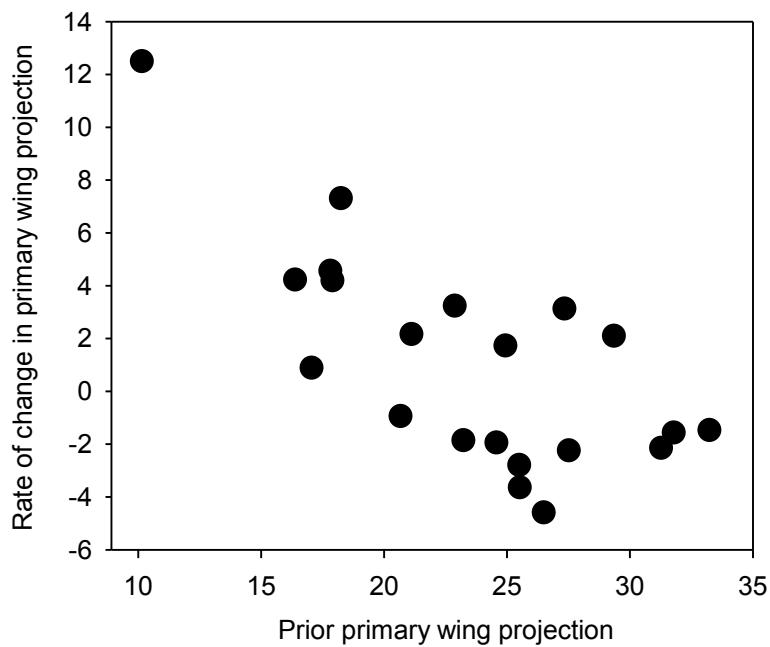


Figure 3.2. Change in the primary wing projection with increasing prior primary projection, for 21 species; each point represents a species. Prior primary wing projection estimates were the primary projections predicted for 1900, as $b - 0.5c$, where b = primary wing projection in 1950 and c = rate of change in primary projection per 100 years, from Desrochers (2010). The primary wing projection was measured as $100([w - a] / w)$, where a = distance from the carpal joint of the wing to the distal end of the outermost secondary feather, and w = distance from the carpal joint of the wing to the wing tip. Note that a higher primary projection indicates higher mobility.

sedentary species (species A, Figure 3.1) and increased the cost:benefit ratio of mobility for mobile species (species B, Figure 3.1). The higher costs of mobility for more mobile species are due to their more frequent interaction with matrix, and the higher benefits of mobility for sedentary species are due to their greater risk from inbreeding depression, competition, and predation. This is the first study to suggest that a species' evolutionary response to human landscape change depends on its prior mobility. Interestingly, Van Houtan et al. (2007) found similar changes in the mobility of tropical birds immediately following habitat loss; i.e. less mobile tropical birds tended to disperse farther following habitat loss, while more mobile birds dispersed shorter distances. Although Van Houtan et al. (2007) measured the immediate response to habitat loss rather than an evolutionary change, their study supports my suggestion that prior mobility influences the species response to a given landscape alteration, such as habitat loss.

Although a species' prior primary wing projection and rate of change in primary projection were estimated from the same data set and statistical model (Desrochers 2010), this did not create the strong, negative, cross-species correlation between these two estimates. If this correlation was a statistical artifact, parameter estimates in the statistical model would have to be biased, such that the actual (population-level) rate of change in primary projection was overestimated when the prior primary projection was small, and the actual rate of change in primary projection was underestimated when the prior primary

projection was large. Simulations confirmed that cross-species correlations were not biased (Appendix D).

Although other things can cause the primary wing projection to change over time, none of these explain the negative relationship between the prior primary projection and its rate of change. For example, habitat loss is expected to drive selection for decreased mobility, and habitat gain to drive selection for increased mobility (Travis and Dytham 1999, Bonte et al. 2006, 2010, Ahlroth et al. 2010). However, this could only cause the observed relationship between the prior projection and its rate of change if the most mobile species were losing habitat and the least mobile species were gaining habitat. This is not likely, because my study species are generally losing habitat, irrespective of mobility: the dominant change in North American land cover in the 20th century was conversion from native land cover classes (e.g. forest, wetland) to human-dominated ones (Hobson et al. 2002, Drummond and Loveland 2010, Sleeter et al. 2013), and my study species avoid intensively developed areas (Appendix E). We also found no support for a cross-species relationship between prior mobility and an index of habitat loss (i.e. the population trend, assuming greater rates of habitat loss are related to greater declines in population abundance; Appendix F).

Another potential explanation for changes in the primary wing projection of a species over time is a shift in the migration behaviour of that species, because migratory individuals tend to have more pointed wings (i.e. higher primary projections) than non-migratory individuals (Marchetti et al. 1995, Lockwood et al.

1998). However, this would only cause the observed relationship between the prior primary projection and its rate of change if migratory species became less migratory, and non-migratory species became more migratory. I can think of no reason why non-migratory species would become more migratory. In fact, studies suggest a warming climate should favor a non-migratory strategy (Rivalan et al. 2007, Pulido and Berthold 2010). There was also no empirical support for a relationship between the rate of change in primary projection and migration status for these species (Appendix G). Therefore my inference that habitat loss and the increasing intensity of human land uses over the past century had different effects on mobile and sedentary species is the most likely explanation for the observed relationship.

An interesting implication of my result is that it suggests there has been a decline over time in the variation in mobility among species. This is supported by a strong, negative correlation between the variance in primary wing projection estimates among species and time ($r = -0.79$, $p = 0.002$; Figure 3.3). One of the known consequences of human land use is that it homogenizes biotic communities, resulting in reduced genetic, taxonomic, or functional diversity (McKinney and Lockwood 1999). Much focus has been on how human-mediated extinction of some species and range expansion of others homogenizes bird communities (Blair and Johnson 2008, Davey et al. 2012). However, human land use can also homogenize communities by driving selection for similar traits across species. For example, previous study suggests that habitat specialization of bird species is declining over time, homogenizing species habitat preferences

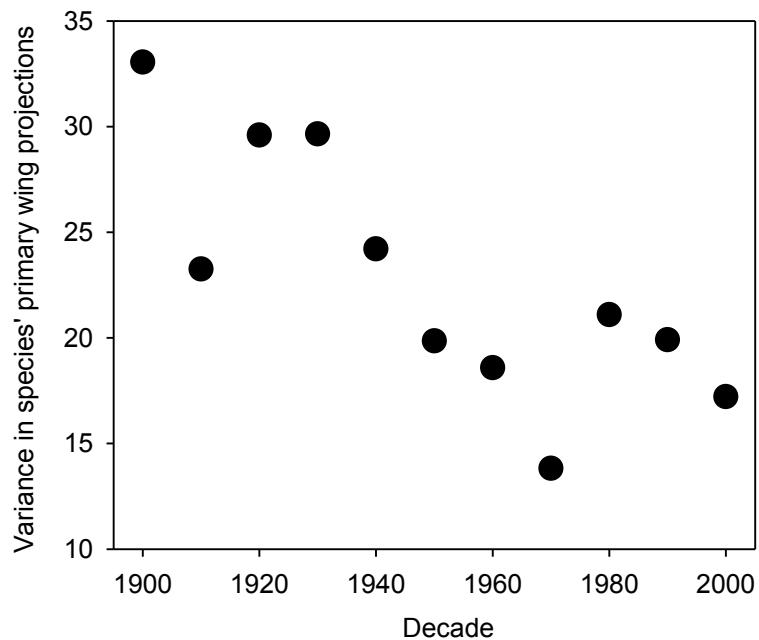


Figure 3.3. Variability in the primary wing projection among species declines over time. Variability in the primary wing projection was estimated as the variance in species' mean primary projections in each decade. The mean primary projection for each species in each decade was calculated from all individuals sampled in that decade. The primary wing projection was measured as $100([w - a] / w)$, where a = distance from the carpal joint of the wing to the distal end of the outermost secondary feather, and w = distance from the carpal joint of the wing to the wing tip.

(Barnagaud et al. 2011). My study is the first to suggest a similar trend in species mobility, with human land use driving selection of intermediate mobility across species.

My inference that habitat loss and land use intensification increase the costs of mobility more for mobile than sedentary species also has implications for species conservation, because it implies that mobility influences the relative risks of human landscape change to species (Figure 3.1). When the rate of human landscape change is faster than the species' evolutionary response to that change, larger increases in the costs of mobility for mobile species should put them at greater risk than more sedentary species. This indirectly supports theoretical and empirical findings that extinction risk increases with species mobility in human-altered landscapes (Gibbs 1998, Casagrandi and Gatto 1999, Fahrig 2001, Shahabuddin and Ponte 2005). Thus the most mobile species should be prioritized for conservation action.

Chapter 4 – Reconciling contradictory relationships between mobility and extinction risk in human-altered landscapes

4.1 Abstract

Some empirical and theoretical studies suggest that more mobile species are less at-risk in human-altered landscapes, while others suggest they are more at-risk. I propose two novel hypotheses to explain these contradictory findings: (1) extinction risk increases with increasing mobility when mobility is measured as emigration, but decreases with increasing mobility when mobility is measured as immigration; and (2) the most mobile species in unaltered landscapes are least mobile in human-altered landscapes, so the relationship between mobility and extinction risk is opposite when mobility is measured in unaltered and human-altered landscapes. I also test a third hypothesis that had been previously theorized, but never tested: that some landscape structures drive evolution of mobility-related characteristics that increase both mobility and risk, while others drive evolution of characteristics that increase mobility and decrease risk. To test these three hypotheses, I created an individual-based, spatially explicit simulation model to simulate population dynamics, evolution of mobility-related characteristics, and the population response to habitat loss. My simulations supported the first and third hypotheses. Extinction risk increased with emigration rate but decreased with immigration rate. Species in landscapes with historically more abundant, less fragmented habitat and more frequent disturbance had increased extinction risk and mobility during habitat loss, while species in

landscapes with lower non-habitat (i.e. matrix) quality had increased extinction risk and decreased mobility. This is the first study to investigate why some studies find that more mobile species are less at-risk in human-altered landscapes, while others find the opposite. My results suggest that these contradictory relationships occur because of differences in how mobility is measured in these studies, or differences in the historic structure of species' landscapes. Understanding how mobility and the landscape structure influence the extinction risk of species in human-altered landscapes can help us identify species of conservation concern and target them for management. My results suggest that we should focus on species with high emigration rates but low immigration rates, and those that evolved in landscapes with non-fragmented habitat and high-risk matrix.

4.2 Introduction

If we could predict which species are most at-risk in human-altered landscapes, we would be able to focus limited resources for conservation on these species. Empirical studies suggest that large-bodied, specialist species with low fecundity and limited geographic ranges are most at-risk of extinction in human-altered landscapes (Vance et al. 2003, Sekercioğlu et al. 2004, Cardillo et al. 2005, Kotiaho et al. 2005, Jiguet et al. 2007, Davidson et al. 2009, Fritz et al. 2009). In addition, several studies suggest that extinction risk is related to species mobility, but these studies report both greater extinction risk (Gibbs 1998, Shahabuddin and Ponte 2005, Van Houtan et al. 2007) and lower

extinction risk (Jones et al. 2003, Kotiaho et al. 2005, Reinhardt et al. 2005, Sekercioğlu 2007, Jiguet et al. 2007, Mattila et al. 2008, Pöyry et al. 2009, Öckinger et al. 2010, Garrard et al. 2012) for more mobile species. The purpose of this study was to evaluate three hypotheses, described below, that might explain these contradictory findings: (a) the metric type hypothesis, (b) the historic landscape hypothesis, and (c) the metric context hypothesis.

4.2.1 *Metric type hypothesis*

There is little consensus on how to measure mobility. Metrics include direct measurements of emigration rate, dispersal distance, and immigration rate (Van Houtan et al. 2007, Jiguet et al. 2007, Öckinger et al. 2009), and indirect measures such as expert opinion, wing shape, and wing size (Kotiaho et al. 2005, Reinhardt et al. 2005, Shahabuddin and Ponte 2005). I hypothesize that whether a mobile species is more or less vulnerable to human landscape change than a sedentary species depends on whether the measure of mobility is essentially related to emigration or immigration (Figure 4.1). This hypothesis predicts that mobility increases extinction risk when mobility is measured as emigration, and mobility decreases extinction risk when mobility is measured as immigration. This is because the emigration rate reflects the impact of dispersal mortality on population persistence, while the immigration rate reflects the population's ability to recolonize local extinctions and rescue small populations (Brown and Kodric-Brown 1977, Hanski 1998, Fahrig 2001).

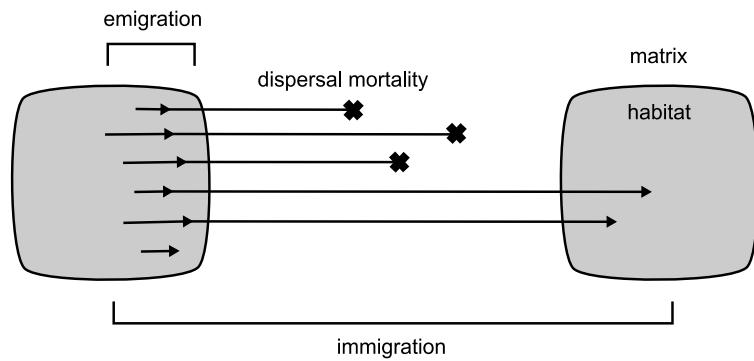


Figure 4.1. Depiction of emigration, i.e. exit from the current home range or territory, and immigration, i.e. when the individual leaves its current home range or territory and settles in a different habitat patch. Emigration does not equal immigration, because emigrants can settle in a new location within their home habitat patch, or die during dispersal.

4.2.2 *Historic landscape hypothesis*

The historic landscape hypothesis argues that a species' mobility-related characteristics depend on the landscape in which it evolved, i.e. its 'historic' landscape (Fahrig 2007b). Extinction risk in human-altered landscapes will then depend on these evolved mobility-related characteristics. Differences in the mobility-extinction risk relationship will arise if some historic landscape attributes drive evolution of mobility-related characteristics that increase both mobility and extinction risk in human-altered landscapes, while others drive evolution of characteristics that increase mobility and decrease extinction risk in human-altered landscapes.

4.2.3 *Metric context hypothesis*

The metric context hypothesis proposes that the relationship between mobility and extinction risk in human-altered landscapes depends on whether the measure of mobility was taken in a human-altered landscape or in an unaltered landscape that resembles the species' historic landscape. Altering the landscape, e.g. through habitat loss, changes the mobility of a species. Species that were more mobile in their historic landscapes will be particularly vulnerable to dispersal mortality in the altered landscape, causing the mobility of these species to be reduced (Van Houtan et al. 2007, Chapter 3). If this effect is large, the most mobile species before landscape change might become the least mobile species after landscape change. This would mean that the relationship between mobility and extinction risk would be opposite if mobility is measured in an unaltered

landscape versus if mobility is measured in a human-altered landscape. In particular, extinction risk would (1) increase with emigration rate when emigration rate is measured in human-altered landscapes (see Metric type hypothesis, above), but decrease with emigration rate when measured in unaltered landscapes, and (2) decrease with immigration rate when immigration rate is measured in human-altered landscapes, but increase with immigration rate when measured in unaltered landscapes.

4.3 Methods

To address my three hypotheses, proposed to explain the contradictory findings on the role of mobility in extinction risk, I created an individual-based, spatially explicit simulation model in NetLogo (Wilensky 1999). I simulated population dynamics and evolution of mobility-related characteristics in different historic landscape types, varying in habitat amount, habitat fragmentation, matrix (i.e. non-habitat) quality, and disturbance frequency. I then subjected each landscape (and its population with optimal, evolved mobility-related characteristics) to habitat loss. For the metric type hypothesis, I measured mobility during habitat loss as both emigration and immigration, and related extinction risk to mobility measured in both ways. For the landscape type hypothesis, I compared the mobility-extinction risk relationships for different historic landscape types. For the metric context hypothesis I again related extinction risk to mobility measured as emigration and immigration, but this time I

took measurements in landscapes both before habitat loss began and during habitat loss.

4.3.1 Simulated evolution of mobility-related characteristics in historic landscapes

I simulated population dynamics and evolution of mobility-related characteristics in artificial landscapes over 1000 generations. Four characteristics were modelled as independent, heritable traits: (1) dispersal probability, i.e. the probability that an individual leaves its current habitat location, (2) path straightness in matrix, (3) path straightness in habitat, and (4) probability of boundary crossing, i.e. the probability of crossing from habitat to matrix when a dispersing individual encountered a habitat-matrix boundary. See Figure 4.2a and Appendix H for flow charts and summary of model parameters.

Each simulation started with creation of an artificial, historic landscape and an initial population. Each historic landscape was defined by its habitat amount, habitat fragmentation, matrix quality, and disturbance frequency. The landscape was a square 127×127 (16,129) grid of habitat and matrix cells. The differences between habitat and matrix were that reproduction could only occur in habitat cells, and dispersal mortality was lower in habitat than matrix. I used a fractal surface, generated through midpoint displacement (Saupe 1988), to assign cells as habitat or matrix (Figure 4.3). I did this by superimposing the fractal surface on the landscape, and assigning the required proportion of cells (as defined by the habitat amount parameter) with the highest fractal values as habitat. All

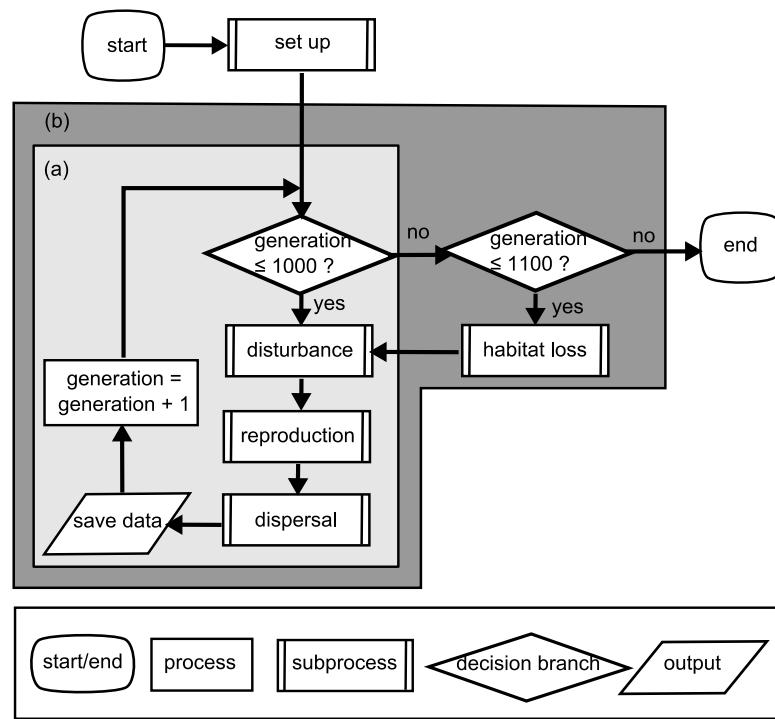


Figure 4.2. The sequence of events for the simulation model, simulating (a) evolution of mobility-related characteristics in historic landscapes, and (b) extinction risk in response to habitat loss. See Appendix H for flow charts for each of the five subprocesses.

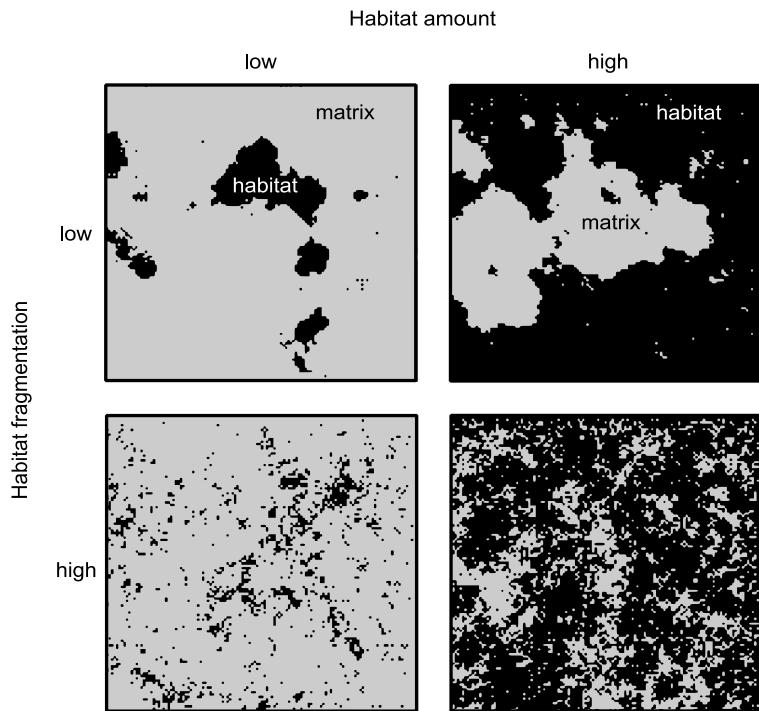


Figure 4.3. Examples of the simulated historic landscapes, varying in habitat amount, i.e. the proportion of the landscape in habitat, and habitat fragmentation, i.e. how clumped or distributed habitat is, for a given habitat amount. Cells in a 127×127 grid landscape were assigned as either habitat or matrix (i.e. non-habitat), based on values of a fractal surface, generated through midpoint displacement (Saupe 1988). The fractal surface was superimposed on the landscape, and the proportion of cells with the highest fractal values were assigned as habitat (i.e. the habitat amount). All remaining cells were matrix. Habitat fragmentation was controlled by the Hurst exponent (H) for the fractal surface, where lower H result in more fragmented habitat.

remaining cells were matrix. Habitat fragmentation was controlled by the Hurst exponent (H), where H determines the autocorrelation in the fractal surface. Matrix quality was assigned as the probability of mortality in matrix cells. I then identified habitat patches as groups of contiguous habitat cells, based on a Moore neighborhood rule, and assigned each patch a disturbance interval, i.e. number of generations until disturbance. Each disturbance interval was randomly drawn from a Poisson distribution, with a mean equal to the disturbance frequency. For each simulation run I seeded the landscape with one individual per habitat cell. Each individual was assigned a random value for each of its four genetically-determined mobility-related characteristics.

Each generation involved (1) habitat disturbance, (2) reproduction, including transfer and mutation of dispersal genotypes, and (3) dispersal, i.e. movement of individuals from their birth place, resulting in either dispersal mortality or settlement in a new location.

Disturbance caused death of all individuals in a habitat patch. When a habitat patch reached its disturbance interval it was disturbed, after which a new disturbance interval was selected from the Poisson distribution.

After disturbance, adults in habitat reproduced, assuming an asexual, haploid species. The number of offspring produced by each adult was randomly drawn from a Poisson distribution, where the mean for cell i in generation t was:

$$\mu_{i,t} = \lambda / (1 + a \times N_{i,t}) \quad \text{equation 4.1}$$

where $a = (\lambda - 1)/k$, λ = intrinsic growth rate, k = cell carrying capacity, and $N_{i,t}$ = number of adults in cell i at generation t (Hassell 1975). Offspring inherited the parental genotype for the four mobility-related characteristics. Genes could mutate during reproduction. A mutation randomly increased or decreased the value of the mobility-related characteristic by 0.01. All adults died after reproducing.

Each juvenile dispersed or not, depending on its genetically-determined dispersal probability. A dispersing individual kept moving until it either settled in a new habitat cell, or died. Dispersal could be within or between habitat patches, but was limited to movements within the bounds of the landscape. Dispersal was modelled as a series of movement steps of one cell-length each. The change in direction between consecutive steps was randomly drawn from a wrapped Cauchy distribution with a mean of zero and a concentration parameter (ρ), where ρ was genetically determined for each individual, with different values for habitat and matrix. If a movement step would cause the individual to cross from habitat to matrix, whether it actually crossed or not depended on its genetically-determined boundary-crossing response. If the individual decided not to cross, it would move in a randomly selected direction within habitat or, if no such option existed, it remained in its current location. Dispersal mortality was applied after each movement step. If the individual moved between a habitat cell and a matrix cell, the probability of mortality was the average of the probabilities in habitat and matrix. After each movement step, if the individual landed in a habitat cell with fewer than k individuals it settled there; otherwise it took another movement step.

This initial simulation phase lasted for 1000 generations. At the end of the initial phase, the population's mobility-related characteristics had evolved to the optimal levels for the given historic landscape type.

4.3.2 Simulated extinction risk in response to habitat loss

Following the initial simulation phase, I subjected each landscape, and its population with optimally evolved mobility-related characteristics, to habitat loss for 100 generations, or until the population went extinct (Figure 4.2b). Habitat disturbance, reproduction, and dispersal were simulated as described above. In each generation prior to reproduction, a proportion of the remaining habitat cells were converted to matrix. This habitat loss was simulated as encroachment of matrix into habitat; cells converted from habitat to matrix were on the edges of habitat patches, i.e. they had at least one neighbouring matrix cell.

4.3.3 Testing the hypotheses

I simulated population dynamics, evolution of mobility-related characteristics, and population response to habitat loss in 1000 different historic landscapes. For each simulation I measured mobility in the historic landscape and in the human-altered landscape, measuring mobility as the (1) emigration rate, i.e. proportion of the population that left their initial habitat cell and did not return, per generation, and (2) immigration rate, i.e. proportion of the population that settled in a different habitat patch, per generation. To measure mobility in the historic landscape I averaged each of the two mobility metrics over the final 50

generations before habitat loss. To measure mobility in the human-altered landscape, I averaged each of the two mobility metrics over the 100 generations during habitat loss, or over all generations until the population went extinct.

I repeated simulations with slow, moderate, and fast rates of habitat loss, selected based on the percentage of populations that went extinct within 100 generations in preliminary simulation runs. For slow loss, 0.03 of habitat was lost per generation, and 15.6% of populations went extinct. For moderate loss, 0.05 of habitat was lost per generation, and 56.8% of populations went extinct. For fast loss, 0.07 of habitat was lost per generation, and 90.4% of populations went extinct. I evaluated the hypotheses for each rate of habitat loss.

To test the metric type hypothesis, I compared the relationship between the extinction risk (i.e. probability of extinction during habitat loss) and emigration rate to the relationship between extinction risk and immigration rate. The hypothesis would be supported if the former relationship was positive and the latter was negative.

For the landscape type hypothesis I compared the relationship between extinction risk and a landscape attribute to the relationship between mobility and the landscape attribute, repeated for each of the four attributes of the historic landscapes (habitat amount, habitat fragmentation, matrix quality, and disturbance frequency), using each of the two mobility metrics. The hypothesis would be supported if some historic landscape attributes increased both risk and mobility, while other historic landscape attributes increased risk and decreased mobility in the altered landscape.

For the metric context hypothesis, I compared the mobility-extinction risk relationships for emigration and immigration rates measured in the historic landscapes, i.e. during the 50 generations before habitat loss began, to the mobility-extinction risk relationships for emigration and immigration rates measured during habitat loss. The hypothesis would be supported if (1) extinction risk increased with emigration rate when emigration rate was measured during habitat loss, but decreased with emigration rate when measured before habitat loss, and (2) extinction risk decreased with immigration rate when immigration rate was measured during habitat loss, but increased with immigration rate when measured before habitat loss.

4.4 Results

Extinction risk increased with emigration rate, but decreased with immigration rate, supporting my metric type hypothesis (Figure 4.4a). The direction of the relationship between the extinction risk and mobility was consistent for all rates of habitat loss, but the strength of the relationship changed. The emigration rate-extinction risk relationship was stronger with faster habitat loss, while the immigration rate-extinction risk relationship was weaker with faster habitat loss (Figure 4.4a).

Some historic landscape attributes increased both extinction risk and mobility in the human-altered landscapes, while others increased risk but decreased mobility, supporting my landscape context hypothesis (Figure 4.5). Specifically, I found higher probabilities of extinction and higher emigration rates

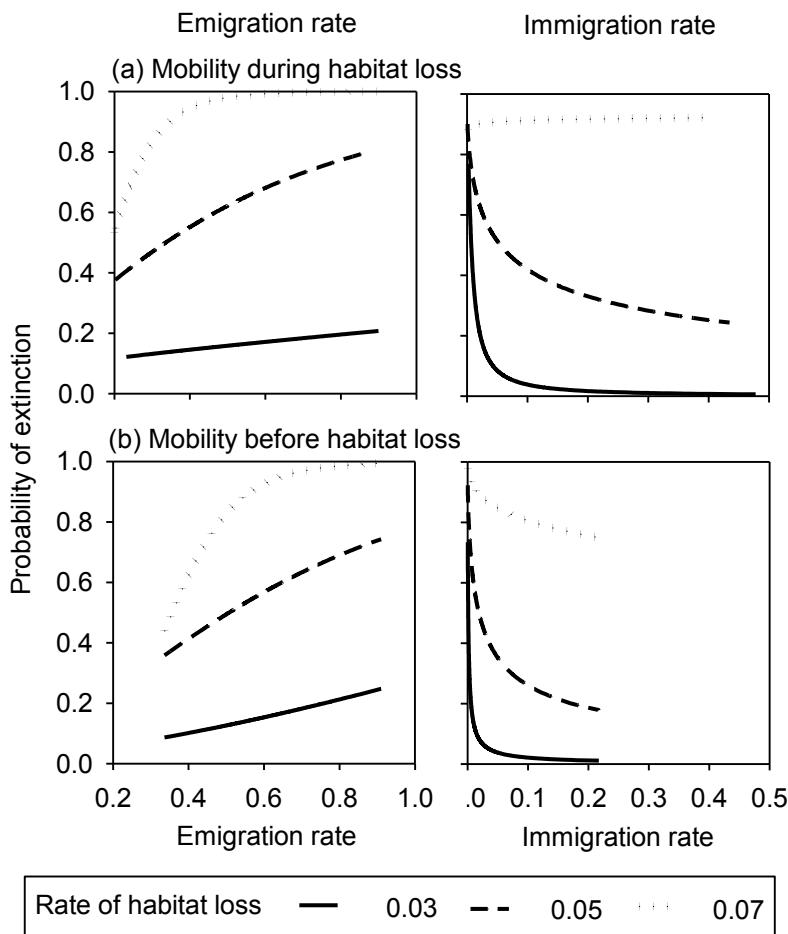


Figure 4.4. Relationships between the probability of extinction within 100 generations and species mobility, when mobility was measured (a) during habitat loss and (b) before habitat loss. Mobility was measured as the emigration rate (left column) and immigration rate (right column). Relationships were modelled by logistic regression in R (R Core Team 2014), using square-root-transformed emigration rates and ln-transformed immigration rates (back-transformed prior to plotting), for the 1000 simulated populations at each of three rates of habitat loss: 0.03, 0.05, and 0.07 of habitat lost per generation.

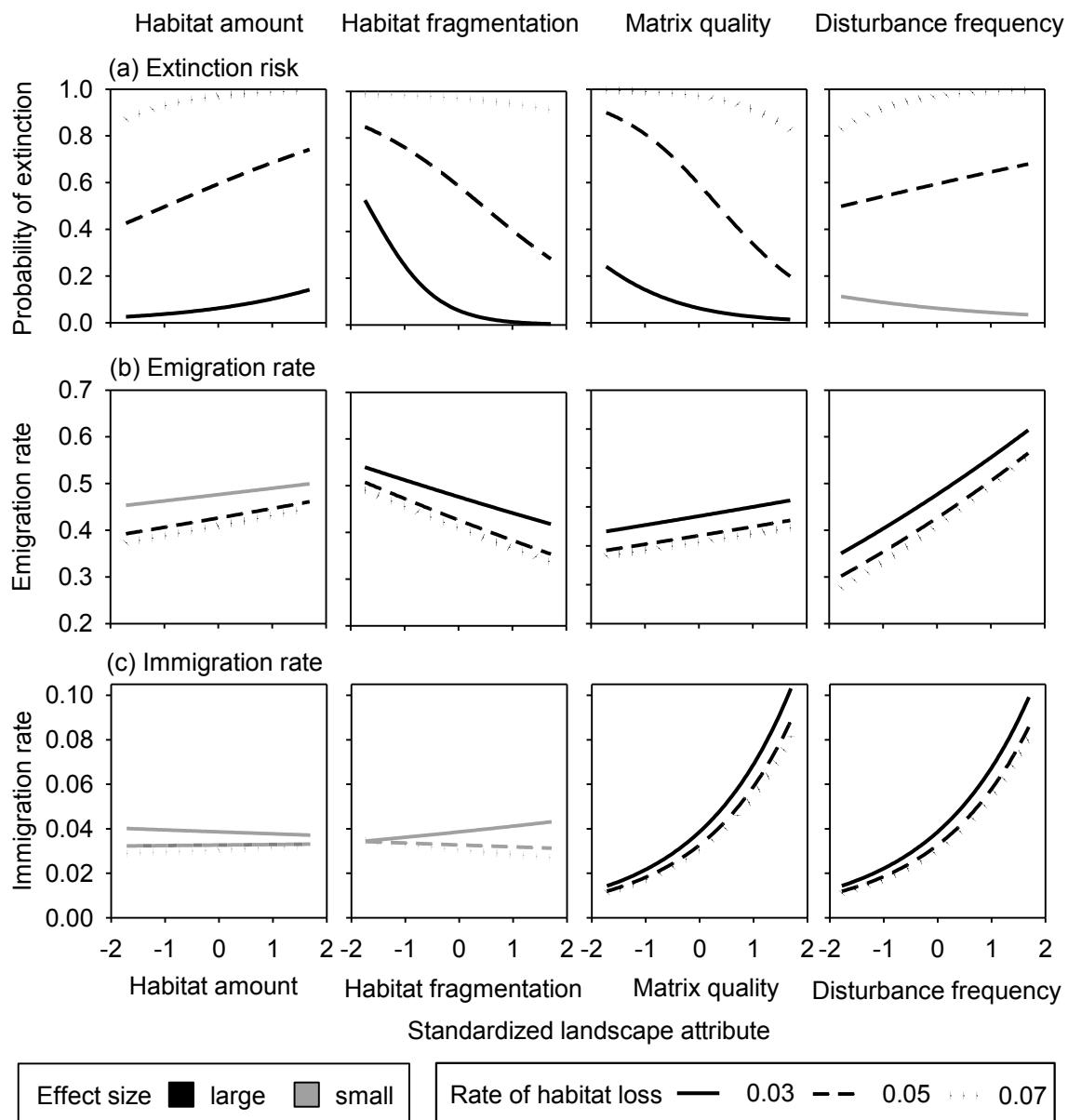


Figure 4.5. Relationships between the (a) probability of extinction during 100 generations of habitat loss, (b) emigration rate, and (c) immigration rate, and each of four historic landscape attributes, when holding all other landscape attributes at their mean values. Standardized landscape attribute values were scaled such that larger values indicate more habitat, more fragmented habitat, (continued on the following page)

higher matrix quality, and more frequent disturbance. Relationships between the probability of extinction and the standardized landscape attributes were modelled by multiple logistic regression in R (R Core Team 2014). Relationships between each measure of mobility and the standardized landscape attributes were modelled by multiple linear regression, using square-root-transformed emigration rates and ln-transformed immigration rates (back-transformed prior to plotting). These analyses were repeated three times, using the 1000 simulated populations at each of three rates of habitat loss: 0.03, 0.05, and 0.07 of habitat lost per generation. To simplify, I focus on relationships with moderate to large effects, i.e. those where the estimated probability of extinction changed by more than 0.1 across the range of modelled landscape attribute values, or where the estimated mobility changed by more than 0.05 across the range of modelled landscape values.

for species with historically more abundant and less fragmented habitat. Disturbance frequency also drove a positive mobility-extinction risk relationship, with higher extinction risk, and higher emigration and immigration rates, for species in landscapes with more frequent habitat disturbance. In contrast, the historic matrix quality drove a negative mobility-extinction risk relationship, with higher extinction risk but lower emigration and immigration rates for species in landscapes with historically lower matrix quality.

I found no support for my metric context hypothesis. The direction of the relationship between the extinction risk and a given measure of species mobility was the same when mobility was measured prior to habitat loss (Figure 4.4b) as when mobility was measured during habitat loss (Figure 4.4a).

4.5 Discussion

4.5.1 *Metric type hypothesis*

My simulations support the metric type hypothesis, suggesting that extinction risk in human-altered landscapes increases with increasing mobility when mobility is measured as emigration, but decreases with increasing mobility when mobility is measured as immigration. Emigration puts populations at risk because dispersers are more likely to die in a human-altered landscape than sedentary individuals, thus higher emigration results in higher mortality rates. However, successful movement among habitat patches (immigration) allows rescue of small populations and recolonization after local extinction, reducing extinction risk. Therefore species that emigrate frequently, but rarely move

successfully between habitat patches may be most at-risk in human-altered landscapes.

Other theoretical studies also showed greater risk for more mobile species when mobility was measured as emigration (Casagrandi and Gatto 1999, Heino and Hanski 2001, Fahrig 2001), and less risk for more mobile species either when mobility was measured as immigration or when there was no dispersal mortality (Hill et al. 2002, Grimm et al. 2004, Reed 2004). However, comparisons to empirical studies are limited, because few studies directly measured dispersal. One empirical study of French birds supported my findings: species with longer dispersal distances and, presumably, more movement among habitat patches, were at less risk in human-altered landscapes (Jiguet et al. 2007). A study on tropical birds found species with higher immigration rates were at greater extinction risk (Van Houtan et al. 2007), in contrast to my model predictions. However, in that study mobility was confounded with foraging strategy, i.e. more mobile species were more likely to be group foragers than less mobile species (Van Houtan et al. 2006, 2007). Group foragers may be at greater risk than solitary foragers, because of their larger area requirements or feeding behaviour (e.g. ant-following), and thus these species may have been more at-risk because of their foraging strategy (Van Houtan et al. 2006).

Unexpectedly, I found that the emigration-extinction risk relationship was stronger, and the immigration-extinction risk relationship weaker, with faster habitat loss. I suggest this is because (a) emigration increases local extinction while immigration determines recolonization (see Appendix I), and (b) the rate of

local extinction is more important than the recolonization rate when habitat loss is very rapid. Under most circumstances recolonization events are critical for population persistence (Fahrig and Merriam 1994); however, when recolonization is rare the local extinction rate drives extinction risk, because following local extinction that habitat is essentially lost to the population. Recolonizations become rarer with faster habitat loss because, in any given generation, there are fewer dispersers, fewer and smaller habitat patches, and larger distances among patches than in a landscape with slower habitat loss (Fahrig 2007a).

4.5.2 *Landscape context hypothesis*

My results support the hypothesis that the relationship between mobility and extinction risk in human-altered landscapes depends on the historic landscape structure in which the species' mobility-related characteristics evolved (Fahrig 2007b). Species in landscapes with historically more abundant habitat, less fragmented habitat, and more frequent disturbance had increased extinction risk and mobility in human-altered landscapes, while species in landscapes with lower matrix quality had increased extinction risk and decreased mobility in human-altered landscapes.

Species whose historic landscapes had more abundant, less fragmented habitat were at greater extinction risk in human-altered landscapes than species from landscapes with rarer, more fragmented habitat. Quantitative data on species' landscape structure prior to human alteration is rare, making comparisons to empirical study difficult. However, my simulations are consistent

with the observed greater sensitivity of tropical species to forest loss and fragmentation relative to temperate species (Bregman et al. 2014). Temperate forest species should be better able to disperse in a human-altered landscape than tropical forest species, because tropical species evolved in forests that were historically larger and less fragmented than temperate forests (Baldi 1996). My results may also help explain why habitat fragmentation frequently has positive effects on species occurrence and abundance (Fahrig 2003). Positive fragmentation effects may reflect my finding that species with historically more fragmented habitat were better adapted to dispersal in the human-altered landscape than species with historically less fragmented habitat. However, this assumes that landscapes with historically more fragmented habitat also tend to have more fragmented habitat after human landscape alteration (relative to landscapes with historically less fragmented habitat).

Species whose historic landscapes were more frequently disturbed were more at-risk from habitat loss than species from less frequently disturbed landscapes. This was somewhat unexpected, because disturbance-tolerant species are typically thought to be more resilient to human landscape change. However, these species are generally considered disturbance-tolerant because they are able to colonize human-dominated areas of the landscape (Davis et al. 2007), and are thus likely experiencing habitat gains rather than habitat losses. Previous simulations also suggest extinction risk increases with more frequent disturbance (Boughton and Malvadkar 2002). The costs of higher emigration rates for species from landscapes with historically frequent disturbance are likely

greater than the benefits of higher immigration for these same species when habitat loss is fast (as discussed in the previous section), thus increasing their risk relative to the less mobile species from landscapes with infrequent disturbance. Additionally, more frequent disturbance may increase species extinction risk from habitat loss because species in landscapes with more frequent disturbance require more habitat than species in landscapes with less frequent disturbance. This is because more frequent disturbance causes a larger proportion of the remaining habitat to become temporarily unavailable to species, exacerbating the effects of habitat loss on extinction risk.

Species that evolved in landscapes with lower matrix quality had mobility-related characteristics that increased risk and decreased mobility in human-altered landscapes. Historic matrix quality had stronger effects on immigration rates in the human-altered landscape than on emigration rates, with greater increases in immigration than emigration with increasing matrix quality. Thus more mobile species from landscapes with higher-quality matrix were at less risk in human-altered landscapes, because their mobility-related characteristics allowed them to maintain high immigration rates during habitat loss. This is consistent with empirical observations of greater rates of inter-patch movement and longer dispersal distances in landscapes with higher-quality matrix (Haynes and Cronin 2003, Schooley and Wiens 2004).

4.5.3 *Metric context hypothesis*

My results did not support the hypothesis that the relationship between

mobility and extinction risk in human-altered landscapes depends on whether the measure of mobility was taken in a human-altered landscape or in an unaltered landscape that resembles the species' historic landscape. The direction of the relationship between extinction risk and species mobility was the same whether mobility was measured prior to habitat loss or during habitat loss. This is in agreement with empirical evidence, which suggests that changes in mobility in response to habitat loss may not be extreme enough to cause the previously most mobile species to become least mobile (Van Houtan et al. 2007). Therefore I conclude that the metric context does not explain the contradictory findings on the role of mobility in extinction risk.

4.5.4 Conclusions

My simulations reconcile contradictory findings on the mobility-extinction risk relationship in human-altered landscapes. First, my simulations suggest that the relationship between mobility and extinction risk depends on how you measure mobility. If mobility is measured as emigration, extinction risk increases with increasing mobility, but if mobility is measured as immigration, extinction risk increases with decreasing mobility. My simulations also suggest that the relationship between mobility and extinction risk depends on the rate of habitat loss, because the emigration-extinction risk relationship was stronger, and the immigration-extinction risk relationship weaker, with faster habitat loss. Finally, the relationship between mobility and extinction risk in human-altered landscapes depends on the species' historic landscape, because some historic landscape

structures drive evolution of mobility-related characteristics that increase both mobility and extinction risk in human-altered landscapes, while others drive evolution of characteristics that increase mobility and decrease risk.

In addition, my simulations have implications for conservation and management in human-altered landscapes. First, they suggest that species with frequent emigration but infrequent movement between habitat patches (i.e. immigration) will be most at-risk, because of the combined effects of higher mortality and lower recolonization rates. My simulations also suggest that mobile species should generally be at greater risk than sedentary species in landscapes with rapid habitat loss, because the costs of emigration are greater than the benefits of immigration when habitat loss is rapid. Finally, my results suggest that consideration of the species' historic landscape structure can help identify species most at-risk in human-altered landscapes, i.e. species that evolved in landscapes with abundant, un-fragmented, dynamic habitat, and low-quality matrix. If the model predictions are valid, conservation efforts should focus on these species.

Chapter 5 – Estimating dispersal distance using time-lagged synchrony in species abundance

5.1 Abstract

Dispersal is important for species persistence in human-altered landscapes. However, reliable estimates of dispersal are relatively rare, likely because of the difficulties inherent to studying dispersal. In this study I tested a method proposed to indirectly estimate dispersal distances using time-series of abundance estimates, which assumes that dispersal between two locations can result in positive, one-year-lagged correlations in population abundances between those locations. I tested how well this population synchrony dispersal index (PSDI) estimates dispersal distances for United Kingdom birds by comparing my estimates to those from independent mark-recapture data. I found a strong, positive correlation between PSDI and dispersal distance estimates from the mark-recapture study, although PSDI estimates tended to be larger. My study suggests that PSDI are meaningful and can be used to infer relative dispersal distances between species. This also has implications for our understanding of population synchrony, supporting the idea that dispersal can cause a one year lag in population synchronization. Additionally, both PSDI and mark-recapture estimates suggest that United Kingdom bird species disperse long distances; over half of my species were estimated to typically disperse at least 25 km. This suggests that dispersal limitation may be less important for

species risk from habitat loss or climate change than habitat availability for most United Kingdom bird species.

5.2 Introduction

Dispersal, i.e. the movement of an individual away from its current home range or territory, is important for species persistence in human-altered landscapes. The risk of mortality during dispersal may exacerbate population declines caused directly by human landscape change (Gibbs 1998, Shahabuddin and Ponte 2005). Alternatively, dispersal may decrease risk by allowing greater rates of recolonization after local extinction, rescue of small populations, and shifts in distribution in response to climate change (Kotiaho et al. 2005, Barbet-Massin et al. 2012). Greater dispersal may also increase invasion rates of pest species (Phillips et al. 2006).

Reliable estimates of dispersal are relatively rare, likely because of the difficulties inherent to studying dispersal. Collection of individual movement data by methods such as mark-recapture sampling, radio-telemetry, or GPS telemetry is costly. These methods often require many field researchers or expensive technology. Large study areas are required, to ensure that long distance dispersal events are captured (Schneider 2003). Large sample sizes may be needed to observe relatively few dispersal events, particularly in species with low dispersal probabilities. Large sample sizes are also needed because of high inter-individual variability in dispersal probabilities and dispersal distances (Stevens et al. 2010). Genetic techniques for estimating dispersal are also costly,

requiring large sample sizes and expensive equipment to process samples. Use of genetic dispersal estimates is also limited by restrictive assumptions of models relating genetic structure to dispersal (Whitlock and McCauley 1999), and lags between dispersal and its observable impact on population genetic structure (Landguth et al. 2010). Finally, morphological traits, such as body size or wing length, have been used as indices of dispersal (Gibb et al. 2006). However, comparisons between direct estimates of dispersal and morphological traits suggest they are not reliable indices for some species (Paradis et al. 1998).

Tittler et al. (2006, 2009) proposed a method for estimating the typical dispersal distance using longitudinal data sets of count data or abundance estimates. I use the term ‘typical’ to stress that the method does not attempt to estimate the shape of the distribution of dispersal distances, but rather the distance(s) to which the species most frequently disperses. This method assumes that directional movement between two locations can result in positive, one-year-lagged correlations in population abundances between those locations. For example, if individuals move readily from population A to population B, and population A increases, the increased number of dispersers from population A to B in that year is detected as an increase in population B in the following year (Figure 5.1). By using a large number of paired sites, separated by different distances, one can determine the distances the species disperses by finding the distances at which such one-year-lagged correlations occur.

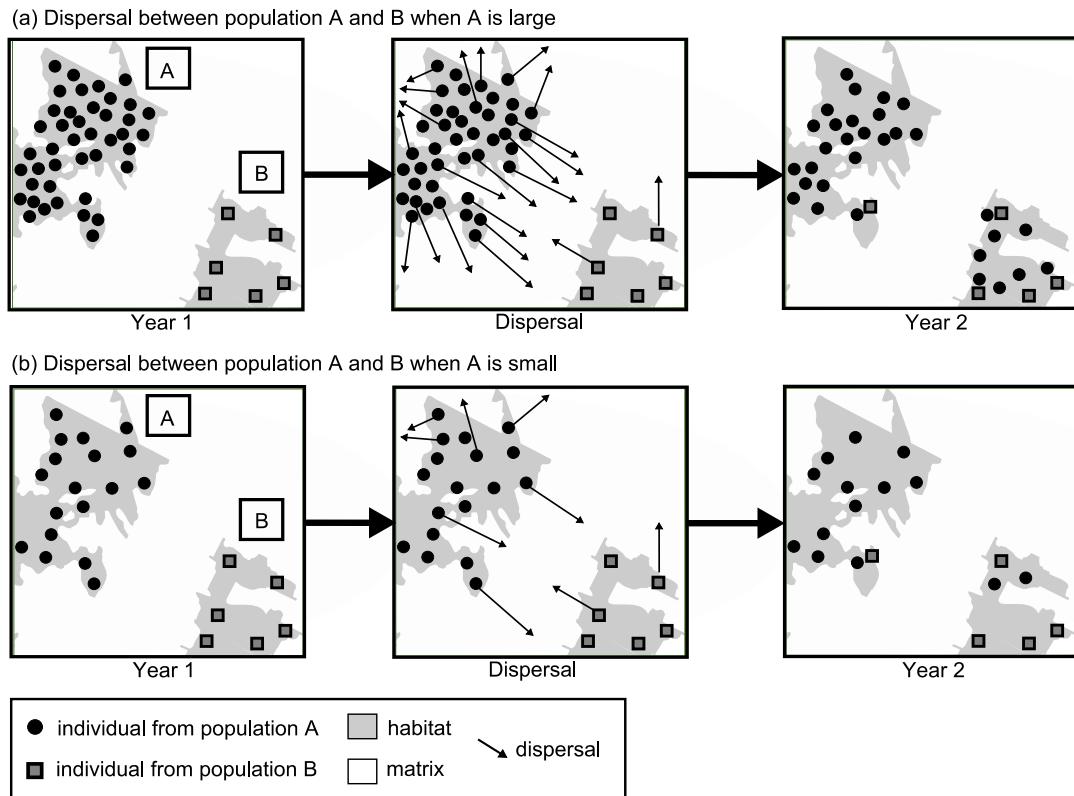


Figure 5.1. Example showing how positive, one-year-lagged correlations in population abundances can result from movement between those locations. If individuals disperse readily from population A to population B, (a) when population A is larger, a larger number of dispersers from A to B is detected as a larger population B in the following year, and (b) when A is smaller, a smaller number of dispersers from A to B is detected as a smaller population B in the following year.

Prior study supports the suggestion that dispersal causes correlation in population abundances, i.e. population synchrony (Paradis et al. 1999, Powney et al. 2011, 2012, Chevalier et al. 2014); however, there are some concerns with its use to estimate dispersal distances. The main concern is that population synchrony can result from factors other than dispersal, and thus the estimates may reflect distances at which one, or a combination, of these factors act. For example, populations may be synchronized if there is synchrony in their environmental conditions, such as weather (Post and Forchhammer 2002). Populations may also be synchronized by synchrony in their predators or prey; simultaneous increases in predator abundance or decreases in prey abundance for two populations may drive down the abundances of both (Satake et al. 2004). A second concern is that estimation of dispersal distance may be error-prone if a given population receives dispersers from multiple sources.

In this study I test how well typical dispersal distances estimated according to the Tittler et al. (2006, 2009) method, hereafter called the population synchrony dispersal index (PSDI), correlate with independent estimates of mean dispersal distances. I compared PSDI estimates for United Kingdom breeding birds to dispersal distances estimated from a mark-recapture study (Paradis et al. 1998).

5.3 Methods

5.3.1 Overview

To test how well PSDI can predict the relative and actual dispersal

distances estimated from an independent empirical study, I calculated PSDI for United Kingdom breeding birds and compared them to geometric mean dispersal estimates from a mark-recapture study (Paradis et al. 1998). The PSDI uses one-year-lagged synchrony in species abundance estimates between sampling sites as an indicator of dispersal distances. I estimated the PSDI by binning pairs of sampling sites into distance classes, and determining the distance class, or classes, with a significantly higher proportion of positive, one-year-lagged correlations than expected by chance. As the α -level used to determine significance is arbitrary, I calculated four PSDI for each species, using four different α : 0.005, 0.01, 0.05, and 0.1. I then compared each of my four PSDI estimates to each of two Paradis et al. (1998) estimates – natal dispersal and breeding dispersal – for a total of eight comparisons. For each comparison I evaluated (1) the relative concordance between estimates using the Spearman rank correlation (r_s), and (2) the absolute concordance between estimates as the difference between them.

5.3.2 *Data sets*

To estimate the PSDI for each species I used United Kingdom Breeding Bird Survey (UK BBS) data. The UK BBS is an annual breeding bird monitoring scheme, with standardized bird counts at approximately 3000, 1 km squares (Gregory et al. 2004). Volunteers record counts of all birds seen or heard along two, 1 km transects within the sampling square. Bird observations are recorded in one of four classes; three are based on estimated distance of the bird from the

transect line (0 – 25 m, 25 – 100 m, and 100 m+), and the fourth is for birds in flight. As this fourth category includes a range of behaviours from foraging to overflying, with individuals that are not obviously associated with the sampling square, I did not include them in my analyses. Bird counts are carried out twice per year. I used UK BBS data for 1994 – 2013, including all locations with available geographic coordinates (Figure 5.2). To produce an annual count for each sampling site I summed the counts for the three distances, across the two samples taken per year.

Independent estimates of typical dispersal distances, estimated as the geometric mean dispersal distances, were taken from Paradis et al. (1998). Distances between marking and recapture locations for birds banded by the British Trust for Ornithology were gathered for birds from 1909 – 1994. Dispersal records were divided into either natal dispersal, if the individual was marked in its year of birth and recaptured at breeding age, or breeding dispersal, if the recaptured individual was marked at breeding age. For full details, see Paradis et al. (1998).

5.3.3 *Population synchrony dispersal index*

I estimated the PSDI for each species recorded in the UK BBS. For each species, I tested for positive, one-year-lagged correlations in the time series of counts for all pairs of UK BBS sampling sites, according to Tittler et al. (2009). Since I did not know *a priori* the dominant direction of dispersal between any two sites, for each pair of sites I calculated correlations between site A at time t (A_t)

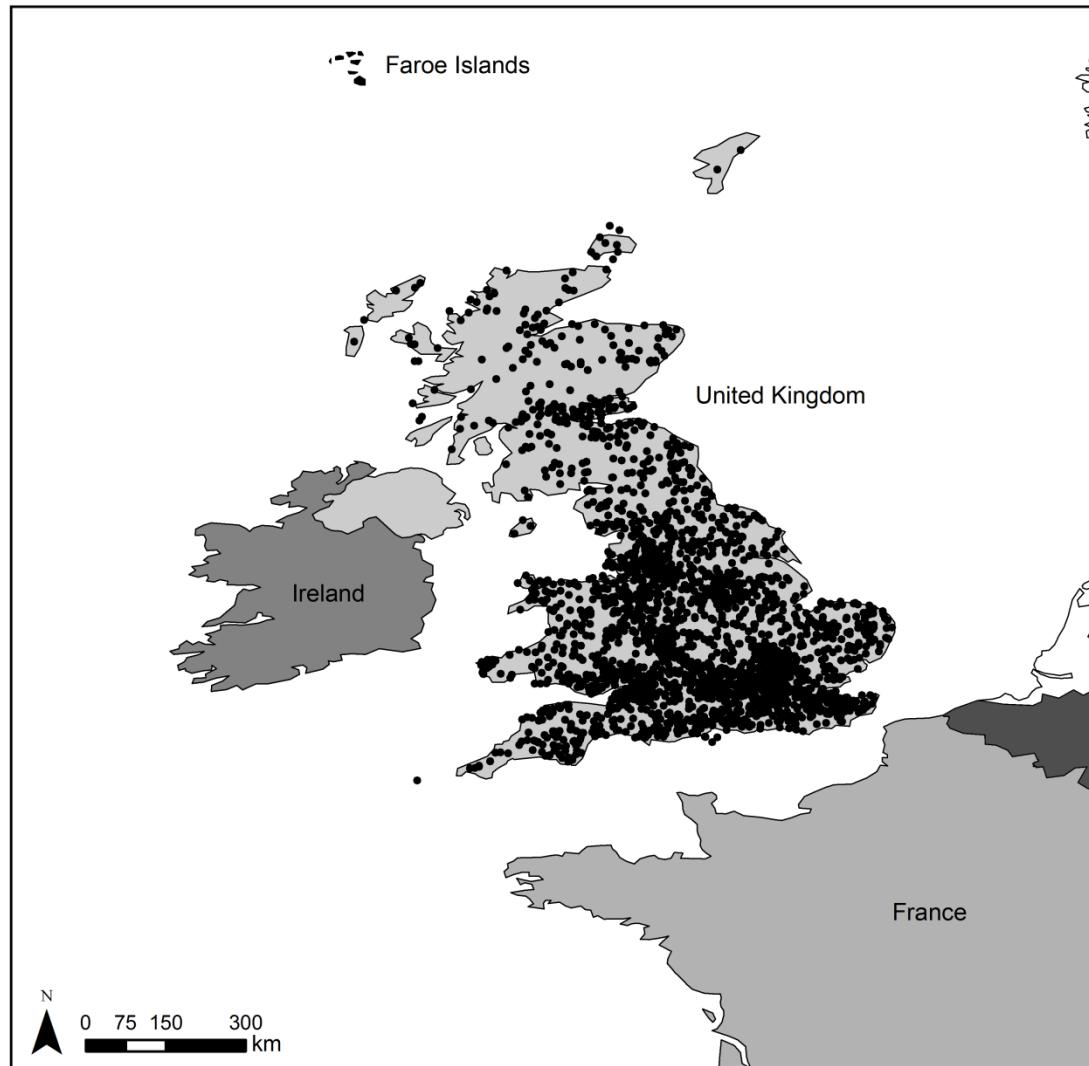


Figure 5.2. Distribution of sampling sites in the British Trust for Ornithology/Joint Nature Conservation Committee/Royal Society for the Protection of Birds Breeding Bird Survey.

and site B at time $t-1$ (B_{t-1}), and between A_{t-1} and B_t . I controlled for factors other than dispersal that may cause positive correlations between pairs of sites as follows. Due to spatial autocorrelation in environmental conditions (e.g. weather), I expect positive correlations between species counts at two sites in the same year (A_t and B_t). Furthermore, due to temporal autocorrelation in environmental conditions, I expect positive correlations between species counts at the same site from one year to the next (A_{t-1} and A_t). Therefore, I expect a positive correlation between A_t and B_{t-1} due to the correlations between A_{t-1} and B_{t-1} and between A_{t-1} and A_t that cannot be attributed to dispersal. To control for this, I included A_{t-1} in the multiple regression equation examining the relationship between A_t and B_{t-1} :

$$A_t = m_1 B_{t-1} + m_2 A_{t-1} + b \quad \text{equation 5.1}$$

where m_1 estimates the correlation between A_t and B_{t-1} . Only correlations for pairs of sites with at least 10 years of data and at least 0.25 of the years in the times series with a non-zero count were used in subsequent steps of this analysis.

All pairs of samples were then binned into distances classes and, for each distance class, I determined the proportion of correlations in that class that were positive; i.e. had a coefficient m_1 significantly greater than zero at $\alpha = 0.05$ (Figure 5.3). I used a bin width of 10 km. Tittler et al. (2009) suggested some species may have a PSDI greater than 100 km. Therefore I conservatively set

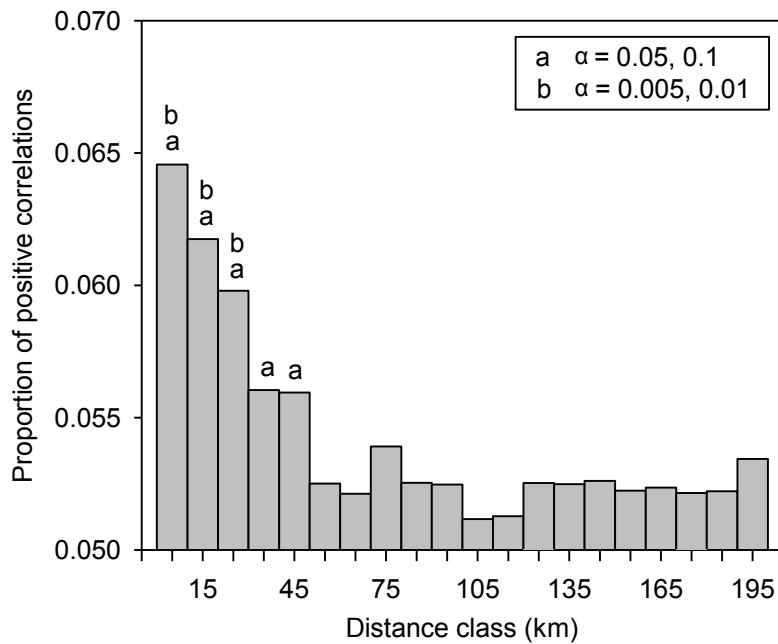


Figure 5.3. Example estimation of the population synchrony dispersal index for *Carduelis chloris*, showing the proportion of positive, one-year-lagged correlations for each distance class. Letters indicate the distance classes with significantly larger proportions of positive one-year-lagged correlations than expected by chance, based on each of the four tested α .

the maximum distance evaluated to 200 km. In total, I analyzed 20 distance classes, from 0 – 10 to 190 – 200.

To determine whether there was dispersal at a given distance, I tested whether the proportion of positive, time-lagged correlations in that distance class was greater than expected by chance. I conducted a test of significance for each distance class, comparing the proportion of positive time-lagged correlations to an empirically-derived null distribution. To generate a null distribution, I (1) selected a random set of paired sampling sites, equal to the sample size for the distance class, (2) conducted multiple regressions to determine the number of positive, time-lagged correlations (as described above), and (3) calculated the proportion of positive, time-lagged correlations. These three steps were repeated 5000 times to create a distribution of proportions. I then compared the proportion of positive, time-lagged correlations for the distance class to this distribution, using a one-tailed test. If the probability of getting the proportion of positive time-lagged correlations for the distance class, or something larger, was less than α I considered this evidence of species dispersal at this distance. To ensure sample sizes were large enough to allow for reasonable variation in the null distribution, I only included species that had 10 distance classes with at least 10 paired sample locations. I removed 171 of the 268 species monitored by the UK BBS from further analysis because they did not meet this criterion.

The PSDI was estimated based on the distance class, or classes, with a significant proportion of positive, time-lagged correlations. If there was a significant proportion of positive, time-lagged correlations at only a single

distance class, the PSDI was estimated as the center of that distance class. If there were significant proportions of positive, time-lagged correlations at multiple distance classes, the PSDI was estimated as the median of the range of the significant distance classes. For example, if significant for bins 0 – 10, 10 – 20, and 20 – 30, the median distance would be estimated as 15.

I calculated four PSDI for each species, each using a different α -level – 0.005, 0.01, 0.05, and 0.1 – to identify distance classes with significant proportions of positive, time-lagged correlations. If there were no distance classes with significant proportions of positive, time-lagged correlations at a given α , I removed the species from further analysis. I removed these species because there was no way to determine whether the lack of significance for all distance classes resulted from (a) an insufficient sample size, (b) negligible rates of dispersal, or (c) similar rates of dispersal at all distances.

5.3.4 Data analysis

To test whether the PSDI can predict the relative dispersal distances of species estimated in Paradis et al. (1998), I calculated r_s between the PSDI and Paradis et al. (1998) estimates for my species. Comparisons were made between each of the four PSDI (calculated at $\alpha = 0.005, 0.01, 0.05$ and 0.1) and each of the two Paradis et al. (1998) estimates (natal and breeding dispersal), for a total of eight comparisons. For each comparison I transformed the estimated distances into phylogenetically independent contrasts (Felsenstein 1985), to account for phylogenetic non-independence. To account for uncertainty in the

phylogenetic relationships among species, I obtained a random sample of 5000 phylogenetic trees for my species, chosen from the pseudoposterior distribution of trees with a Hackett backbone (Jetz et al. 2012). I then conducted the above analyses 5000 times, each with a different phylogeny. To determine whether there were significant, positive correlations between estimates, I calculated the median statistical test results (i.e. median r_s and median p-value) for the 5000 analyses. Significant, positive correlations would suggest that the PSDI predicts similar relative dispersal distances to those estimated in the independent mark-recapture study.

To test whether the PSDI can predict the actual (rather than relative) mean dispersal distances estimated in Paradis et al. (1998), I used a phylogenetic paired t-test to compare PSDI and Paradis et al. (1998) estimates for my species (Lindenfors et al. 2010). I used the phylogenetic trees estimated by Jetz et al. (2012), and repeated analyses 5000 times. To determine whether there were significant differences between estimates I calculated the median statistical test results (i.e. median t and median p-value) for the 5000 analyses. Non-significant differences may suggest that the PSDI predicts the dispersal distances estimated from independent study; however, non-significant differences may also result from type II error. To assess this possibility I estimated the probability of type II error (β) using power analysis for each test where the difference between the PSDI and Paradis et al. (1998) estimates was non-significant, given the sample size, α -level, and effect size for the comparison. The effect size was estimated as the phylogenetic mean difference divided by the

standard deviation for the phylogenetic mean difference. Non-significant differences were only interpreted as evidence that the PSDI predicts the dispersal distance when β was less than 0.20.

All data analyses were conducted in R (R Core Team 2014), using the ‘ape’ (Paradis et al. 2004), ‘phytools’ (Revell 2012), ‘picante’ (Kembel et al. 2014), and ‘pwr’ (Champely 2012) packages.

5.4 Results

The number of species that I could calculate a PSDI for depended on the stringency of the α -level, with more PSDI calculated as α increased, ranging from 24 species, when $\alpha = 0.005$, to 92, when $\alpha = 0.1$ (Appendix J). This resulted in variation in the number of species per comparison between the PSDI and dispersal estimate from Paradis et al. (1998). Only species with an estimated PSDI and a dispersal distance estimate in Paradis et al. (1998) could be used in analysis. The number of species per comparison thus ranged from 19, when comparing the PSDI at $\alpha = 0.005$ to either the natal or breeding dispersal estimate, to 60, when comparing the PSDI at $\alpha = 0.1$ to the natal dispersal estimate (Appendix J).

The PSDI produced estimates of relative dispersal distances of species similar to those estimated by Paradis et al. (1998), with stronger relationships between the estimates as α decreased. There were significant, positive correlations between the PSDI and Paradis et al. (1998) estimates for all comparisons, except for the comparison between the PSDI at $\alpha = 0.1$ and the

natal dispersal estimate ($r_s = 0.19$, $p = 0.08$; Figure 5.4a). At the most stringent α ($\alpha = 0.005$), there was a 0.87 ($p < 0.001$) correlation between the PSDI and the natal dispersal estimate, and a 0.55 ($p = 0.01$) correlation between the PSDI and the breeding dispersal estimate (Figure 5.4a).

PSDI tended to estimate longer dispersal distances than Paradis et al. (1998), with greater differences between the PSDI and Paradis et al. (1998) estimates as α increased. The mean difference between the PSDI and Paradis et al. (1998) estimates ranged from 5.1 km, when comparing the PSDI at $\alpha = 0.005$ and the natal dispersal distance, to 78.8 km, when comparing the PSDI at $\alpha = 0.1$ to the breeding dispersal distance (before controlling for phylogeny). The PSDI were significantly larger than Paradis et al. (1998) dispersal estimates, except when the PSDI was estimated at $\alpha = 0.005$ (Figure 5.4b). The estimated probability of type II error was negligible for comparisons of the PSDI at $\alpha = 0.005$ to both natal and breeding dispersal distances ($\beta < 0.001$); therefore I interpret the non-significant test results as evidence that the PSDI estimated at $\alpha = 0.005$ were no different from dispersal estimates based on mark-recapture sampling.

5.5 Discussion

This is the first study to show that the PSDI developed by Tittler et al. (2006, 2009) estimates relative dispersal distances similar to those from a large-scale mark-recapture study (Paradis et al. 1998). This is consistent with the explanation that the PSDI estimates dispersal distances from population

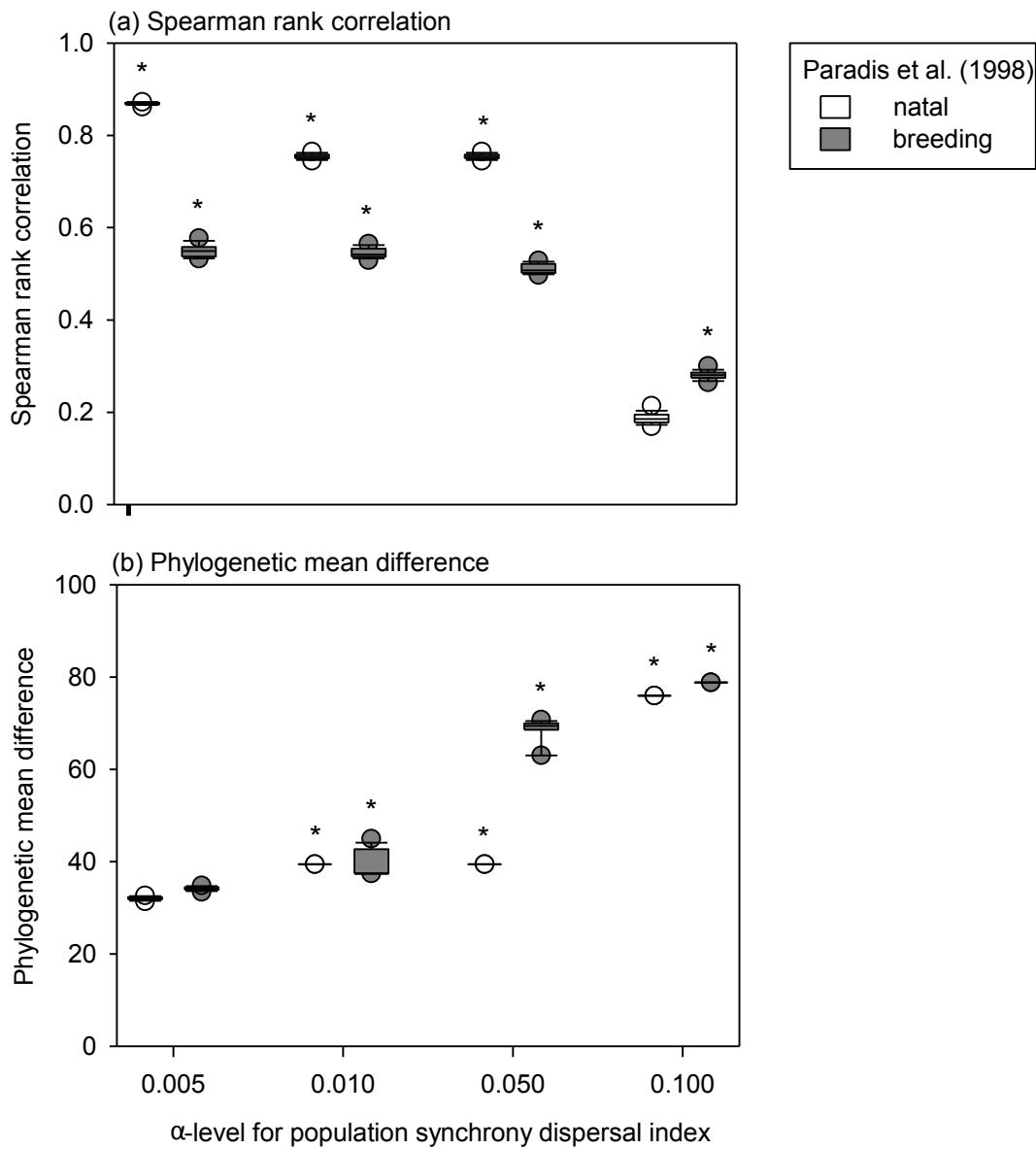


Figure 5.4. (a) Spearman rank correlations and (b) mean differences between the population synchrony dispersal index estimated from breeding bird surveys and the geometric mean dispersal distance (km) for natal and breeding dispersal estimated from marked bird recaptures, after controlling for phylogenetic non-independence. Variability in correlations and mean differences results from uncertainty in the phylogenetic relationships among species ($n = 5000$ possible phylogenies). * = median correlation or difference is significant at $\alpha = 0.05$.

synchrony caused by dispersal among populations. Directional movement between two locations results in positive, one-year-lagged correlations in population abundances between those locations. If individuals move readily from population A to population B, and population A increases, the increased number of dispersers from population A to B in that year is detected as an increase in population B in the following year (Figure 5.1). However, if individuals infrequently or never disperse the distance between two populations, such time-lagged synchrony is unlikely.

PSDI are not likely an artifact of spatial and temporal autocorrelation in factors unrelated to dispersal. Spatial autocorrelation in environmental conditions (e.g. weather; Post & Forchhammer 2002) can cause positive correlations between species counts at two sites in the same year (A_t and B_t). Temporal autocorrelation in environmental conditions, caused by effects that carry over from the previous year (e.g. food availability, weather; Clotfelter et al. 2007, Pearce-Higgins et al. 2015), can cause positive correlations between species counts at the same site from one year to the next (A_t and A_{t-1}). Although such spatial and temporal autocorrelation could cause a positive lagged correlation between population A (A_t) and population B in the previous year (B_{t-1}), the PSDI eliminates this effect by including A_{t-1} in the multiple regression equation.

In fact, three conditions would need to hold for the cross-species correlation between the PSDI and mark-recapture dispersal distance to be caused by an unknown factor: (a) that factor has a one-year-lagged correlation between distant locations, (b) the distance of that one-year-lagged correlation

varies between species, and (c) the distance of that one-year-lagged correlation is longer for species with longer dispersal distances. I am not aware of any factor that meets all of these criteria. For example, while weather conditions are temporally and spatially autocorrelated, there is no known mechanism by which weather would create time-lagged correlations in abundances between populations at different distances for different species in a manner that correlates with the species' dispersal distances. Similarly, lags in the spread of human land management practices or landscape change (e.g. urbanization; Carrion-Flores & Irwin 2004) may affect bird abundances (Marzluff 2001). However, if lags in human land use determined PSDI, PSDI should have occurred at similar distances for species with similar habitat, i.e. the distance at which human land use affected their habitat. This was not the case (Appendix K). Additionally, there is no evidence that one year lags in the spread of human land use are longer for species with longer dispersal distances. Similarly, one could imagine that one-year-lagged synchrony in the abundance of a predator or prey species drives changes in bird populations. However, to create the cross-species correlation between PSDI and dispersal distance, there would need to be a cross-species correlation between predator and prey dispersal distances, leading to similar PSDI for species with similar prey. This was not supported by my data (Appendix L). Finally, negative density dependence, which is widespread in these species (Eglington and Pearce-Higgins 2012), causes a negative correlation in a given population's abundances over time. One might imagine that this could influence PSDI estimation, because I only explicitly controlled for positive temporal

autocorrelation in my analysis (see previous paragraph). However, this could only cause the cross-species correlation between the PSDI and mark-recapture dispersal distance if there was also spatial autocorrelation in the strength of negative density dependence among populations, and if the change in strength with distance were related to dispersal distance. There is no evidence that either of these conditions is met. Therefore I conclude that the cross-species correlation between PSDI and dispersal distance occurs because PSDI reflects the typical distance of between-population dispersal, and not because of an unknown factor.

Although the PSDI estimated similar relative dispersal distances to those from Paradis et al. (1998), I found that the PSDI tended to estimate longer dispersal distances than Paradis et al. (1998). This could occur because the PSDI estimates are based on the median of the range of significant distance classes. If dispersal distances have a fat-tailed or negative exponential distribution, dispersal distances would be overestimated using this method because the actual dispersal distance is at the shorter end of this range. This explanation is supported by the fact that reducing α reduced the differences between the PSDI and Paradis et al. (1998) estimates. Reducing α tended to remove the longer distance classes, which weighted the PSDI towards the shorter distance classes.

Overall, my study shows that PSDI can be used to estimate typical dispersal distances of bird species, particularly in cases where the relative, rather than absolute, dispersal distances are required. This is because I found strong, positive correlations between the PSDI and independent estimates of natal and

breeding dispersal distances. Furthermore, although the PSDI for a given species depended on the α -level, its dispersal relative to other species did not. There were strong correlations between PSDI calculated at different α (Appendix M). This further supports my conclusion that the PSDI can be used to estimate the relative dispersal distances of species.

5.5.1 *Limitations*

Although the PSDI successfully estimated the relative dispersal distances of bird species, there may be species groups for which the PSDI would not be appropriate, even if a large-scale data set such as the UK BBS were available. For example, this method would not be appropriate for species found at low densities, as the regression modelling component of the PSDI method requires there not be an overabundance of species absences (i.e. zeros) at sampling locations. In addition, the PSDI would not likely be estimable if a species rarely disperses, because rare dispersal events are not likely to change the recipient population size enough to cause positive time-lagged correlations between populations. This method may also be inappropriate if species dispersal is inversely density-dependent (Matthysen 2005). This is because, if a smaller proportion of population A disperses when population A is large, there may be a smaller number of dispersers from population A to B, causing a decrease in population B in the following year, i.e. a negative lagged correlation. Finally, this method may not be appropriate if species do not have annual dispersal, as one-

year-lagged correlations between populations would not be detected if dispersal occurred at irregular or multi-year intervals.

PSDI appear to consistently overestimate mean dispersal distances of species from independent mark-recapture study. Therefore, this index is best used in cases where only the relative dispersal distances of species are needed, or cases where the PSDI can be calibrated using known dispersal distances. If there are independent dispersal distance estimates for a subset of the species of interest, these can be used to estimate the PSDI-dispersal distance relationship. Then this relationship can be used to predict dispersal distances for the rest of the species. To demonstrate this, I calibrated my PSDI estimates at $\alpha = 0.05$ using dispersal estimates from Paradis et al. (1998), and predicted natal dispersal distances for 23 species and breeding dispersal distances for 25 species not included in Paradis et al. (1998; Appendix N).

5.5.2 *Implications*

Although previous studies have suggested that dispersal can synchronize populations (Paradis et al. 1999, Powney et al. 2011, 2012, Chevalier et al. 2014), this is the first to show that the distance at which dispersal most strongly synchronizes populations is correlated with empirical estimates of dispersal distance. Additionally, this finding suggests that dispersal can cause one year lags in population synchrony. This provides indirect support for Bearup et al. (2013), which suggested that Moran effects on population synchrony could be

distinguished from dispersal effects on population synchrony because the former causes within-year synchrony and the latter causes one-year-lagged synchrony.

I also show that the PSDI can be used to estimate the relative dispersal distances of bird species. Reliable estimates of dispersal are relatively rare; my study suggests that researchers can take advantage of large-scale, longitudinal, multi-species data sets, like the UK BBS, to estimate relative dispersal distances. Such data sets are therefore of high value not only for estimating population trends, population sizes, and relationships between species or communities and environmental conditions (e.g. Newson et al. 2005, 2009), but also for estimating dispersal distances.

In addition to estimating the relative dispersal distances of species, the PSDI could be used to address other questions about the relationship between dispersal distance and the landscape context. For example, one could subset the data temporally, and estimate dispersal distances within different time periods; such estimates could then be used to detect changes in dispersal distances over time in relation to land use changes. One could also subset the data geographically and estimate a species' PSDI in different regions. These estimates could be used to detect differences between dispersal distances within the core and edges of a species range, to model the change in dispersal distance with latitude, or to estimate differences in dispersal distances between regions with different rates of landscape change.

Like Paradis et al. (1998), my PSDI estimates suggest that many United Kingdom bird species disperse relatively long distances. Over half of my species

were estimated to typically disperse at least 25 km in a year. Mark-recapture sampling similarly suggested that birds are capable of long-distance dispersal, detecting dispersal events of over 200 km for a number of species (Paradis et al. 1998). The current analysis also indirectly supports the PSDI estimates made for North American birds (Tittler et al. 2009), which suggested that North American birds also typically disperse over much longer distances than previously thought.

Long dispersal distances have implications for species responses to habitat loss and climate change, as this suggests that species risk is driven by habitat availability, not dispersal limitation. Consistent with this statement, Barbet-Massin et al. (2012) predict that, although dispersal will not limit most European bird species' abilities to track shifts in breeding habitat with climate change, breeding ranges will be reduced in size for most species. Empirical study also suggests that habitat generalist bird species have been better able to track climate change than habitat specialists (Jiguet et al. 2007, Davey et al. 2012), likely because generalists have more available habitat at the expanding edge of their current range than specialists. Efforts should therefore focus on conserving and restoring habitat for habitat specialists, rather than prioritizing species based on mobility.

Chapter 6 – Habitat specialist bird species disperse farther than habitat generalist bird species

6.1 Abstract

Some theories predict habitat specialists should be less dispersive and migratory than generalists, while other theories predict the opposite. I evaluated the cross-species relationship between habitat specialization, dispersal distance, and migration status in 202 bird species breeding in North America or the United Kingdom. I found that habitat specialists dispersed farther than habitat generalists, but I found no difference in migratory status between specialists and generalists. This suggests that habitat specialist bird species need to move farther than habitat generalists, to locate resources and avoid genetic and demographic isolation. To my knowledge this is the first large-scale, multi-species study to demonstrate a positive relationship between habitat specialization and dispersal and, interestingly, it is opposite to the pattern found for invertebrates. This relationship has implications for species conservation. If generalist birds have weaker dispersal abilities than specialist birds, placing conservation priority on habitat specialists will not conserve dispersal-limited species. Further study should focus on the relative importance of habitat specialization and dispersal limitation for species risk in human-altered landscapes.

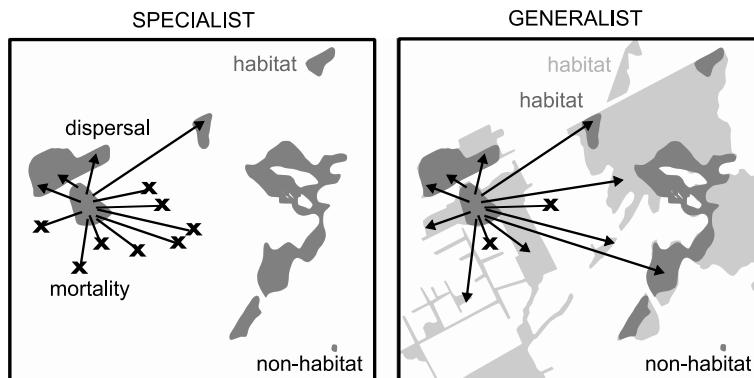
6.2 Introduction

Cost-benefit trade-offs between species traits should cause certain traits to co-occur, as investment of resources in one trait means reduced investment in another. Selection for one species trait may also alter the costs and benefits associated with a second trait, influencing the selective pressure on the second trait. For example, studies suggest co-occurrence of short lifespan, early reproduction, high fecundity, and low mobility (Gunn et al. 1988, Gu et al. 2006, Blomquist 2009).

Several theories suggest a trade-off between habitat specialization and dispersal, predicting that habitat specialists are less dispersive than habitat generalists. One hypothesis is that higher costs of movement among sparsely distributed resource patches lead to selection for less dispersal (Figure 6.1a; Stevens et al. 2014). A second suggests that, if habitat specialists can outcompete habitat generalists for a given resource, higher dispersal allows generalists to access resources unavailable to the specialist, and thus avoid competition (Kisdi 2002, Nagelkerke and Menken 2013). Thirdly, a negative association between dispersal and habitat specialization could occur if high dispersal leads to high rates of gene flow across the landscape, decreasing local adaptation (Venail et al. 2008).

Conversely, some theory suggests the opposite: that habitat specialists have stronger dispersal abilities. The idea here is that dispersal compensates for local resource scarcity. In a heterogeneous landscape, as species habitat

(a) Habitat generalists disperse farther than specialists, because of higher dispersal costs for specialists



(b) Habitat specialists disperse farther than generalists, because habitat patches are farther apart for specialists

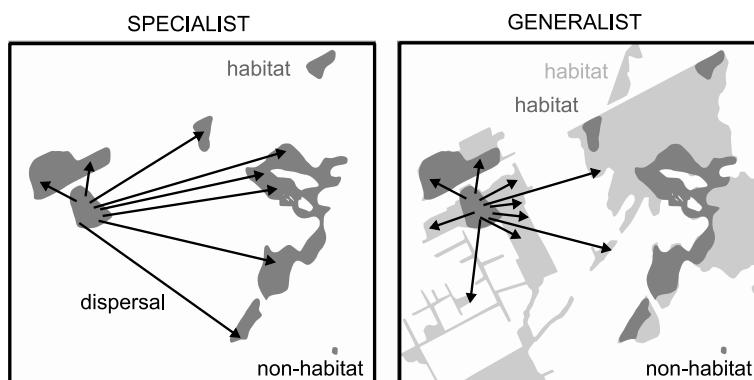


Figure 6.1. Examples illustrating why (a) habitat generalists may be more dispersive than specialists, because dispersal costs increase with habitat specialization, and (b) habitat specialists may be more dispersive than generalists, because specialists need to be able to move farther to locate habitat.

specialization increases, its habitat becomes rarer and more isolated. Thus a habitat specialist needs to move more frequently and farther than a habitat generalist, to locate resources and avoid genetic and demographic isolation (Figure 6.1b; Samways and Lu 2007, Centeno-Cuadros et al. 2011).

Empirical studies comparing habitat specialization to dispersal are limited. Most studies include few species, use expert opinion classifications that could confound habitat specialization and dispersal, or lack statistical support (e.g. Brouat et al. 2003, Samways and Lu 2007, Öckinger et al. 2009, Stevens et al. 2012). Rigorous studies so far suggest that specialists are less dispersive than generalists (Bonte et al. 2003, Entling et al. 2011, Sekar 2012, Carnicer et al. 2013, Dapporto and Dennis 2013, Stevens et al. 2014, Dahirel et al. 2015). However, these negative habitat specialization-dispersal relationships have only been observed in invertebrates.

It has also been suggested that non-migratory species are more likely to be habitat specialists than migratory species. Non-migratory species can select breeding habitat before migrants return, so migrants who can take advantage of multiple land cover classes can minimize direct competition for resources with non-migrants. For example, in *Erithacus rubecula* and *Sylvia atricapilla*, non-migratory individuals dominate in forest and migratory individuals use both forest and shrubland (Pérez-Tris and Tellería 2002, Tellería and Pérez-Tris 2004). However, the opposite is also possible (Stevens et al. 2014). Non-migratory species may adapt to fluctuation in resource availability by becoming habitat

generalists, whereas migrants avoid declines in local resource availability through migration (Cox 1985, Holt and Fryxell 2011).

The purpose of this study was to evaluate the cross-species relationship between habitat specialization and dispersal, and between habitat specialization and migration status, in temperate breeding birds in North America (NA) and the United Kingdom (UK).

6.3 Methods

6.3.1 Overview

Analyses were conducted on bird species breeding in NA or the UK (Figure 6.2a). I estimated habitat specialization using the species specialization index (SSI; Julliard et al. 2006, Davey et al. 2012), which models specialization as the coefficient of variation in the estimated species densities among different land cover classes. For NA birds I measured dispersal distance using the population synchrony dispersal index (PSDI; Tittler et al. 2006, 2009), which reliably estimates the relative dispersal distances of bird species (Chapter 5). For UK birds I used mean natal and breeding dispersal distances estimated by mark-recapture sampling (Paradis et al. 1998). Each species was categorized as either migratory or non-migratory, from BirdLife International (2014).

For each region I related the SSI to the estimated dispersal distance and migration status (migratory or non-migratory). I used multimodel inference based on the small-samples Akaike Information Criterion (AICc) to compare among four models, relating the SSI to (1) dispersal distance + migration status, (2) dispersal

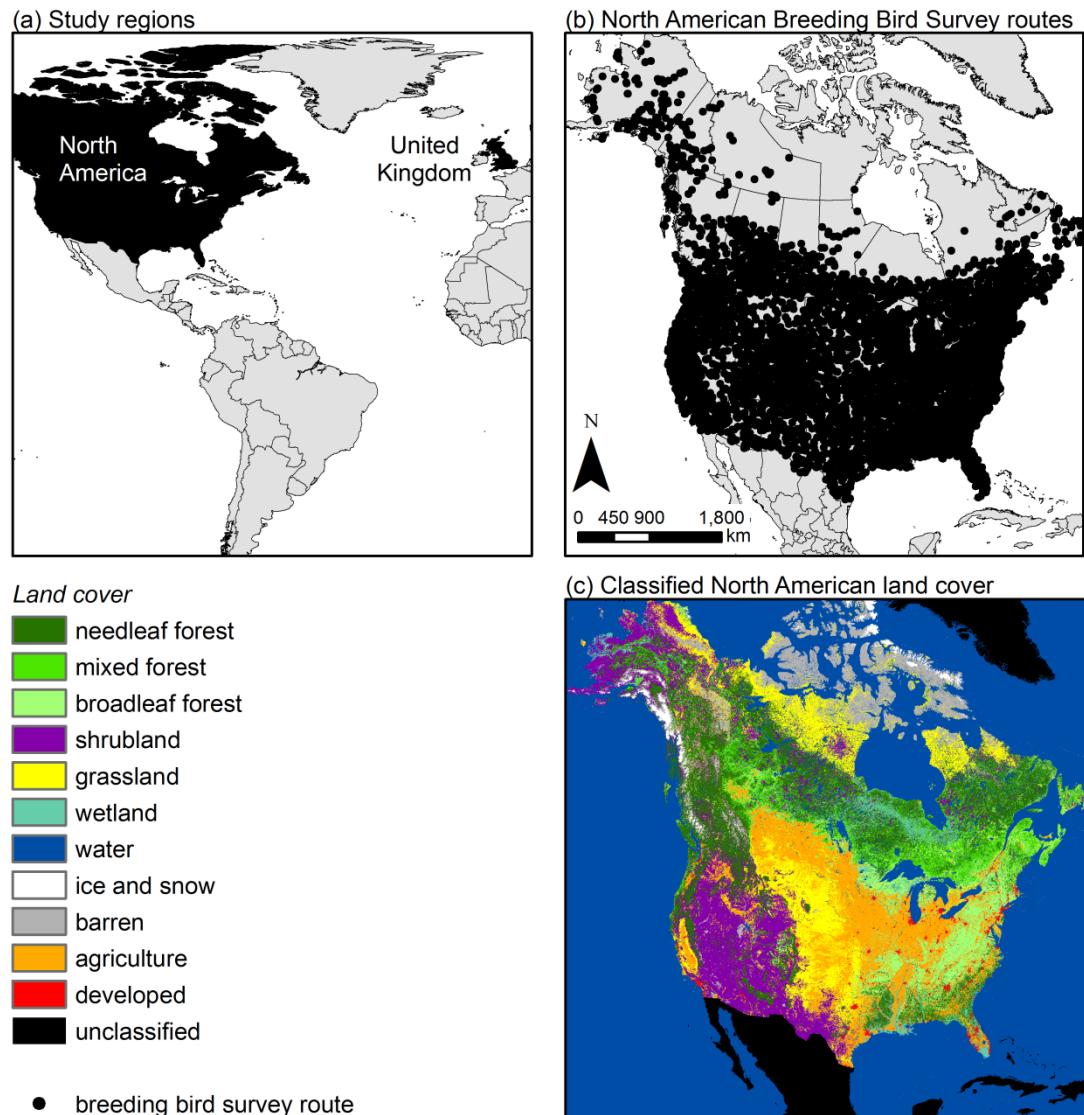


Figure 6.2. (a) Study locations in North America and the United Kingdom. (b) Distribution of North American Breeding Bird Survey routes, used to determine the species specialization indices and population synchrony dispersal indices. (c) Classified land cover, used to calculate the species specialization indices for North American breeding birds.

distance, (3) migration status, and (4) the null model. To account for phylogenetic non-independence I modelled these relationships using a phylogenetic generalized least squares model (Martins and Hansen 1997).

6.3.2 *Estimation of the species specialization index*

6.3.2.1 *North America*

I used the North American Breeding Bird Survey (NA BBS) to calculate the SSI for NA birds. The NA BBS provides a continent-wide, multi-year data set of species counts for NA breeding birds, begun in 1966 (Figure 6.2b; Pardieck et al. 2014). Point counts are conducted at 50 stops spaced along each of the approximately 4100, 39.4 km-long roadside survey routes once each year during the breeding season. At each point count, all birds seen or heard within a 0.4 km radius are recorded over a 3-minute interval. Surveys begin approximately half an hour before sunrise.

To calculate the SSI for each NA species, I first estimated the density of each species in each land cover class. I used 11 land cover classes, derived from an existing, classified raster GIS data set which classified land cover at a pixel size of 250m (Figure 6.2c; NRCan et al. 2005). Classification was based on Moderate Resolution Imaging Spectroradiometer imagery for 2005, combining classifications of national land cover performed by the United States, Canada, and Mexico, as part of the North American Agreement on Environmental Cooperation (NRCan et al. 2005). Species counts were taken from the first stop of each NA BBS route sampled in 2003 – 2007. The first stop is the only stop for

each route with reliable latitude-longitudes for all routes. I selected 2003 – 2007 to bracket the year of land cover data (2005). I estimated the density of a species in a land cover class as the number of individuals observed in that land cover between 2003 and 2007, divided by the number of first-stops in that land cover within the species range. The species range was estimated as the minimum convex polygon around all routes where the species was detected at least once during the entire time series of the NA BBS.

The SSI was then calculated as the coefficient of variation (standard deviation / mean) in the estimated densities among the land cover classes found in the species range. This produced a continuous index of habitat specialization, where habitat specialist species had higher coefficients of variation in the estimated densities than habitat generalist species (Figure 6.3). To ensure sample sizes were large enough to allow for reasonable estimation of the species densities in different land cover classes, I only included species observed at the first stop of at least 10 routes between 2003 and 2007.

6.3.2.2 United Kingdom

For UK birds SSI values were taken from Davey et al. (2012). These were based on the same methods as described above, using the species counts and land cover classifications from the UK Breeding Bird Survey co-ordinated by the British Trust for Ornithology/Joint Nature Conservation Committee/Royal Society for the Protection of Birds. The main differences between this and my NA SSI calculations were that, in the UK estimates, (a) the number of sample locations in

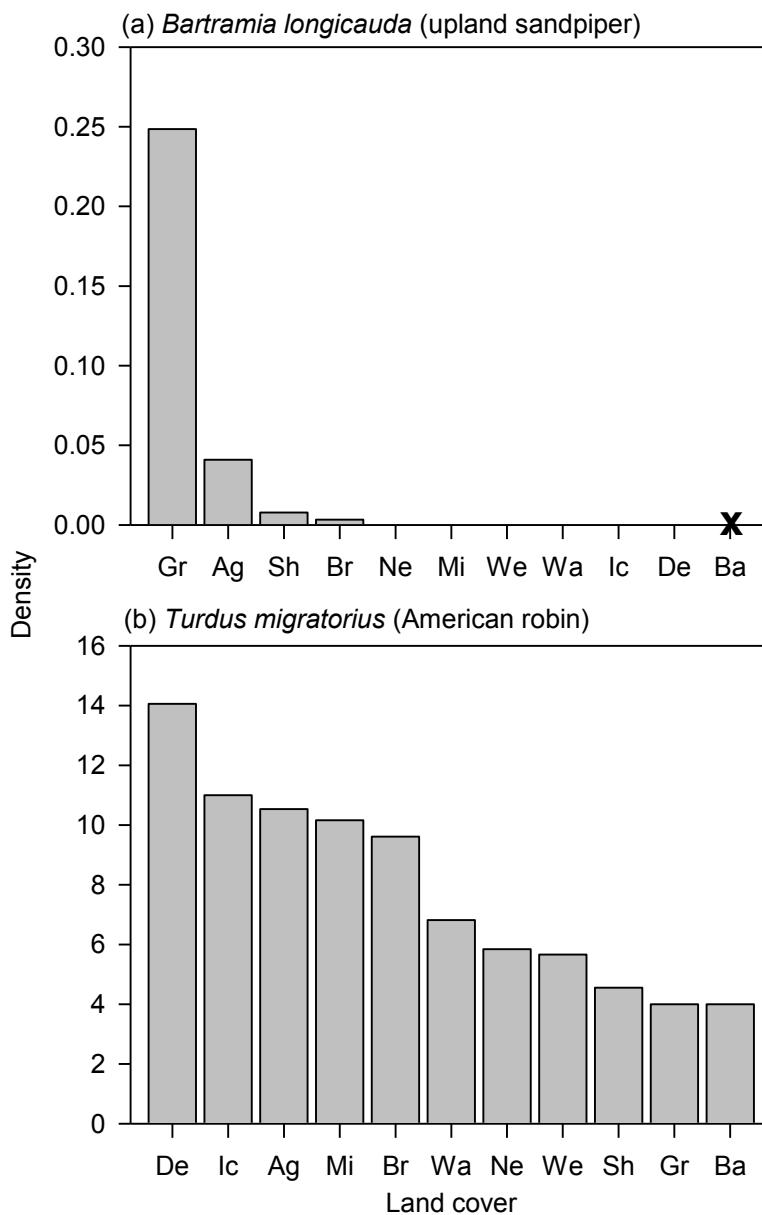


Figure 6.3. Example estimation of the species specialization index (SSI) for (a) *Bartramia longicauda* (upland sandpiper), a habitat specialist ($SSI = 2.59$), and (b) *Turdus migratorius* (American robin), a generalist ($SSI = 0.43$). The SSI was calculated as the coefficient of variation in densities among land cover classes found within the species range. Ne = needleleaf forest; Mi = mixed forest;

(continued on the following page)

Br = broadleaf forest; Sh = shrubland; Gr = grassland; We = wetland; Wa = water; Ic = ice and snow; Ba = barren; Ag = agriculture; De = developed; **X** = land cover not found in the species range.

a given land cover class were not explicitly limited to those within the species range, and (b) density estimates in each land cover class were based on a longer time series (1994 – 2008; details in Davey et al. 2012).

6.3.3 *Estimation of dispersal distances*

6.3.3.1 *North America*

I estimated the PSDI of each species observed in the NA BBS, using the method developed by Tittler et al. (2006, 2009). The PSDI determines the distances between sampling sites at which there are positive, one-year-lagged correlations in abundance estimates, under the assumption that directional dispersal between two locations can result in positive, one-year-lagged correlations in population abundances between those locations. For example, if individuals disperse readily from population A to population B, and population A increases, this increases the number of dispersers from population A to B, which is detected as an increase in population B in the next year. However, if individuals rarely disperse between two populations, such time-lagged synchrony is unlikely.

For each species, I first tested for positive, one-year-lagged correlations in the time series of counts for all pairs of NA BBS routes. For each route I used the summed counts for the first 10 stops for each year of sampling (which I refer to as a “site”), to produce a sufficient number of years with non-zero counts for model fitting (described below). Since I did not know *a priori* the dominant direction of dispersal between any two sites, for each pair of sites I calculated

correlations between site A at time t-1 (A_{t-1}) and site B at time t (B_t), and between A_t and B_{t-1} . I controlled for factors other than dispersal that may cause positive one-year-lagged correlations between pairs of sites, as follows. Due to spatial autocorrelation in environmental conditions, I expect positive correlations between species counts at two sites in the same year (A_t and B_t). Due to temporal autocorrelation in environmental conditions, I expect positive correlations between species counts at the same site from one year to the next (A_{t-1} and A_t). Therefore, I expect a positive correlation between A_t and B_{t-1} that cannot be attributed to dispersal, but instead is caused by correlations between A_{t-1} and A_t and between A_{t-1} and B_{t-1} . To control for this, I included A_{t-1} in the multiple regression equation examining the relationship between A_t and B_{t-1} :

$$A_t = m_1 B_{t-1} + m_2 A_{t-1} + b \quad \text{equation 6.1}$$

where m_1 estimates the correlation between A_t and B_{t-1} . Only correlations for pairs of sites with at least 10 years of data and at least 0.25 of the years in the times series with a non-zero count were used in subsequent steps of this analysis.

All pairs of samples were binned into distance classes and, for each distance class, I determined the proportion of correlations in that class that had significant, positive, time-lagged correlations, i.e. m_1 significantly greater than zero at $\alpha = 0.05$. I used a bin width of 10 km. I did not examine distances less than 10 km because the samples were composed of 10 stops along a 7.9 km

transect, and I judged it invalid to examine distances between samples that were similar to, or less than the distances between point locations within a given sample. In total, I analyzed 19, 10 km-wide distance classes, from 10 to 200 km.

To detect dispersal at a given distance, I determined whether the proportion of positive, time-lagged correlations in that distance class was greater than expected by chance. I tested significance by comparing the observed proportion of positive time-lagged correlations in a distance class to an empirically-derived null distribution. To generate the null distribution, I (1) selected a random set of paired sampling sites, equal to the observed number of pairs in the distance class, (2) conducted multiple regressions on this random set to determine the number of significant, positive, time-lagged correlations (as described above), and (3) calculated the proportion of significant, positive, time-lagged correlations. These three steps were repeated 5000 times to create a distribution of proportions. I then compared the actual proportion of positive, time-lagged correlations for the distance class to this distribution, using a one-tailed test. If the probability of getting at least the observed proportion was less than $\alpha = 0.05$ I considered this evidence of species dispersal at this distance. To ensure sample sizes were large enough to produce reasonable variation in the null distribution, I only included species with at least 10 paired sample sites in more than 10 of the distance classes. Two hundred and twenty-three species monitored by the NA BBS met this criterion.

The PSDI was estimated based on the distance class(es), with a significant proportion of positive, time-lagged correlations. If there was a

significant proportion of positive, time-lagged correlations at a single distance class, the PSDI was the center of that distance class. If there were multiple distance classes with significant proportions of positive, time-lagged correlations, the PSDI was estimated as the median of the range of the significant distance classes. For example, if significant for bins 10 – 20 and 20 – 30, the median distance would be estimated as 20. If a species had no distance classes with significant proportions of positive, time-lagged correlations, I removed the species from further analysis (89 of 223 [40 %] species).

6.3.3.2 United Kingdom

Natal and breeding dispersal distances were estimated by mark-recapture sampling, from Paradis et al. (1998). Distances between marking and recapture locations for birds banded by the British Trust for Ornithology were gathered from 1909 to 1994. Dispersal records were divided into either natal dispersal, if the individual was marked in its year of birth and recaptured at breeding age, or breeding dispersal, if the recaptured individual was marked at breeding age. Geometric mean dispersal distances were estimated for all species with at least 10 sampled dispersal events (details in Paradis et al. 1998).

6.3.4 Data analysis

I tested for a relationship between the SSI, dispersal distance, and migration status separately for NA and UK species. For UK birds, the analysis was conducted using each of the natal and breeding dispersal distance

estimates. I used multimodel inference based on the small-samples Akaike Information Criterion (AICc) to compare among four candidate models, relating the SSI to (1) dispersal distance + migration status, (2) dispersal distance, (3) migration status, and (4) the null model, using a generalized least squares model. To satisfy model assumptions, I ln-transformed the SSI and dispersal distance estimates. To account for phylogenetic non-independence I included a covariance matrix, where covariance between a given pair of species was based on a phylogenetic tree and Brownian model of evolution (Martins and Hansen 1997). The phylogenetic tree used in the model was based on Jetz et al. (2012). To account for uncertainty in the phylogenetic tree, I obtained a random subset of 5000 trees, chosen from the pseudoposterior distribution of trees with a Hackett backbone phylogeny (for more details, see Jetz et al. 2012), and fit each of the candidate models 5000 times, each with a different phylogeny. To determine the support for a given model I used the median results of multimodel inference, i.e. the median AICc, ΔAICc , and model weight from the 5000 analyses. I also quantified the relationship between the SSI, dispersal distance, and migration status using the median model-averaged regression coefficients and unconditional 95% confidence intervals.

Data analyses were conducted in R (R Core Team 2014), using the ‘ape’ (Paradis et al. 2004), ‘nlme’ (Pinheiro et al. 2014), and ‘MuMIn’ (Barton 2014) packages.

6.4 Results

I calculated SSI for 240 NA bird species and PSDI for 134 species (Appendix O). Analyses of NA birds included the 131 species for which I had estimates of all three variables: habitat specialization, dispersal distance, and migration status. For UK birds I included 75 species in my analyses when using the natal dispersal distance estimates, and 67 species when using breeding dispersal distance estimates.

For both NA and UK birds, species with narrower habitat requirements (i.e. larger SSI) had longer dispersal distances than species with more flexible habitat requirements (i.e. smaller SSI). Models relating the SSI to dispersal distance, or dispersal distance + migration status, had the strongest support of all models in the candidate model set, and the null model was not included in the most supported model set (i.e. $\Delta\text{AICc} \leq 2$; Table 6.1). Additionally, the unconditional 95% confidence interval around the model-averaged regression coefficient for the relationship between the SSI and dispersal distance did not include zero (Figure 6.4a).

I found little evidence of differences in the degree of habitat specialization between migratory and non-migratory species. Although the model relating the SSI to both dispersal distance and migration status was included in the most supported model set for both NA and UK species (Table 6.1), the unconditional 95% confidence interval around the model-averaged coefficient for the relationship between the SSI and migration status included zero in all analyses (Figure 6.4b).

Table 6.1. Results of multimodel inference, modelling the relationship between the species specialization index, dispersal distance, and migration status (either migratory or non-migratory) for (a) 131 North American breeding bird species, (b) 75 United Kingdom bird species, using natal dispersal distances, and (c) 67 United Kingdom bird species, using breeding dispersal distances. Relationships were modelled by the generalized least squares model, with a covariance matrix to account for phylogenetic relationships among species. Presented are the degrees of freedom (df), small-samples Akaike Information Criterion (AICc), change in AICc (ΔAICc), and weight for all subsets of the global model (dispersal distance + migration status). AICc, ΔAICc , and weights are the medians from the set of 5000 analyses conducted with different possible phylogenetic trees.

Model	df	AICc	ΔAICc	Weight
(a) North America				
dispersal distance	3	181.60	0.00	0.53
dispersal distance + migration status	4	181.86	0.37	0.44
migration status	3	189.74	8.27	0.01
null	2	190.74	9.19	0.01
(b) United Kingdom (natal dispersal)				
dispersal distance	3	119.52	0.00	0.38
dispersal distance + migration status	4	119.49	0.07	0.38
null	2	121.53	2.15	0.14
migration status	3	122.35	3.02	0.09

(continued on the following page)

Table 6.1 continued.

Model	df	AICc	ΔAICc	Weight
(c) United Kingdom (breeding dispersal)				
dispersal distance + migration status	4	105.76	0.00	0.50
dispersal distance	3	106.68	0.81	0.33
null	2	109.18	3.27	0.10
migration status	3	109.76	3.90	0.07

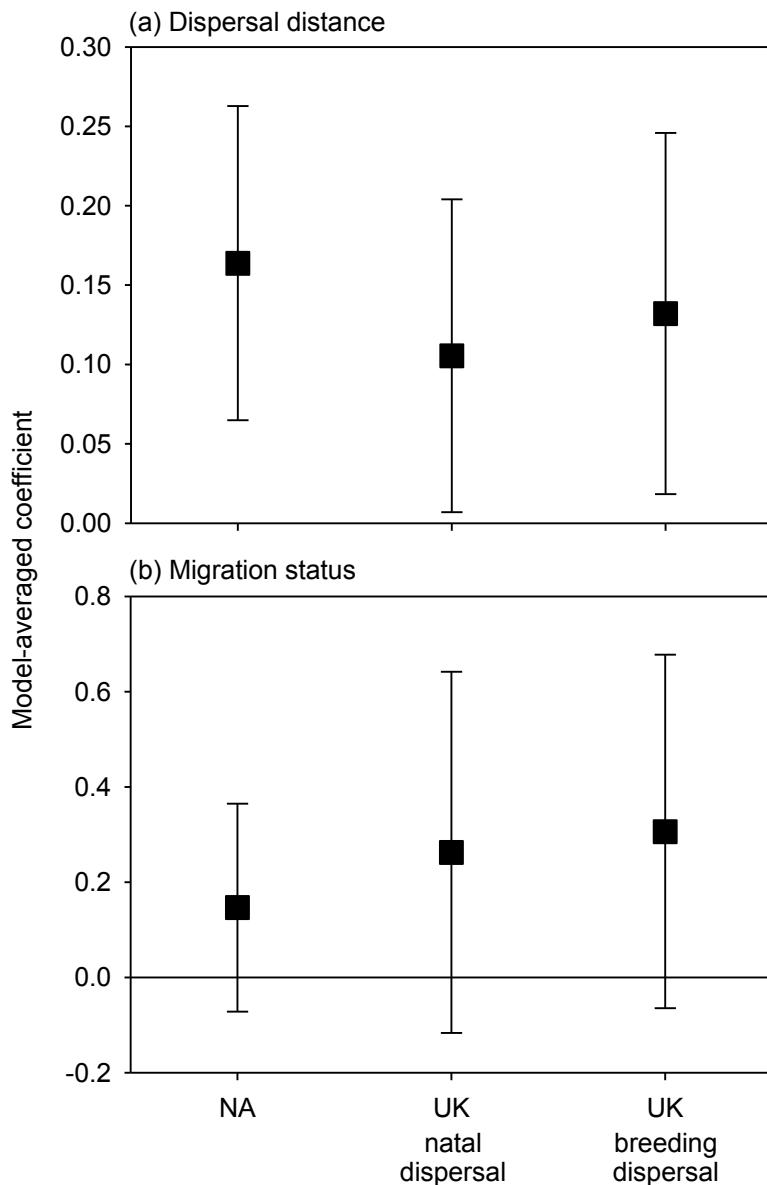


Figure 6.4. Model-averaged regression coefficients, and the unconditional 95% confidence intervals, for (a) the relationship between the species specialization index (SSI) and the estimated dispersal distance, and (b) the difference between the SSI of non-migratory and migratory species, where a positive value indicates higher SSI for non-migratory species. Coefficients were estimated for North American (NA) breeding birds, and for United Kingdom (UK) breeding birds, using natal and breeding dispersal distance estimates.

6.5 Discussion

My results suggest that temperate breeding birds with narrower habitat requirements typically disperse farther than birds with more flexible habitat requirements. I infer that this relationship occurs because dispersal compensates for resource scarcity. When a habitat specialist is restricted to sparsely distributed patches of habitat in an unsuitable matrix, it needs to move farther to locate resources and avoid genetic and demographic isolation (Figure 6.1b; Samways and Lu 2007, Centeno-Cuadros et al. 2011). To my knowledge this is the first large-scale, multi-species study to find a positive relationship between habitat specialization and dispersal.

It is unlikely that the positive relationship between habitat specialization and dispersal distance in my study was an artifact of the data sets or the methods for measuring habitat specialization or dispersal distance. The SSI has advantages over other measures of habitat specialization because it (1) is based on empirical data, rather than expert opinion, (2) takes into account both the number of land cover classes a species occupies and the relative densities of the species in them, and (3) is independent of differences in abundance among species (Julliard et al. 2006). Although typical dispersal distances for NA species were estimated indirectly via the PSDI, I previously showed that the PSDI can estimate the relative dispersal distances of birds (Chapter 5). Additionally, the positive relationship between the SSI and dispersal distances for UK birds supports my findings for NA birds, because in the UK birds I found the same

habitat specialization-dispersal relationship using dispersal distances based on mark-recapture data.

The relationship I found between habitat specialization and dispersal distance for birds was opposite to previously reported relationships for invertebrates (Bonte et al. 2003, Entling et al. 2011, Sekar 2012, Carnicer et al. 2013, Dapporto and Dennis 2013, Stevens et al. 2014, Dahirel et al. 2015). I speculate that these two taxa may differ in other traits that affect the specialization-dispersal relationship. For example, since the energetic costs of endothermy are much higher than ectothermy (Nagy 1987), ectotherms are likely to be better adapted to survive periods of food scarcity than endotherms (Pough 1980). This suggests that endotherms are more sensitive to local resource scarcity than ectotherms, which is consistent with evidence that the abundance and richness of endotherms is more strongly related to local resource availability than the abundance and richness of ectotherms (Buckley et al. 2012). Thus for ectotherms, which can wait out periods of low food availability, the higher costs of movement for specialists should lead to selection for less dispersal than generalists. However, for ectotherms, which need to disperse to avoid starvation, specialists will need to move farther than generalists to locate resource patches.

My finding that specialist birds move farther than generalists is also opposite to what is assumed for tropical bird species, based largely on reduced gap-crossing by tropical forest specialists relative to generalists (Kennedy and Marra 2010, Ibarra-Macias et al. 2011). However, to my knowledge this habitat specialization-dispersal relationship has not been shown in multi-species studies

with empirical estimates of specialization and dispersal. If the relationship is in fact opposite for temperate and tropical species, I speculate that this could be due to an effect of landscape structure on the evolution of the specialization-dispersal relationship. For example, in a stable landscape, where local extinction events are rare, the higher costs of movement for specialists should drive selection for less dispersal. However, in a more spatially or temporally dynamic landscape, the need to disperse to escape locally declining conditions and recolonize after local extinctions may be greater than the costs of dispersal. In these landscapes habitat specialization may drive selection for greater dispersal distances, because specialists need to move farther to locate resources than generalists. Thus habitat specialist birds in the more dynamic temperate regions (Baldi 1996, Saigusa et al. 2008) may evolve to disperse farther than generalists, while habitat generalists in the more stable tropical regions evolve to disperse farther than specialists.

I found little evidence of differences in the degree of habitat specialization between migratory and non-migratory bird species, consistent with previous empirical observations (Wunderle Jr. and Waide 1993, Stevens et al. 2014). This is likely because the fitness advantages gained by tracking temporal variation in the availability and quality of resources drive evolution of migration (Cox 1985, Holt and Fryxell 2011), rather than habitat specialization at the breeding grounds.

6.5.1 *Conclusions*

This is the first large-scale, multi-species study to demonstrate that habitat

specialists are stronger dispersers than habitat generalists. My result for temperate breeding birds is opposite to previous results for invertebrates (Bonte et al. 2003, Entling et al. 2011, Sekar 2012, Carnicer et al. 2013, Dapporto and Dennis 2013, Stevens et al. 2014, Dahirel et al. 2015), and what is expected for tropical bird species (Kennedy and Marra 2010, Ibarra-Macias et al. 2011). This suggests that a trade-off between habitat specialization and dispersal is not consistent across taxa or geographic regions. I speculate that differences in the specialization-dispersal relationship among species groups occur because other species traits or landscape attributes affect the evolution of the habitat specialization-dispersal relationship.

My results have implications for bird conservation in human-altered landscapes. It is thought that species with narrower habitat requirements and limited dispersal should receive higher conservation priority, because they are most sensitive to human landscape change (Julliard et al. 2003, Jiguet et al. 2007, Devictor et al. 2008, Garrard et al. 2012). However, if species with the narrowest habitat requirements are the most dispersive, it becomes unclear whether priority should be placed on the specialist species or the dispersal-limited species. Therefore, further study should evaluate the relative importance of habitat specialization versus dispersal limitation to extinction risk in human-altered landscapes.

Chapter 7 – General discussion

Understanding why some species are at risk of extinction, while others are thriving, can aid our conservation efforts. This is because there is an urgent need for a way to rapidly assess which species are at greatest risk. Species are going extinct at rates far exceeding the background rate of extinction (McCallum 2007, Pimm et al. 2014, Ceballos et al. 2015). Yet the International Union for Conservation of Nature, which has been assessing the conservation status of species for over 50 years, has only been able to assess 4% of the described species (76,199/1,730,725 species; IUCN 2014). Additionally, there is insufficient data to determine extinction risk for many of the assessed species; for example, 15% of the assessed vertebrates (6,006/39,223 species) are considered data-deficient, despite this being the most studied taxonomic group (IUCN 2014).

A species' risk in a human-altered landscape should depend, at least in part, on its traits. Species with traits that are adaptive in a human-altered landscape (e.g. cavity or cliff-nesting birds that nest on buildings; Jokimaki et al. 2014), those with traits allowing for rapid evolution (e.g. short generation times; Thomas et al. 2010), and those with traits allowing for phenotypic flexibility (Hendry et al. 2008) are likely to be at low risk in a human-altered landscape. Thus identifying which species traits are associated with extinction risk in the human-altered landscape can help us identify and prioritize the species of greatest conservation concern.

The overall objective of my thesis was to investigate one species trait – mobility – and why it appears to increase extinction risk in some cases, but

decrease risk in others. To do so, I used an evolutionary perspective, focusing on (a) the interacting effects of the historic landscape structure, human landscape change, and mobility on species extinction risk (Figure 1.1), and (b) co-evolution of species traits, resulting in collinearity between habitat specialization and mobility. In the following section, I outline the key findings of my thesis, and propose future research directions suggested by my findings. I then discuss the conservation implications of my research.

7.1 Key findings and future research directions

The main finding in Chapter 2 was that species behaviour at habitat boundaries evolves in response to the landscape structure; specifically, my simulations suggest that species should evolve higher probabilities of boundary crossing in landscapes with more habitat, less fragmented habitat, higher-quality matrix, and more frequent disturbance. Surprisingly, my simulations also suggested that matrix quality and disturbance frequency have much stronger effects on the evolution of boundary crossing than either habitat amount or habitat fragmentation. Although there have been many theoretical studies of landscape effects on the evolution of mobility-related characteristics (e.g. dispersal probability, path shape; Travis and Dytham 1999, Murrell et al. 2002, Travis et al. 2012), this was the first to investigate landscape effects on the evolution of a boundary-crossing response. Behaviour at habitat boundaries is an important mobility-related characteristic, because it influences the individual's ability to move among populations, and the rates of interaction with human

landscape features such as roads. This chapter contributes to our understanding of how landscape structure influences evolution of mobility-related characteristics, and supports my proposed theoretical framework, suggesting that mobility-related characteristics depend on the attributes of the landscape in which the species evolved (i.e. its historic landscape). It also has implications for empirical research, suggesting that we should not assume that habitat amount or fragmentation drives the evolved boundary-crossing response when these landscape attributes are correlated with either matrix quality or disturbance (Merckx et al. 2003, Schtickzelle and Baguette 2003).

Simulations are useful in ecological research, to refine hypotheses and prioritize future empirical research. This simulation study suggests that future empirical research should focus on the question: ***Do species evolve higher probabilities of boundary crossing in landscapes with higher-quality matrix or more frequent disturbance?*** To study the effects of landscape structure on evolution of behaviour at boundaries, I recommend the ‘common area experiment’ (as in Merckx et al. 2003), i.e. observing boundary-crossing behaviours of the offspring of individuals from landscapes with different attributes, where offspring are reared in a common environment. This study design controls for environmental effects on individual behaviour, thus differences in the behaviour of individuals from different landscapes can be assumed to be heritable. Such a study should use a sampling design that minimizes collinearity between landscape attributes, in order to measure the effects of matrix quality and disturbance frequency on behaviour at boundaries

independent of the effects of habitat amount and fragmentation (Pasher et al. 2013).

In Chapter 3 I found that more mobile North American bird species became less mobile over the last century, while less mobile species became more mobile. This was consistent with my hypothesis that a species' prior mobility affects how its mobility evolves in response to human landscape change, because prior mobility determines whether landscape change increases the costs of mobility more than its benefits. Although previous studies have found rapid changes in the mobility-related characteristics of birds in response to human landscape features (Brown and Brown 2013), this is the first study to suggest that a species' evolutionary response to human landscape change depends on its prior mobility. Interestingly, this interaction between landscape change and prior mobility has resulted in a decline in the variation in mobility among species over time. The homogenization of biotic communities, resulting in reduced genetic, taxonomic, and/or functional diversity, is a well-known consequence of human land use (McKinney and Lockwood 1999). However, my study is the first to suggest that human landscape change is homogenizing species mobility by driving selection for intermediate mobility across species. Thus results from Chapter 3 not only contribute to our understanding of the interacting effects of landscape change and prior mobility on species mobility in the altered landscape, but also identifies a previously unappreciated way in which human landscape change is homogenizing bird communities.

In Chapter 3, I found that evolution of mobility in response to habitat loss and increasing intensities of human land use depended on the species' prior mobility. Therefore, one could also ask the question: ***Does prior mobility affect the evolution of mobility in response to habitat gain?*** Although most species in their native landscapes have lost habitat, there are some that have gained habitat in the human-altered landscape (i.e. human commensals and invasive species). The prediction would be opposite to that for species experiencing habitat loss; i.e. that mobile species are becoming more mobile, while sedentary species are becoming less mobile. If true, this would have implications for species invasions. For example, Phillips et al. (2006) found that invasive cane toads (*Bufo marinus*) in Australia have become more mobile over the 70 years since their introduction, and this was correlated with an increase in the invasion rate. This suggests that more mobile invasive species may be a greater threat to native species than less mobile invaders, because they are likely to become even more mobile when introduced into a landscape with ample habitat.

The results of my simulations in Chapter 4 suggest three reasons why some theoretical and empirical studies find that mobile species are more at-risk than sedentary species, while others report the opposite. First, these simulations suggest that the relationship between mobility and extinction risk depends on what aspect of mobility you measure, because extinction risk increases with increasing mobility when mobility is measured as emigration, but decreases with increasing mobility when mobility is measured as immigration. This is because emigrants are more likely to die in a human-altered landscape than sedentary

individuals, thus mortality rates and extinction risk are higher for species with higher emigration rates. However, successful movement among habitat patches (immigration) allows rescue of small populations and recolonization after local extinction, reducing extinction risk. This finding was supported by previous theoretical studies, where those showing greater risk for more mobile species measured emigration (Casagrandi and Gatto 1999, Heino and Hanski 2001, Fahrig 2001) and those reporting less risk for more mobile species measured immigration or did not include dispersal mortality (in which case emigration equals immigration; Hill et al. 2002, Grimm et al. 2004, Reed 2004).

Unexpectedly, I found that the emigration-extinction risk relationship got stronger with faster habitat loss, and the immigration-extinction risk relationship got weaker with faster habitat loss. This suggests that the mobility-extinction risk relationship may also depend on the rate of habitat loss. Overall, more mobile species should be less at-risk than sedentary species when habitat loss is slow, because the benefits of immigration are greater than the costs of emigration. However, when habitat loss is rapid, mobile species should be more at-risk than sedentary species, because the costs of emigration are greater than the benefits of immigration. Finally, my simulations support the hypothesis that the relationship between mobility and extinction risk depends on the landscapes in which the studied species evolved (Fahrig 2007b). This is because some historic landscape attributes drive evolution of mobility-related characteristics that increase both mobility and extinction risk in human-altered landscapes, while others drive evolution of characteristics that increase mobility and decrease risk.

To my knowledge, this is the first study to test for interacting effects of the historic landscape structure, landscape change, and mobility on species extinction risk, and the first to explain the contradictory findings on the role of mobility in extinction risk.

My simulation model results suggest that future empirical research on the role of mobility in extinction risk should focus on the following: (1) ***Does the mobility-extinction risk relationship depend on how you measure mobility?***; (2) ***Does the mobility-extinction risk relationship depend on the rate of habitat loss?***; and (3) ***Does the mobility-extinction risk relationship depend on the historic landscape structure?*** Such questions could be answered by comparing cross-species mobility-extinction risk relationships for (1) different measures of mobility, (2) species in regions with different rates of habitat loss, and (3) species in regions with different historic landscape attributes.

In Chapter 5 I provide support for the population synchrony dispersal index (PSDI) developed by Tittler et al. (2006, 2009), which indirectly estimates typical dispersal distances using time-series of abundance estimates, under the assumption that dispersal between two locations results in positive, one-year-lagged correlations in abundances between those locations. I found strong, positive correlations between PSDI and independent estimates of mean dispersal distances, although PSDI estimates tended to be larger. Reliable estimates of dispersal are relatively rare; in a recent review, 46% of studies identified the lack of dispersal knowledge as an impediment to research (Driscoll et al. 2014). My study suggests that researchers can take advantage of large-scale, longitudinal,

multi-species data sets to estimate relative dispersal distances. Additionally, this finding advances our understanding of the role of dispersal in population synchronization. Although previous studies have suggested that dispersal can synchronize populations (Paradis et al. 1999, Powney et al. 2011, 2012, Chevalier et al. 2014, Mortelliti et al. 2014), mine is the first to show that the distance at which dispersal most strongly synchronizes populations is correlated with empirical estimates of dispersal distance.

In my final data chapter I found evidence of collinearity between habitat specialization and dispersal distance for temperate breeding birds; specifically, that habitat specialist species disperse farther than habitat generalist species. This is the first large-scale, multi-species study to demonstrate a habitat specialization-mobility relationship in birds, and the first to find that habitat specialists are stronger dispersers than habitat generalists. Interestingly, this finding is opposite to previous results for invertebrates (Bonte et al. 2003, Entling et al. 2011, Sekar 2012, Carnicer et al. 2013, Dapporto and Dennis 2013, Stevens et al. 2014, Dahirel et al. 2015), and opposite to what is expected for tropical bird species (Kennedy and Marra 2010, Ibarra-Macias et al. 2011). Thus this finding is important, because it suggests that the trade-off between habitat specialization and mobility is not consistent across taxa or geographic regions. This in turn suggests that collinearity between habitat specialization and mobility could contribute to the conflicting findings on the role of mobility in extinction risk. If habitat specialization increases extinction risk, then mobility may appear to decrease extinction risk in cases where habitat specialists are the least mobile

species, and mobility may appear to increase extinction risk in cases where habitat specialists are the most mobile species.

However, identifying that the habitat specialization-mobility relationship can vary among species groups is only the first step to showing that collinearity contributes to the conflicting findings on the role of mobility in extinction risk. For habitat specialization to cause a spurious relationship between mobility and risk, we expect habitat specialization to be more important for species extinction risk in a human-altered landscape than mobility. Therefore the next step is to answer the question: ***Is habitat specialization more important for species extinction risk than mobility?*** Habitat specialization may be more important for species extinction risk than mobility. This is because habitat generalists are likely to be more resilient to habitat loss than habitat specialists, regardless of their mobility, because habitat generalists can use more of the land cover classes in a human-altered landscape as habitat. This is supported by evidence that habitat specialists have a more negative response to a given landscape change than habitat generalists (Munday 2004, Devictor et al. 2008). Additionally, ***What is the effect of mobility on extinction risk, independent of the effect of habitat specialization?*** Studies addressing these questions should minimize collinearity between habitat specialization and mobility, to the degree possible, and use the standardized partial regression coefficients from multiple regression to indicate relative importance, as these provide unbiased estimates of relative importance even when predictors are highly correlated (Smith et al. 2009).

Another question prompted by my findings is: ***Why does habitat specialization increase with mobility in some species groups, but decrease with mobility in others?*** In Chapter 6, I proposed two hypotheses. First, I hypothesized that the habitat specialization-mobility relationship depends on the effects of another species trait on the cost-benefit trade-offs of specialization and mobility. In particular, I speculated that ectothermy in invertebrates may favor evolution of increasing mobility with decreasing habitat specialization, while endothermy in birds favors increasing mobility with increasing habitat specialization. This is because endotherms are more sensitive to local resource scarcity than ectotherms (Buckley et al. 2012). Thus for ectothermic specialists, that can wait out periods of low resources, the higher costs of dispersal likely favor reduced mobility relative to generalists. For endothermic specialists, that must disperse to avoid periods of low resource availability, greater mobility is favored because they need to move farther than generalists when searching for resources. Second, I hypothesized that the habitat specialization-mobility relationship depends on the landscape structure in which the species evolved. For example, I speculated that, in a landscape where local extinction events are rare, the higher costs of dispersal for specialists should drive selection for lower mobility than in generalists. However, in a more spatially or temporally dynamic landscape, the need to disperse to escape locally declining conditions and recolonize after local extinctions should drive selection for greater mobility in habitat specialists than in generalists, because specialists need to move farther to locate resources.

7.2 Conservation implications

My simulation results suggest some general implications for species conservation and management in human-altered landscapes, although I stress that simulation results should be supported with empirical study, wherever possible. My simulations suggest that a species' extinction risk depends on its emigration and immigration rates; i.e. species that emigrate but cannot move the long distances among habitat fragments in a human-altered landscape are most at-risk. However, mobile species should generally be at greater risk than sedentary species in landscapes with rapid habitat loss, and sedentary species at greater risk than mobile species in landscapes with slow habitat loss. We may lack the data needed to accurately estimate mobility for many species (Driscoll et al. 2014). For these species, consideration of the historic landscape structure can help identify the most at-risk species, i.e. species that evolved in landscapes with abundant, un-fragmented, dynamic habitat, and low-quality matrix. If the model predictions are valid, conservation efforts should focus on these species.

My empirical data chapters also have conservation implications for temperate breeding birds, particularly the finding of a relationship between habitat specialization and mobility. It is thought that species with narrower habitat requirements and shorter dispersal distances should receive higher conservation priority, because they are most sensitive to human landscape change (Julliard et al. 2003, Jiguet et al. 2007, Devictor et al. 2008, Garrard et al. 2012). However, if species with the narrowest habitat requirements disperse the longest distances,

conserving habitat specialists will not protect the dispersal-limited species. Thus my study suggests that, when conservation resources are limited, we may need to decide whether to prioritize the habitat specialist species, or the dispersal-limited ones.

Future study is required to determine whether habitat specialization or mobility is most important for extinction risk; however, based on the available evidence, I suggest that priority should be placed on temperate bird species with the narrowest habitat requirements. This is because most temperate breeding birds (even the sedentary generalists) are not limited by dispersal (Barbet-Massin et al. 2012). PSDI estimates of typical dispersal distances (Chapters 5 and 6) suggest that most temperate breeding birds should be able to traverse the distances among habitat fragments and track changes in their habitat distribution caused by climate change, with most species able to disperse tens to hundreds of km (Figure 7.1). Mark-recapture sampling supports this, with recorded dispersal events of over 200 km for a number of species (Paradis et al. 1998).

7.3 Conclusions

The relationship between species mobility and extinction risk is not simple: theoretical and empirical studies suggest that mobility increases extinction risk in some cases, but decreases risk in others. My thesis is the first step to understanding why these conflicting mobility-extinction risk relationships occur.

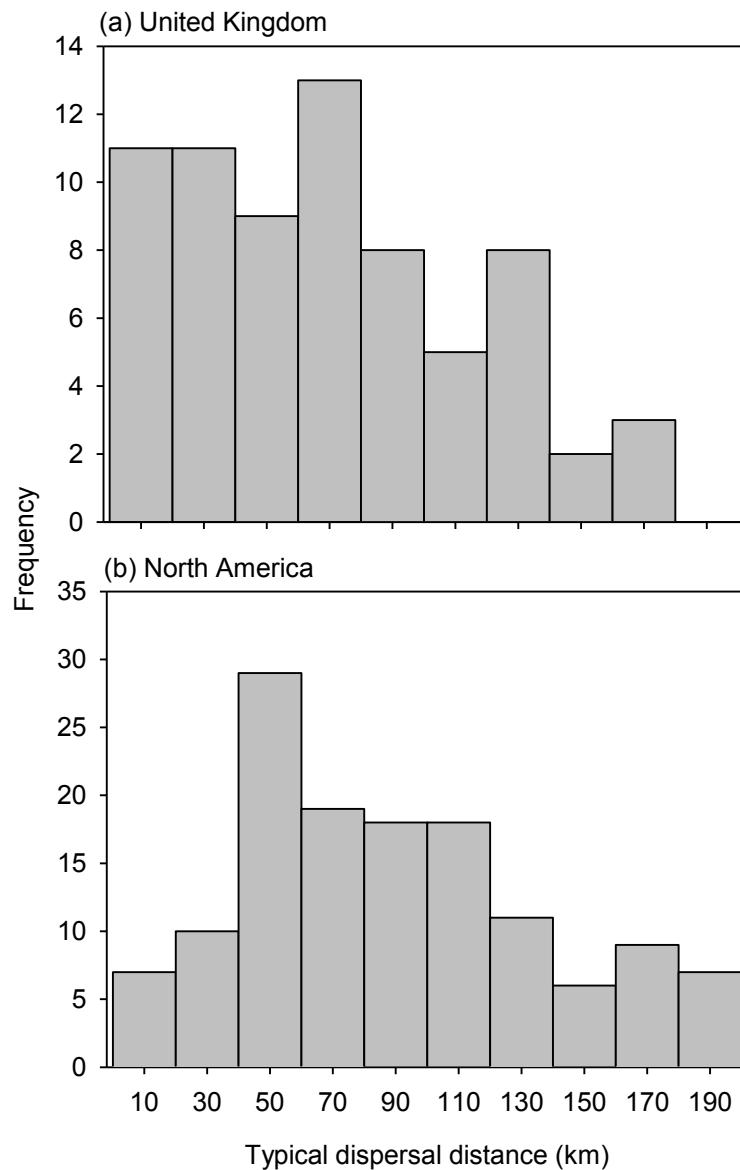


Figure 7.1. Frequency distribution of typical dispersal distances (km), estimated by the population synchrony dispersal index, at $\alpha = 0.05$ for (a) United Kingdom species (estimated in Chapter 5) and (b) North American species (estimated in Chapter 6).

My thesis supports the suggestion that a species' mobility depends on both its evolutionary history and its evolutionary response to human landscape change. I showed that mobility-related characteristics could evolve in response to landscape structure, and that a species' mobility influenced how its mobility changed in response to human landscape change (Chapters 2 and 3). If the historic landscape, human landscape change, and mobility interact such that mobility increases extinction risk in some landscapes but decreases risk in others, this could explain the conflicting findings on the role of mobility in extinction risk. Simulations in Chapter 4 modelled these interactions, and suggested three factors that may influence the mobility-extinction risk relationship: (1) the mobility metric, (2) the rate of landscape change, and (3) the historic landscape structure. I also provided preliminary evidence that collinearity between habitat specialization and species mobility may contribute to the conflicting findings on the role of mobility in extinction risk (Chapter 6).

Future research is required to validate these explanations, and to determine the relative importance of these factors' effects on the mobility-risk relationship. If the mobility-risk relationship could be predicted based on one or a few of these factors, then one could provide relatively simple guidelines for predicting the direction of the mobility-risk relationship for species in different taxa or geographic regions.

My thesis also has implications for species conservation and management in human-altered landscapes. If the model predictions are valid, conservation efforts should focus on species that frequently emigrate but cannot move the

long distances between habitat fragments in a human-altered landscape. This should be particularly important in landscapes where habitat loss is rapid, and the costs of emigration outweigh the benefits of movement between populations.

Appendices

Appendix A Flow charts for each of the five subprocesses in the model simulating evolution of species behaviour at habitat boundaries.

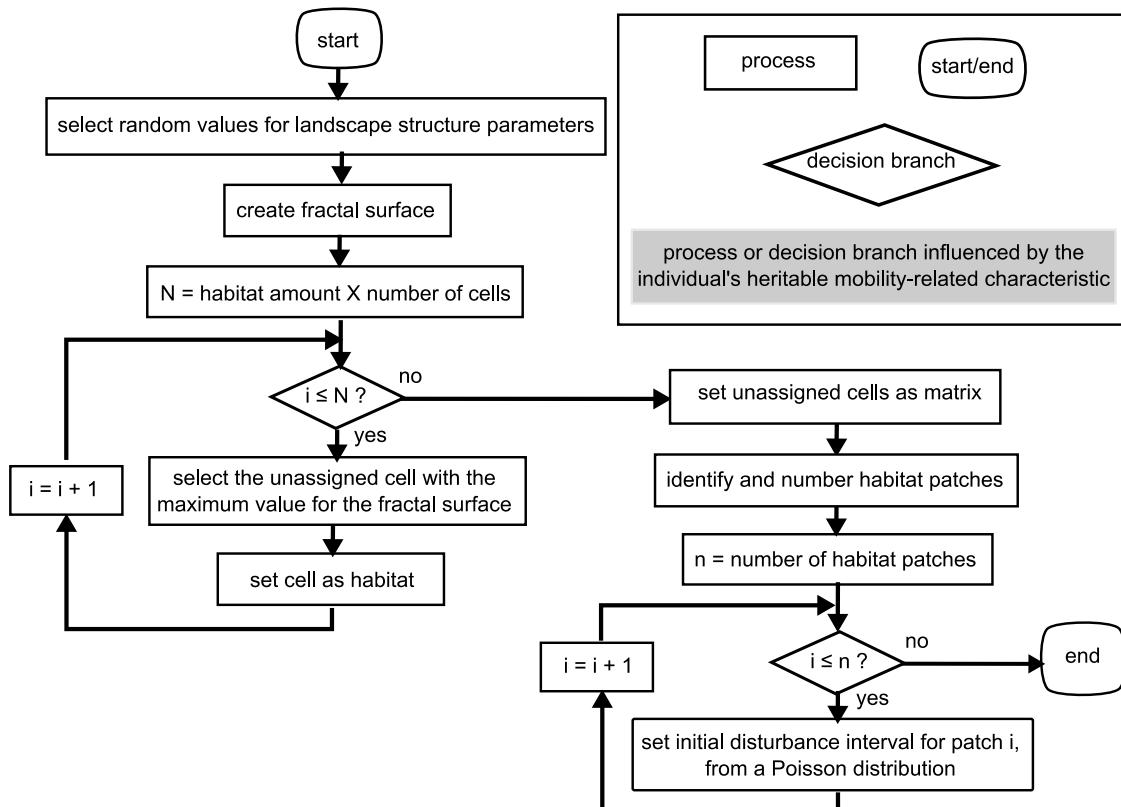


Figure A1. Flow chart for the 'create landscape' subprocess of the simulation model (see Figure 2.2 for the model overview).

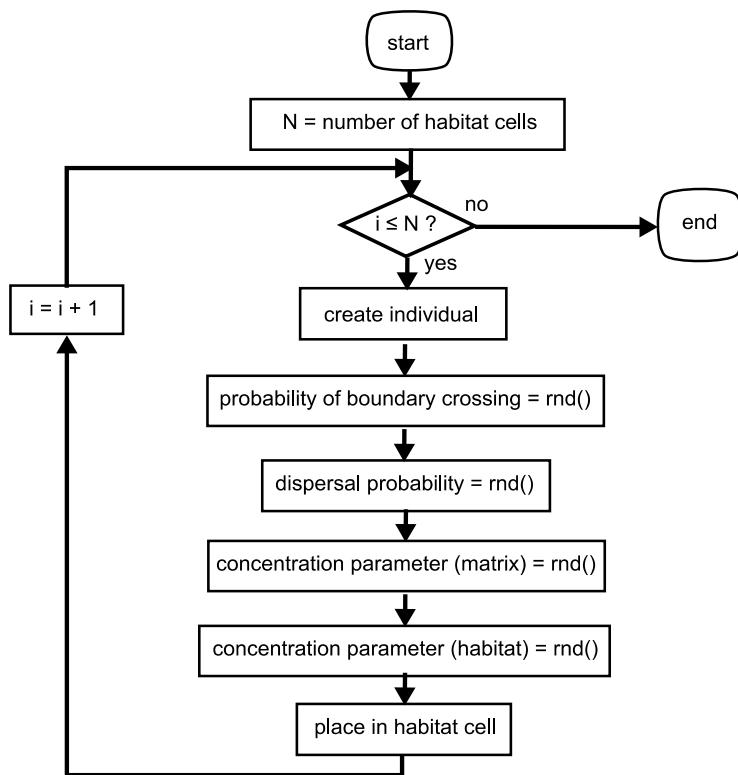


Figure A2. Flow chart for the ‘populate landscape’ subprocess of the simulation model (see Figure 2.2 for the model overview). See Figure A1 for the flow chart legend. $\text{rnd}()$ = random number between 0 and 1, drawn from a uniform distribution.

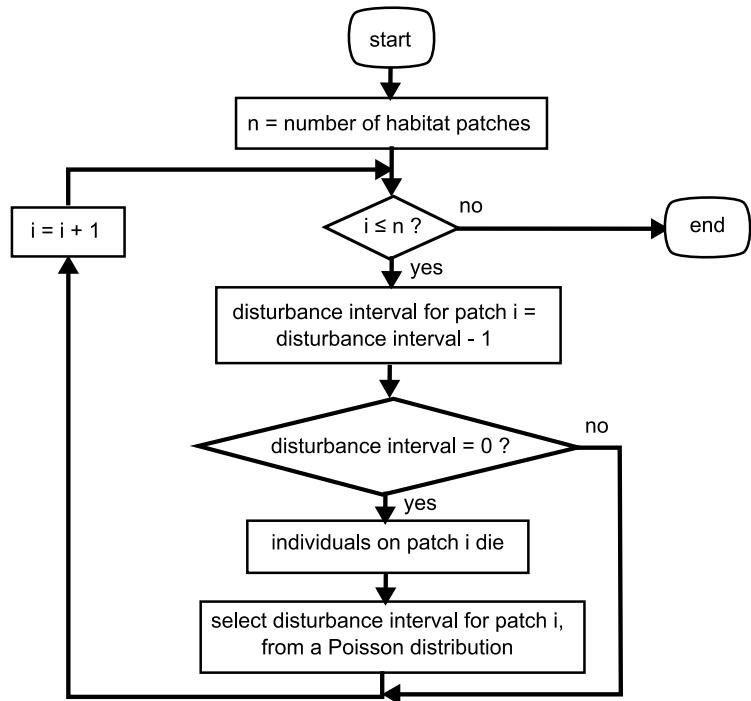


Figure A3. Flow chart for the 'disturbance' subprocess of the simulation model

(see Figure 2.2 for the model overview). See Figure A1 for the flow chart legend.

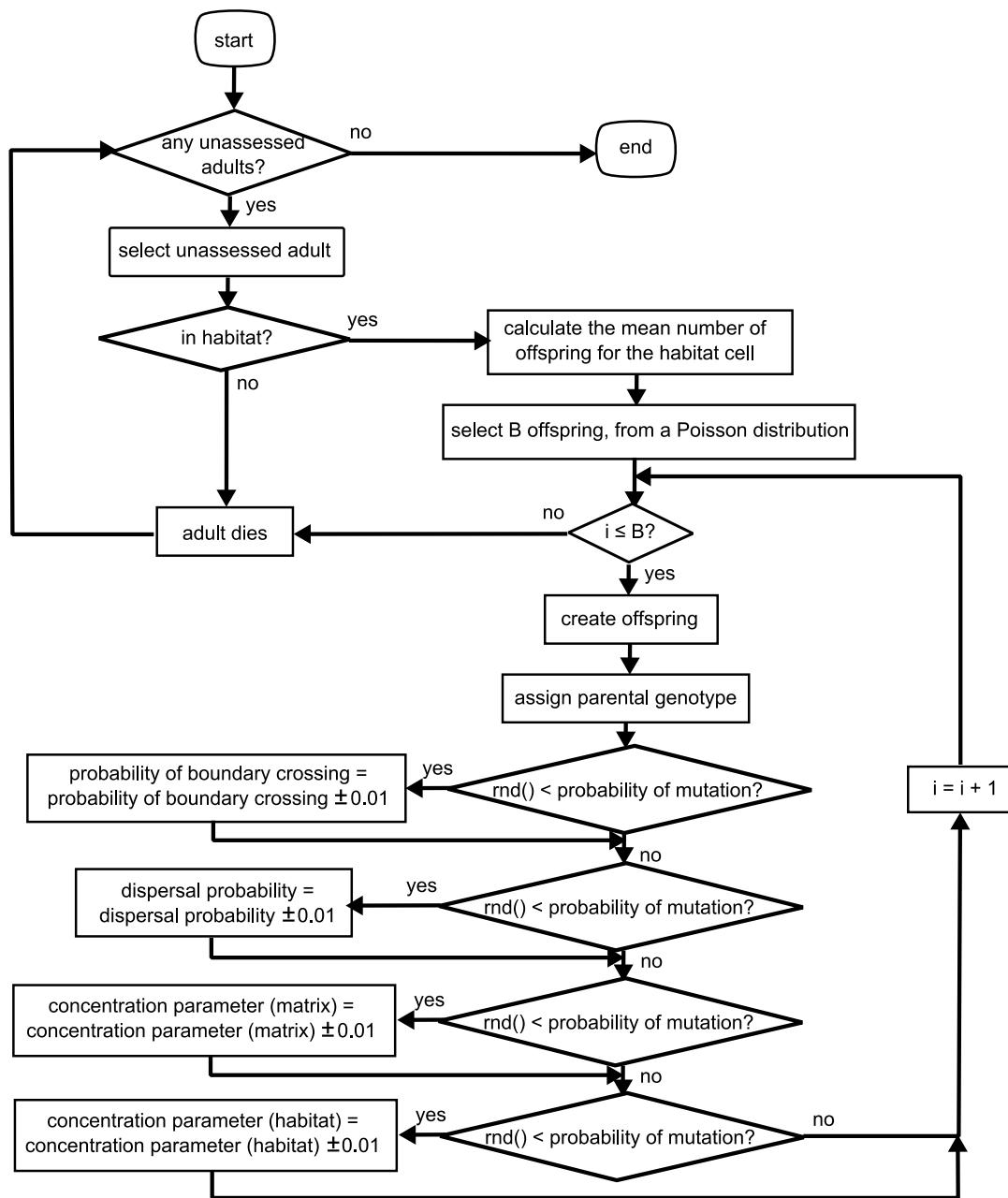


Figure A4. Flow chart for the ‘reproduction’ subprocess of the simulation model (see Figure 2.2 for the model overview). See Figure A1 for the flow chart legend.

`rnd()` = random number between 0 and 1, drawn from a uniform distribution.

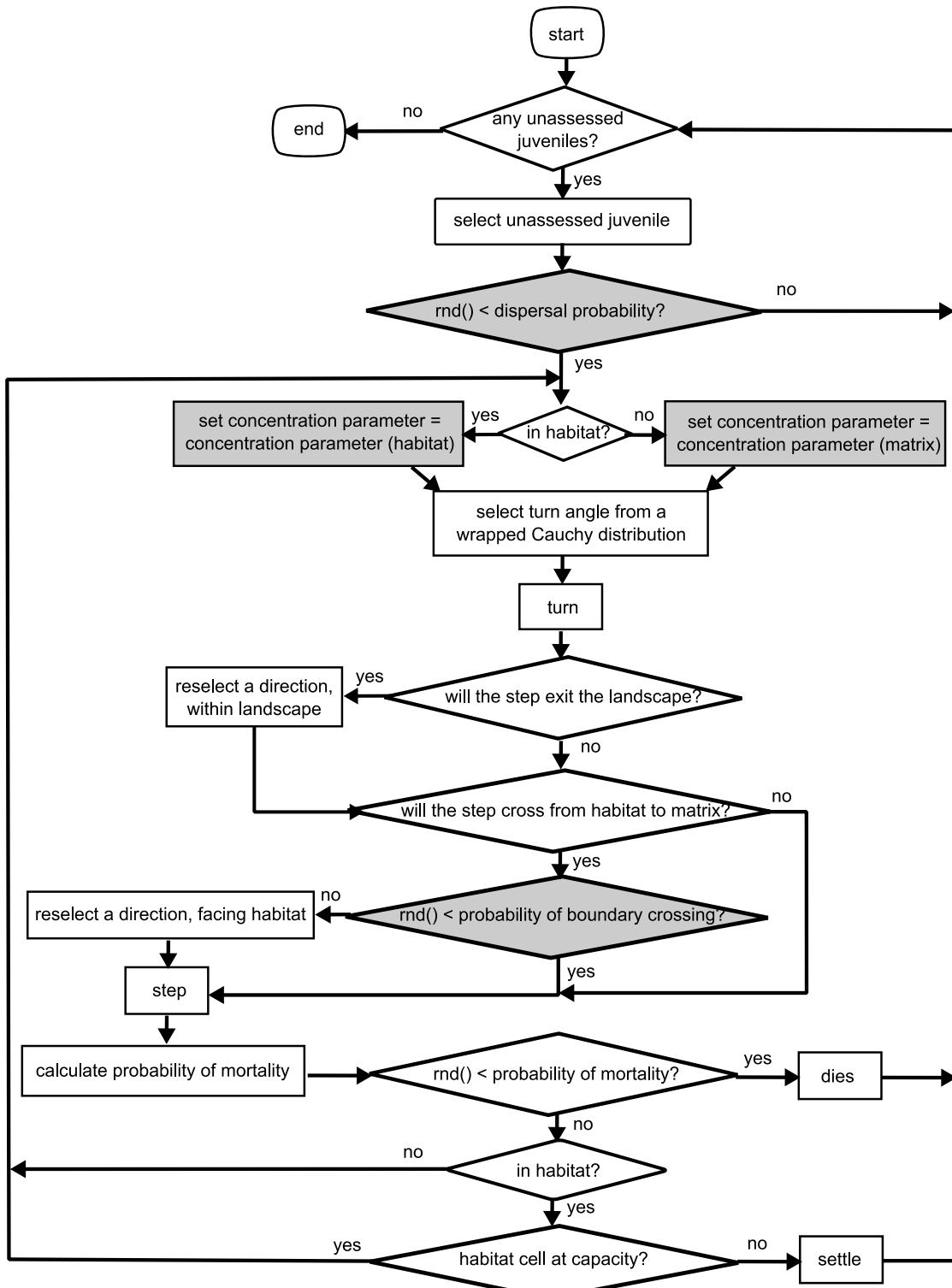


Figure A5. Flow chart for the 'dispersal' subprocess of the simulation model (see Figure 2.2 for the model overview). See Figure A1 for the flow chart legend. $\text{rnd}()$ = random number between 0 and 1, drawn from a uniform distribution.

Appendix B Parameters used in the model simulating evolution of species behaviour at habitat boundaries.

Table B1. Parameters used in the simulation model. Subheadings indicate parameters that were kept constant for all simulation runs (constants), parameters that were varied between simulation runs but were constant within a given run (landscape attributes), and parameters that were allowed to vary among individuals and to evolve in response to the costs and benefits of dispersal (evolved mobility-related characteristics).

Parameter	Description	Value(s)
Constants		
landscape size	number of grid cells (dimensions)	16,129 (127 × 127)
generations		1000
habitat quality	probability of mortality during dispersal across a habitat cell	0.005
intrinsic rate of increase (λ)	variable in the model of the mean number of offspring produced by each adult inhabiting a habitat cell (equation 2.1)	3

(continued on the following page)

Table B1 continued.

Parameter	Description	Value(s)
Constants		
cell carrying capacity (k)	threshold number of offspring supported by a habitat cell, involved in determining the mean number of offspring (equation 2.1) and settlement during dispersal	6
mutation rate	probability of mutation, leading to a change in the value of the target mobility-related characteristic (± 0.01)	0.005
Landscape attributes		
habitat amount	proportion of the grid cells in habitat; smaller values mean less habitat	0.1 – 0.7
habitat fragmentation	Hurst exponent, determining spatial autocorrelation of habitat; smaller values relate to greater fragmentation	0 – 1
matrix quality	probability of mortality during dispersal across a matrix cell; lower probabilities of mortality relate to higher quality	0.006 – 0.2
disturbance frequency	mean number of generations until disturbance, for a Poisson distribution; lower values cause more frequent disturbance	10 – 100

(continued on the following page)

Table B1 continued.

Parameter	Description	Value(s)
Evolved mobility-related characteristics		
probability of boundary crossing	probability of an individual crossing from habitat to matrix when it encounters a boundary	0 – 1
dispersal probability	probability of dispersal in a given generation	0 – 1
path straightness (ρ) in matrix	determines the degree of change in movement direction between successive movement steps originating in matrix, for a wrapped Cauchy distribution	0 – 1
path straightness (ρ) in habitat	determines the degree of change in movement direction between successive movement steps originating in habitat, for a wrapped Cauchy distribution	0 – 1

Appendix C Effects of landscape structure on the evolution of dispersal probability, path shape in matrix, and path shape in habitat.

Table C1. Percent sum of squares (%SS), for a multiple linear regression model of the relationship between the population mean dispersal probability after 1000 generations and the four landscape attributes, for 1000 simulation runs.

Relationships were modelled using square-root-transformed measures of the dispersal probability. I included quadratic terms for each predictor, to account for non-linear relationships. %SS combines the variance explained by both the linear and quadratic terms.

Attribute	%SS
Habitat amount	3.75
Habitat fragmentation	0.64
Matrix quality	0.50
Disturbance frequency	10.03
Residual	85.08

Table C2. Percent sum of squares (%SS), for a multiple linear regression model of the relationship between the population mean path straightness in matrix after 1000 generations and the four landscape attributes, for 1000 simulation runs. Relationships were modelled using square-root-transformed path straightness. I included quadratic terms for each predictor, to account for non-linear relationships. %SS combines the variance explained by both the linear and quadratic terms.

Attribute	%SS
Habitat amount	31.16
Habitat fragmentation	2.52
Matrix quality	0.59
Disturbance frequency	22.80
Residual	42.93

Table C3. Percent sum of squares (%SS), for a multiple linear regression model of the relationship between the population mean path straightness in habitat after 1000 generations and the four landscape attributes, for 1000 simulation runs. Relationships were modelled using square-root-transformed path straightness. I included quadratic terms for each predictor, to account for non-linear relationships. %SS combines the variance explained by both the linear and quadratic terms.

Attribute	%SS
Habitat amount	38.72
Habitat fragmentation	2.78
Matrix quality	1.31
Disturbance frequency	17.11
Residual	40.08

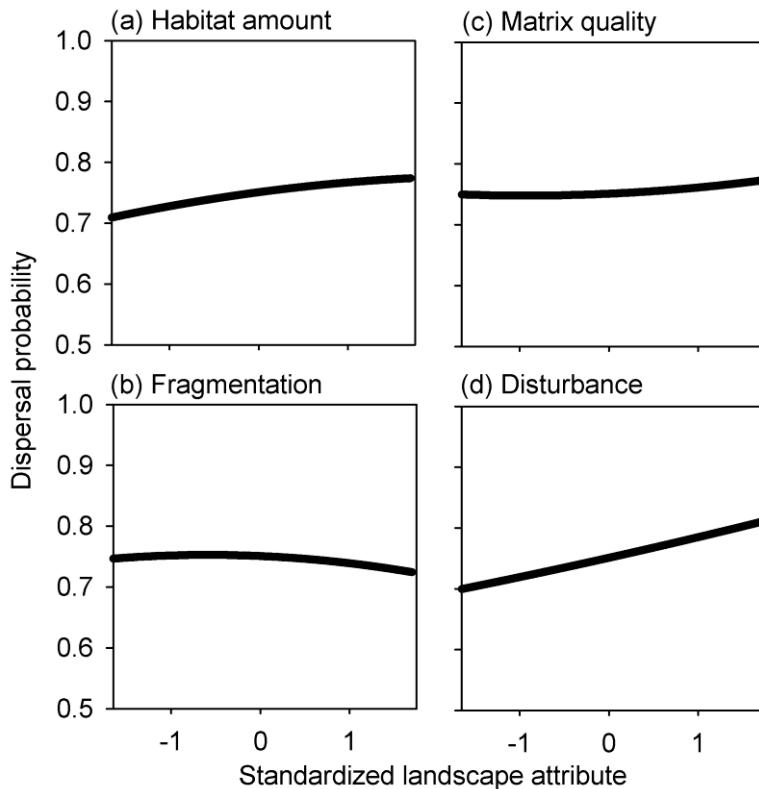


Figure C1. Effects of (a) habitat amount, (b) habitat fragmentation, (c) matrix quality, and (d) disturbance frequency on the evolved dispersal probability, when holding all other landscape attributes at their mean values. Standardized landscape attribute values were scaled such that larger values indicate more habitat, more fragmented habitat, higher matrix quality, and more frequent disturbance. Relationships were modelled by multiple linear regression, using square-root-transformed dispersal probabilities (back-transformed prior to plotting), for the 1000 simulation runs.

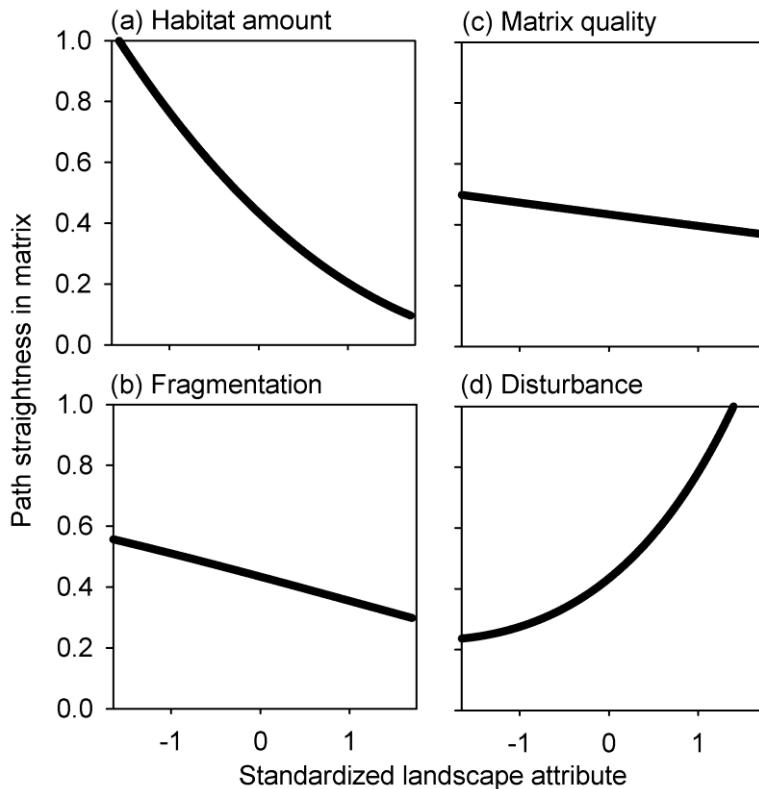


Figure C2. Effects of (a) habitat amount, (b) habitat fragmentation, (c) matrix quality, and (d) disturbance frequency on the evolved path straightness in matrix, when holding all other landscape attributes at their mean values. Standardized landscape attribute values were scaled such that larger values indicate more habitat, more fragmented habitat, higher matrix quality, and more frequent disturbance. Relationships were modelled by multiple linear regression, using square-root-transformed estimates of path straightness (back-transformed prior to plotting), for the 1000 simulation runs.

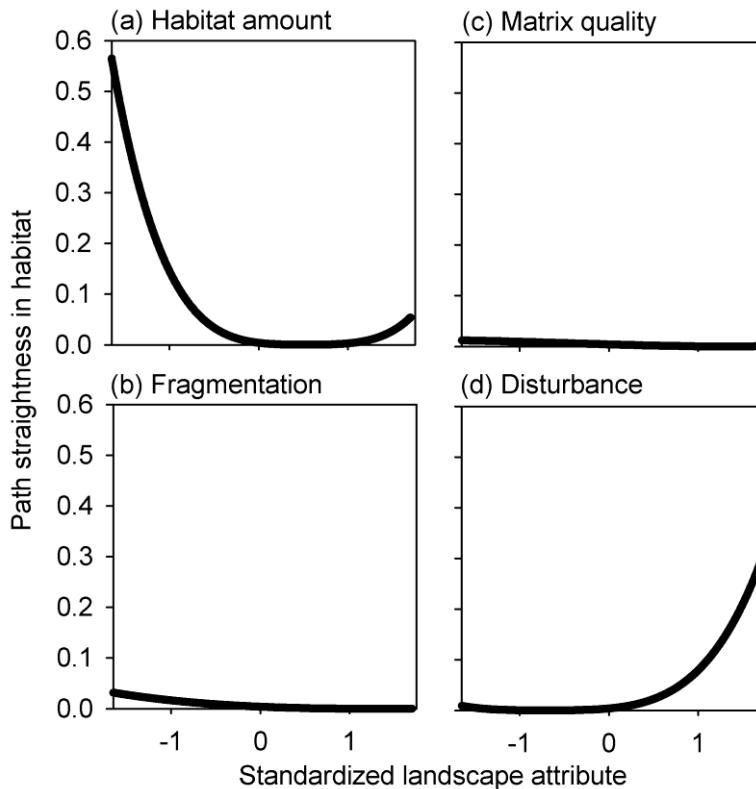


Figure C3. Effects of (a) habitat amount, (b) habitat fragmentation, (c) matrix quality, and (d) disturbance frequency on the evolved path straightness in habitat, when holding all other landscape attributes at their mean values.

Standardized landscape attribute values were scaled such that larger values indicate more habitat, more fragmented habitat, higher matrix quality, and more frequent disturbance. Relationships were modelled by multiple linear regression, using square-root-transformed estimates of path straightness (back-transformed prior to plotting), for the 1000 simulation runs.

Appendix D The relationship between the prior primary wing projection and its rate of change is not a statistical artifact.

Methods

If the negative correlation between the prior primary wing projection and the rate of change in primary projection was a statistical artifact, then parameter estimates in the statistical model would have to be biased, such that the actual (population-level) rate of change in primary projection was overestimated when the prior primary projection was small, and the actual rate of change in primary projection was underestimated when the prior primary projection was large (Figure D1). Such bias should cause the correlation between the actual prior projection and its rate of change to be more positive than the correlation between the model-estimated prior primary projection and its rate of change. To test this, I simulated 1000 data sets with a known cross-species correlation between the prior primary projection and its rate of change and, for each data set, compared this known correlation to the correlation between the prior primary projection and rate of change in primary projection estimated by linear regression.

For each simulation, I: (1) set the actual cross-species correlation between the prior primary projection and rate of change in primary projection ($-1 < r < 1$); (2) selected a prior primary projection and rate of change in primary projection for

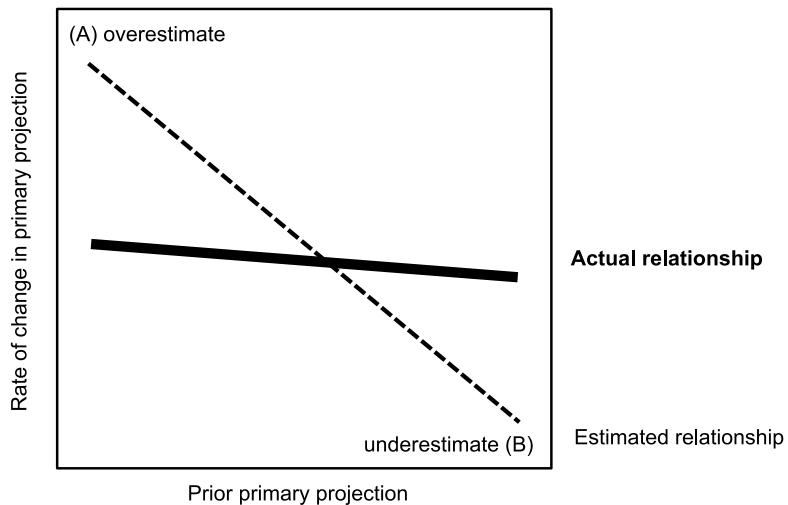


Figure D1. If the negative correlation between the prior primary wing projection and rate of change in primary projection was a statistical artifact, parameter estimates in the statistical model would have to be biased, such that the actual (population-level) rate of change in primary projection was overestimated when the prior primary projection was small (A), and the actual rate of change in primary projection was underestimated when the prior primary projection was large (B).

each of 21 species, to produce the correlation set in step 1; (3) simulated 100 years of primary projection estimates for each species as

$$y = mx + b + \epsilon \quad \text{equation D1}$$

where m = rate of change in primary projection, x = year, b = prior primary projection, and ϵ was normally distributed, with mean = 0 and a standard deviation that varied between simulation runs; and (4) predicted the prior primary projection (i.e. intercept) and rate of change in primary projection (i.e. slope) for each species, from a linear regression model of the relationship between the primary projection and year. I then compared the cross-species correlation between the actual prior primary projection and its rate of change (from steps 1-2, above) to the correlation between the prior primary projection and its rate of change estimated from the model (steps 3-4).

Simulations and analyses were run in R (R Core Team 2014), using the 'MASS' (Ripley et al. 2015) package.

Results

The cross-species correlation between the prior primary wing projection and rate of change in primary projection estimated from the statistical model was just as likely to overestimate the actual correlation as underestimate it (Figure D2).

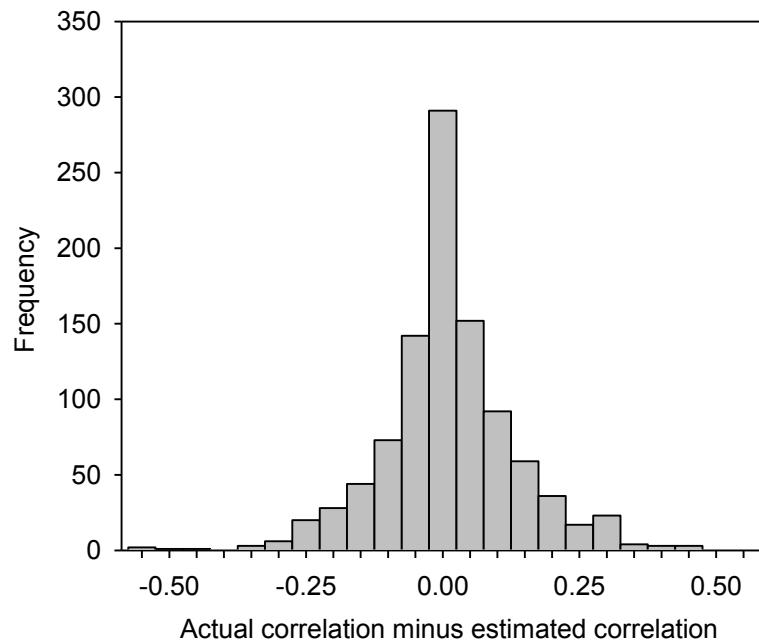


Figure D2. Frequency distribution of the cross-species correlation between the actual prior primary projection and its rate of change (i.e. actual correlation) minus the cross-species correlation of the model-estimated prior primary projection and its rate of change (i.e. estimated correlation).

Appendix E Habitat selection indices for North American breeding birds.**Methods**

To determine the extent to which the study species use, or avoid, human-dominated areas of the landscape, I empirically estimated habitat selection indices for the 21 study species, using the North American Breeding Bird Survey (NA BBS) and a classified land cover data set to calculate habitat selection indices for different native and human-dominated land cover classes. The NA BBS provides a continent-wide, multi-year data set of species counts for breeding birds, beginning in 1966 (Pardieck et al. 2014). Point counts are conducted at 50 stops spaced along each 39.4 km-long roadside survey route once each year during the breeding season. At each point count, all birds seen or heard within a 0.4 km radius are recorded over a 3-minute interval. My sampling sites were the first stop of each NA BBS route sampled in 2003 – 2007, summing the species counts across these years for each sampling site. I used only the first stop, because it was the only stop with reliable latitude-longitudes for all routes. I selected 2003 – 2007 to bracket the year of the land cover data (2005). I defined 11 land cover classes from the 19 classes in the land cover data (Table E1, Figure E1a; NRCan et al. 2005). Classification was based on Moderate Resolution Imaging Spectroradiometer imagery, combining classifications of national land cover from the United States, Canada, and Mexico, as part of the North American Agreement on Environmental Cooperation.

Table E1. Land cover classifications, showing how land cover classes from the original data set (NRCan et al. 2005) were combined to produce the 11 land cover classes used in this study.

Land cover	NRCan et al. (2005)
needleleaf forest	sub-polar taiga needleleaf forest
	temperate or sub-polar needleleaf forest
mixed forest	mixed forest
broadleaf forest	temperate or sub-polar broadleaf deciduous forest
	tropical or sub-tropical broadleaf evergreen forest
	tropical or sub-tropical broadleaf deciduous forest
shrubland	sub-polar or polar shrubland-lichen-moss
	temperate or sub-polar shrubland
	tropical or sub-tropical shrubland
grassland	sub-polar or polar grassland-lichen-moss
	temperate or sub-polar grassland
	tropical or sub-tropical grassland
wetland	wetland
water	water
ice and snow	ice and snow
barren	barren land
	sub-polar or polar barren-lichen-moss
agriculture	cropland
developed	urban and built-up

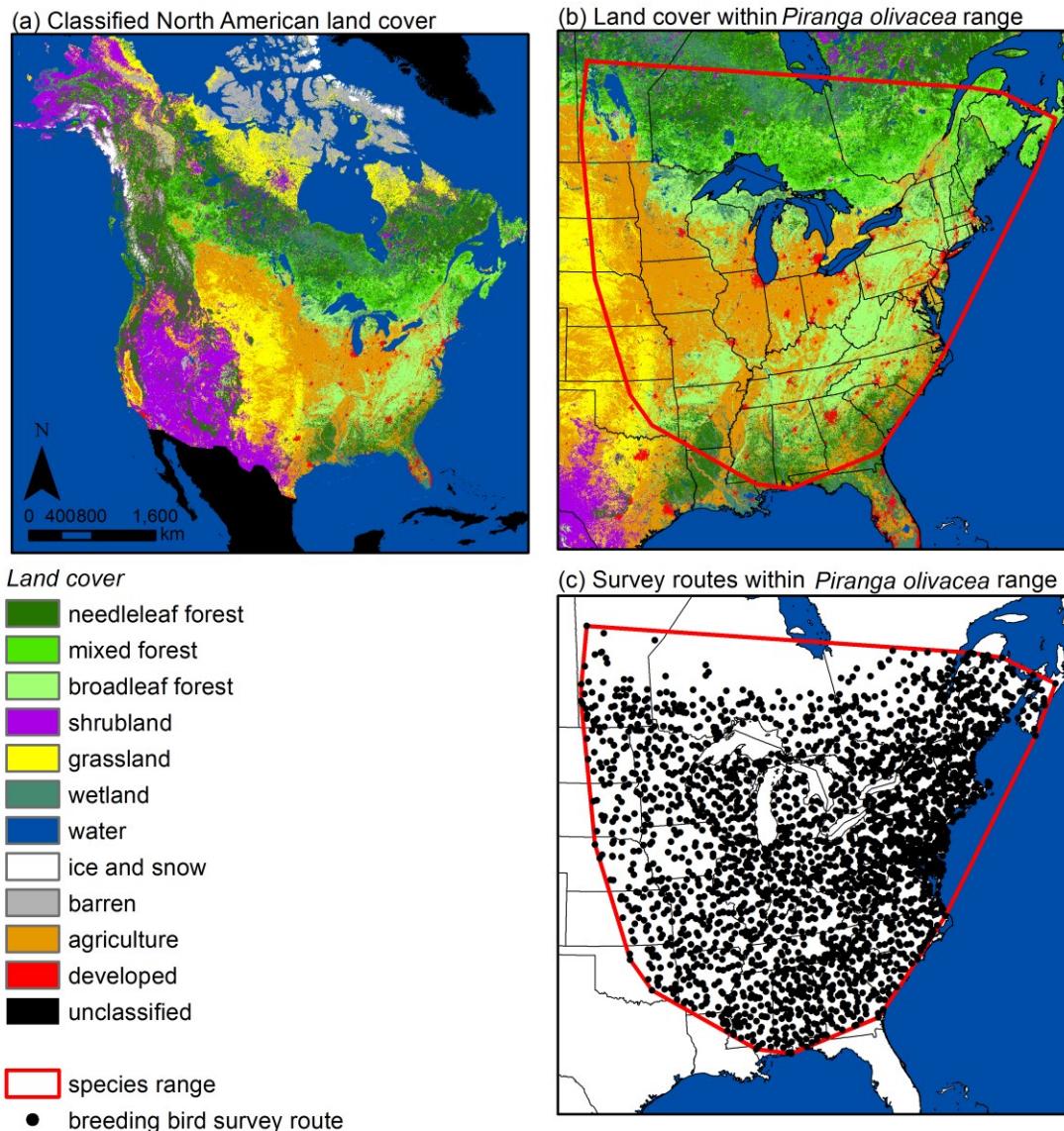


Figure E1. (a) Classified North American land cover, used to calculate habitat selection ratios (HSR_i) for each species. A HSR_i was measured as the proportion of species observations in land cover class i , divided by the proportion of all sampling locations in the species range in land cover class i . For example, HSR_i for *Piranga olivacea* (scarlet tanager) were calculated using only the (b) land cover and (c) North American Breeding Bird Survey data from within the species range.

To estimate the degree to which a species prefers, or avoids, a given land cover class, I calculated a habitat selection ratio (HSR_i) for each of 11 land cover classes for each species. HSR_i was measured as the proportion of species observations in land cover class i , divided by the proportion of all sampling locations in the species range in land cover class i (Kallio 2014), where the species range was estimated as the minimum convex polygon around all routes where the species was detected at least once during the entire time series of the NA BBS (Figure E1b-c). To ensure sample sizes were large enough to allow for reasonable estimation of the HSR_i , I only included species observed at the first stop of at least 10 routes between 2003 – 2007. HSR_i values greater than one indicate habitat preference; i.e. more individuals were observed in the land cover class than expected, given the availability of that land cover class within the species range and set of sampling sites. HSR_i values between zero and one indicate avoidance; i.e. that fewer individuals were observed in the land cover class than expected.

Results

I estimated HSR_i for each land cover class for the 16 species observed at more than 10 routes. Most were forest species (14/16 species), and more than half (10/16 species) were also found in wetlands more often than expected given wetland availability (Figure E2). Few of the study species used human-dominated land cover classes as habitat; $HSR_{\text{agriculture}}$ were greater than one in only 3/16

species (Figure E2a,m,n) and all species avoided intensively developed areas ($\text{HSR}_{\text{developed}} < 1$).

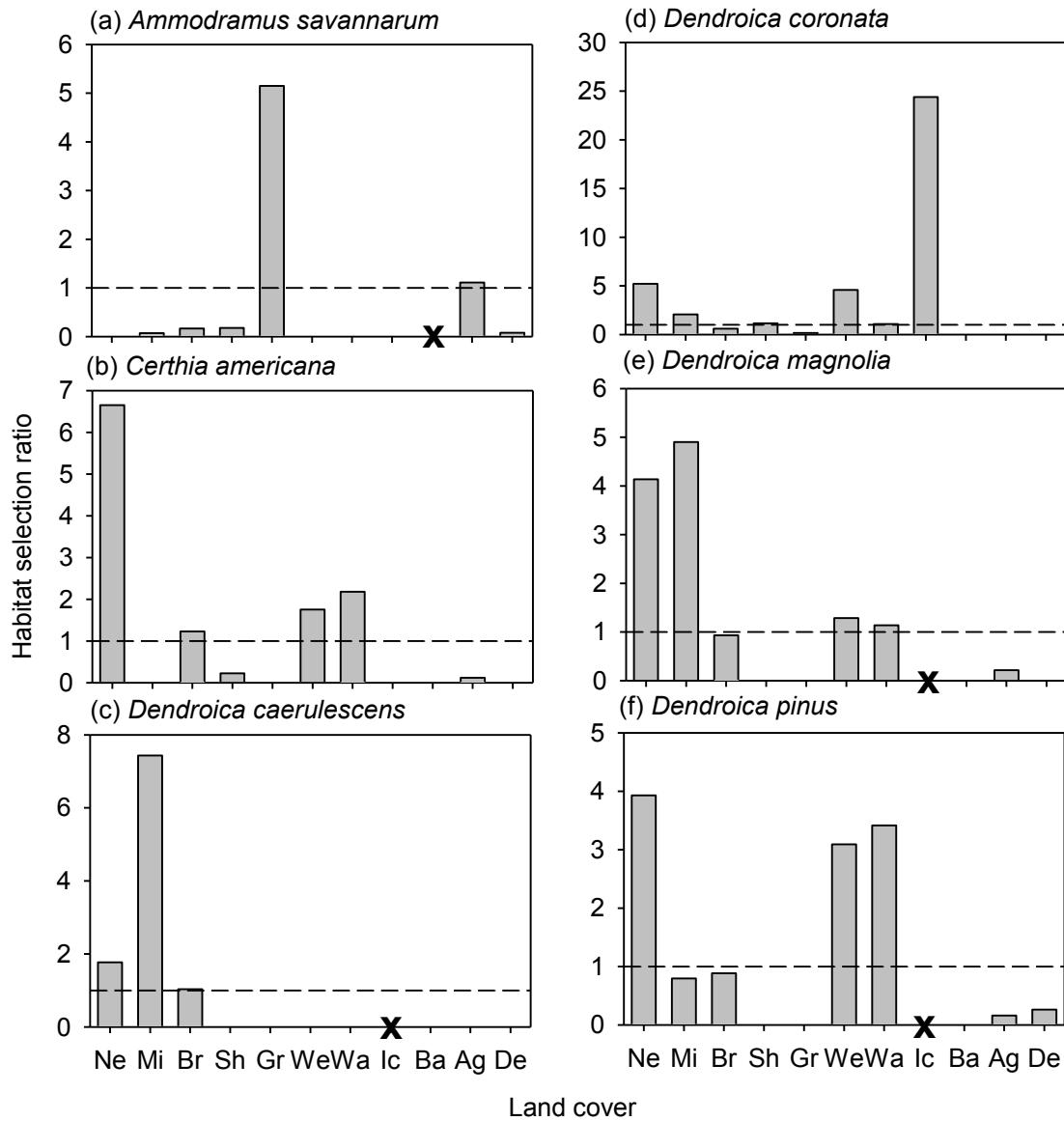
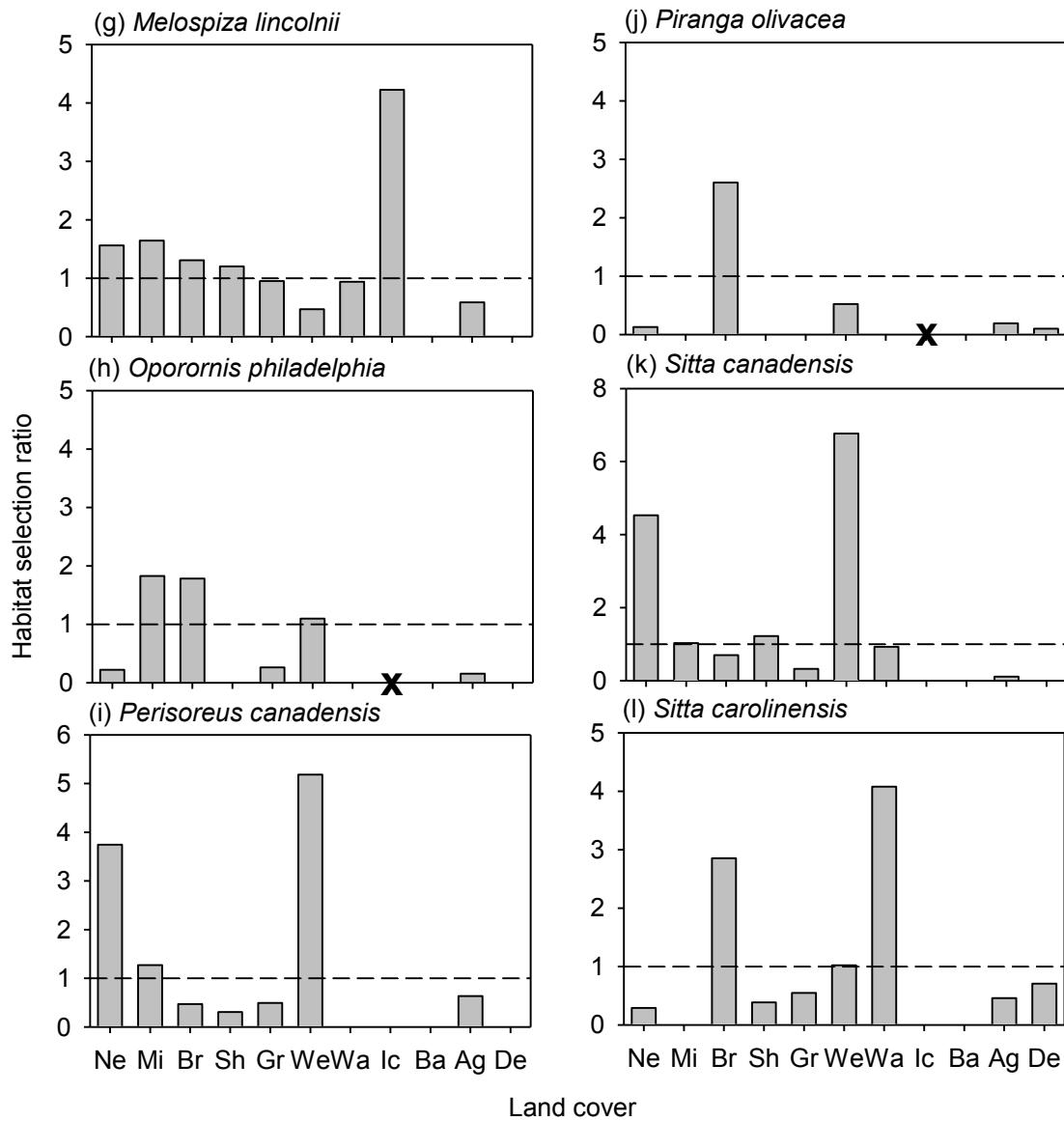


Figure E2. Habitat selection ratios (HSR_i) for each of 16 North American bird species. The HSR_i is the proportion of species observations in land cover class i , divided by the proportion of all sampling locations in the species range in that land cover class. $HSR_i > 1$ indicate preferential use of a land cover relative to its availability. $HSR_i < 1$ indicate avoidance of a land cover. Ne = needleleaf forest;
(continued on the following page)

Mi = mixed forest; Br = broadleaf forest; Sh = shrubland; Gr = grassland; We = wetland; Wa = water; Ic = ice and snow; Ba = barren; Ag = agriculture; De = developed; **X** = land cover not found in the species range.

**Figure E2** continued.

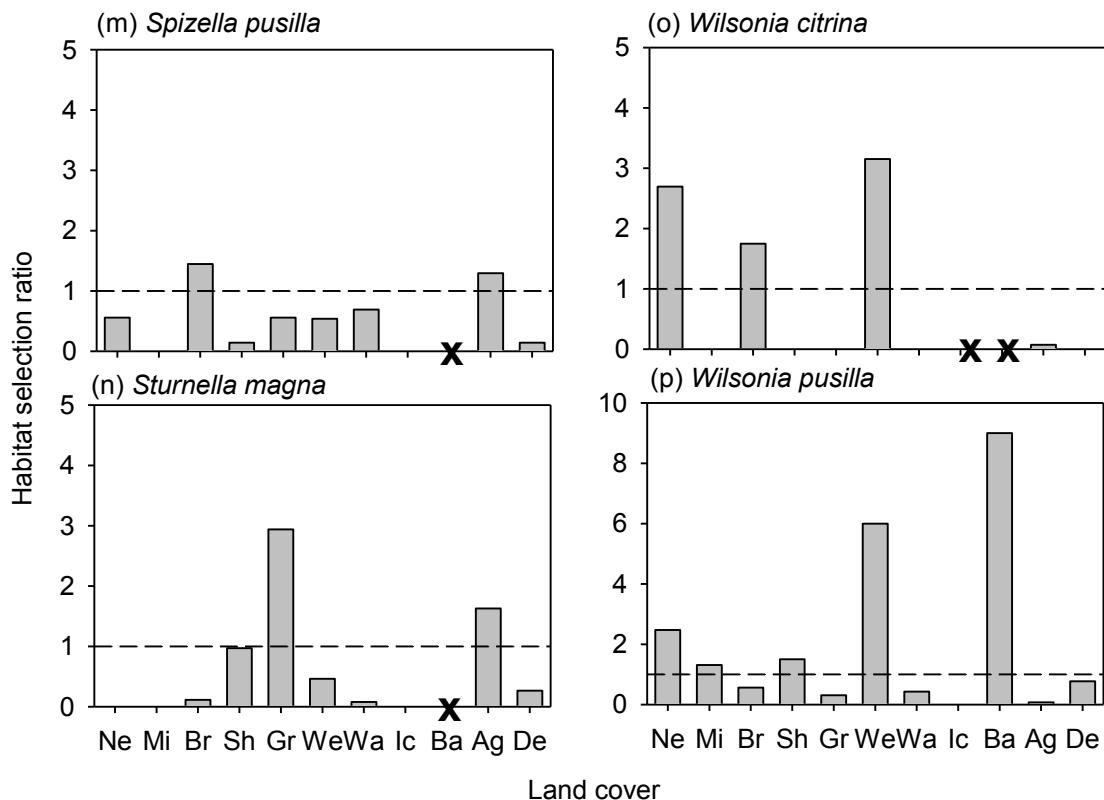


Figure E2 continued.

Appendix F Lack of relationship between the prior primary wing projection and the population trend.

Methods

If the observed relationship between prior mobility and its rate of change was caused by changes in habitat availability, then I expect to find that the most mobile species lost habitat and the least mobile species gained habitat. To investigate this, I tested for a cross-species relationship between prior mobility and an index of changes in habitat availability. In the absence of quantitative estimates of changes in habitat availability over the 20th century, I used the population trend estimated from the North American Breeding Bird Survey (NA BBS) data set as an index of changes in habitat availability (Sauer et al. 2014), assuming greater rates of habitat loss are related to greater declines in abundance.

Estimates of prior mobility were derived from data in Desrochers (2010). Desrochers (2010) used the primary wing projection as an index of species mobility. The primary wing projection is a measure of mobility, and a larger primary projection indicates greater mobility. Desrochers (2010) measured the primary wing projections of museum specimens collected between 1900 and 2008, and used these measurements to estimate the primary projection for each of 21 bird species in a baseline year (i.e. 1950), and the rate of change in primary projection per 100 years. To obtain an estimate of prior mobility for each species, I predicted the primary projection in 1900, i.e. the first year of data collection, as

b - 0.5c

equation F1

where b = primary projection in 1950 and c = rate of change in primary projection per 100 years. Note that for *Sitta canadensis* Desrochers (2010) made separate measurements for boreal and temperate populations; I used only the boreal data for this species.

Population trends were obtained from the NA BBS analysis of the 1966 – 2012 surveys (Sauer et al. 2014). The NA BBS is a continent-wide, multi-year data set of species counts for breeding birds. Point counts are conducted at 50 stops spaced along each of the approximately 4100, 39.4 km-long roadside survey routes once each year during the breeding season. At each point count, all birds seen or heard within a 0.4 km radius are recorded over a 3-minute interval. The trend for each species was the geometric mean of yearly changes in abundance from 1966 to 2012, as predicted by a Bayesian hierarchical model of the NA BBS data set (Sauer and Link 2011).

To test whether prior mobility was related to changes in habitat availability, I tested for a negative correlation between the prior primary wing projection and the population trend. To account for non-independence of observations caused by phylogenetic relatedness I used phylogenetically independent contrasts in my correlation test (Felsenstein 1985). There is uncertainty in the phylogenetic relationships among species. To account for this uncertainty I used a random sample of 5000 possible phylogenetic trees for my species, chosen from the

pseudoposterior distribution of trees with a Hackett backbone (Jetz et al. 2012), and repeated the correlation test 5000 times, each time using a different phylogeny. To determine the support for a relationship between the prior primary projection and the population trend, I calculated the median correlation and p-value from the 5000 analyses.

Data analysis was conducted in R (R Core Team 2014), using the ‘ape’ (Paradis et al. 2004) and ‘picante’ (Kembel et al. 2014) packages.

Results

There was no support for a relationship between prior mobility and the index of change in habitat availability (i.e. the population trend). The relationship between the prior primary projection and population trend was non-significant (Figure F1, $r = 0.18$, $p = 0.78$).

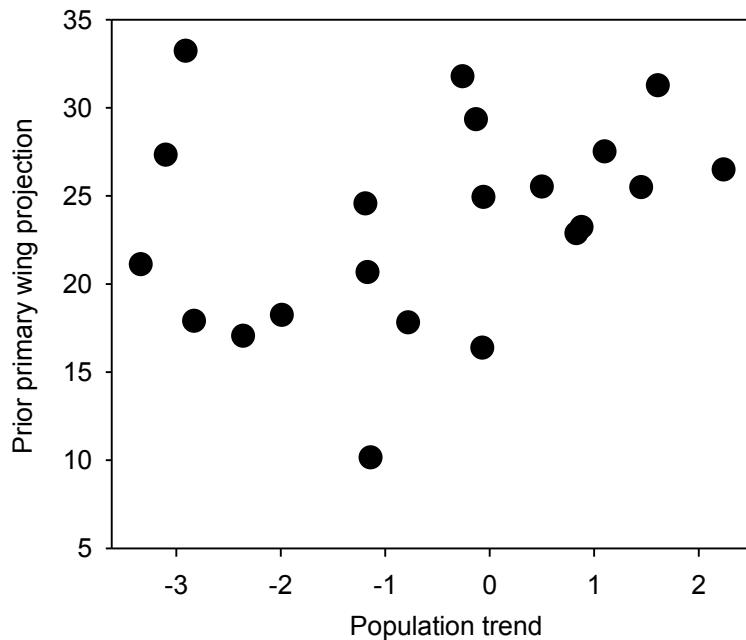


Figure F1. Relationship between the prior primary wing projection and the population trend; each point represents a species. Prior primary wing projection estimates were the primary projections predicted for 1900, as $b - 0.5c$, where b = primary projection in 1950 and c = rate of change in primary projection per 100 years, from Desrochers (2010). The primary wing projection was measured as $100([w - a] / w)$, where a = distance from the carpal joint of the wing to the distal end of the outermost secondary feather, and w = distance from the carpal joint of the wing to the wing tip. The population trend was the geometric mean of yearly changes in abundance from 1966 to 2012 (expressed as a percentage), estimated by a Bayesian hierarchical model of the North American Breeding Bird Survey data set (Sauer and Link 2011, Sauer et al. 2014).

Appendix G Migration status does not explain the rate of change in primary wing projection for North American breeding birds.

Methods

To test whether differences in the rates of change in primary wing projection among species were related to migration status, I modelled the relationship between the rate of change in primary wing projection and the species' migration status.

My estimates of the rate of change in primary projection and migration status were taken from Desrochers (2010). Desrochers (2010) measured the primary wing projections of museum specimens collected between 1900 and 2008, and used these measurements to estimate the rate of change in primary wing projection per 100 years for each of 21 bird species. Desrochers (2010) classified each species as (1) resident, if it remains in its breeding range year-round, (2) short-distance migrant, if it overwinters primarily in the continental United States, or (3) long-distance migrant, if it overwinters in the Caribbean or south of the continental United States. Note that for *Sitta canadensis* Desrochers (2010) made separate primary projection measurements for boreal and temperate populations; I used only the boreal data for this species.

I modelled the relationship between the rate of change in primary projection and the species' migration status using a generalized least squares model, and controlled for non-independence of observations caused by the phylogenetic relatedness of my sampled species by including a covariance

matrix, where covariance between a given pair of species was based on a phylogenetic tree and a Brownian model of evolution (Martins and Hansen 1997). To determine the support for a relationship between the rate of change in primary projection and migration status, I used a likelihood ratio test to compare my model to the null (intercept-only model). To account for uncertainty in the phylogenetic relationships among species, I used a random sample of 5000 phylogenetic trees for my species, chosen from the pseudoposterior distribution of trees with a Hackett backbone (Jetz et al. 2012). I then fit the above model 5000 times, each with a different phylogeny. To determine the support for a relationship between the rate of change in primary projection and migration status, I used the median likelihood ratio and p-value from the 5000 analyses. This relationship would be supported if the model relating the rate of change in primary projection to migration status was significantly more likely than the null model, at $\alpha = 0.05$.

Data analyses were conducted in R (R Core Team 2014), using the ‘ape’ (Paradis et al. 2004) and ‘nlme’ (Pinheiro et al. 2014) packages.

Results

Of the 21 study species, four were classified as resident, seven as short-distance migrant, and 10 as long-distance migrant. The rate of change in primary wing projection did not vary with species’ migration status (Figure G1). The model of the relationship between the rate of change in primary wing projection

and migration status was not more likely than the null (intercept-only) model (LR = 3.08, p = 0.21).

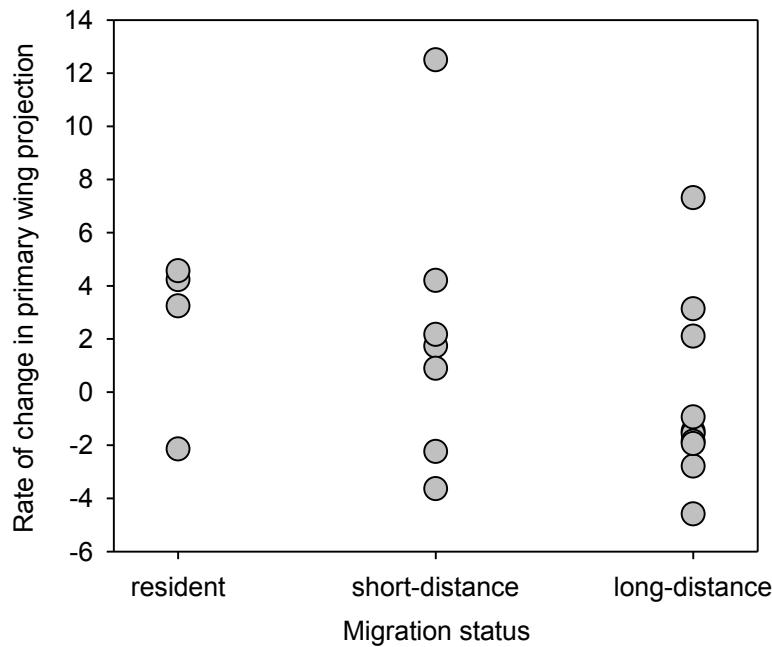


Figure G1. Rates of change in the primary wing projection for resident, short-distance migrant, and long-distance migrant species. Each point represents a species. Prior primary projection estimates were the primary projections predicted for 1900, as $b - 0.5c$, where b = primary wing projection in 1950 and c = rate of change in primary projection per 100 years, from Desrochers (2010). The primary wing projection was measured as $100([w - a] / w)$, where a = distance from the carpal joint of the wing to the distal end of the outermost secondary feather, and w = distance from the carpal joint of the wing to the wing tip.

Appendix H Parameters and flow charts for the model simulating species mobility and extinction risk in human-altered landscapes.

Table H1. Parameters used in the simulation model. Subheadings indicate parameters that were kept constant for all simulation runs (constants), parameters that were varied between simulation runs but were constant within a given run (landscape attributes), and parameters that were allowed to vary among individuals and to evolve in response to the costs and benefits of dispersal (evolved mobility-related characteristics).

Parameter	Description	Value(s)
Constants		
landscape	number of grid cells (dimensions)	16,129
size		(127 × 127)
generations		1000 (before habitat loss) + 100 (during habitat loss)
habitat	probability of mortality during dispersal across a habitat cell	0.005
quality		
intrinsic rate of increase	variable in the model of the mean number of offspring produced by each adult inhabiting a habitat cell (equation 4.1)	3
(λ)		

(continued on the following page)

Table H1 continued.

Parameter	Description	Value(s)
Constants		
cell carrying capacity (k)	threshold number of offspring supported by a habitat cell, involved in determining the mean number of offspring (equation 4.1) and settlement during dispersal	6
mutation rate	probability of mutation, leading to a change in the value for the target mobility-related characteristic; mutation was modelled as a random deviation (± 0.01) from the current characteristic value	0.005
Landscape attributes		
habitat amount	proportion of the grid cells in habitat	0.1 – 0.7
habitat fragmentation	Hurst exponent, determining spatial autocorrelation of habitat (where smaller values relate to greater fragmentation)	0 – 1
matrix quality	probability of mortality during dispersal across a matrix cell (where lower probabilities of mortality relate to higher quality)	0.006 – 0.2

(continued on the following page)

Table H1 continued.

Parameter	Description	Value(s)
Landscape attributes		
disturbance frequency	mean number of generations until disturbance, for a Poisson distribution (where lower values relate to more frequent disturbance)	10 – 100
rate of habitat loss	proportion of habitat converted to matrix in a given generation	0.03, 0.05, 0.07
Evolved mobility-related characteristics		
dispersal probability	probability of dispersal in a given generation	0 – 1
path straightness in matrix (p)	determines the degree of change in movement direction between successive movement steps originating in matrix, for a wrapped Cauchy distribution	0 – 1
path straightness in habitat (p)	determines the degree of change in movement direction between successive movement steps originating in habitat, for a wrapped Cauchy distribution	0 – 1
probability of boundary crossing	probability of crossing from habitat to matrix when a dispersing individual encountered a habitat–matrix boundary	0 – 1

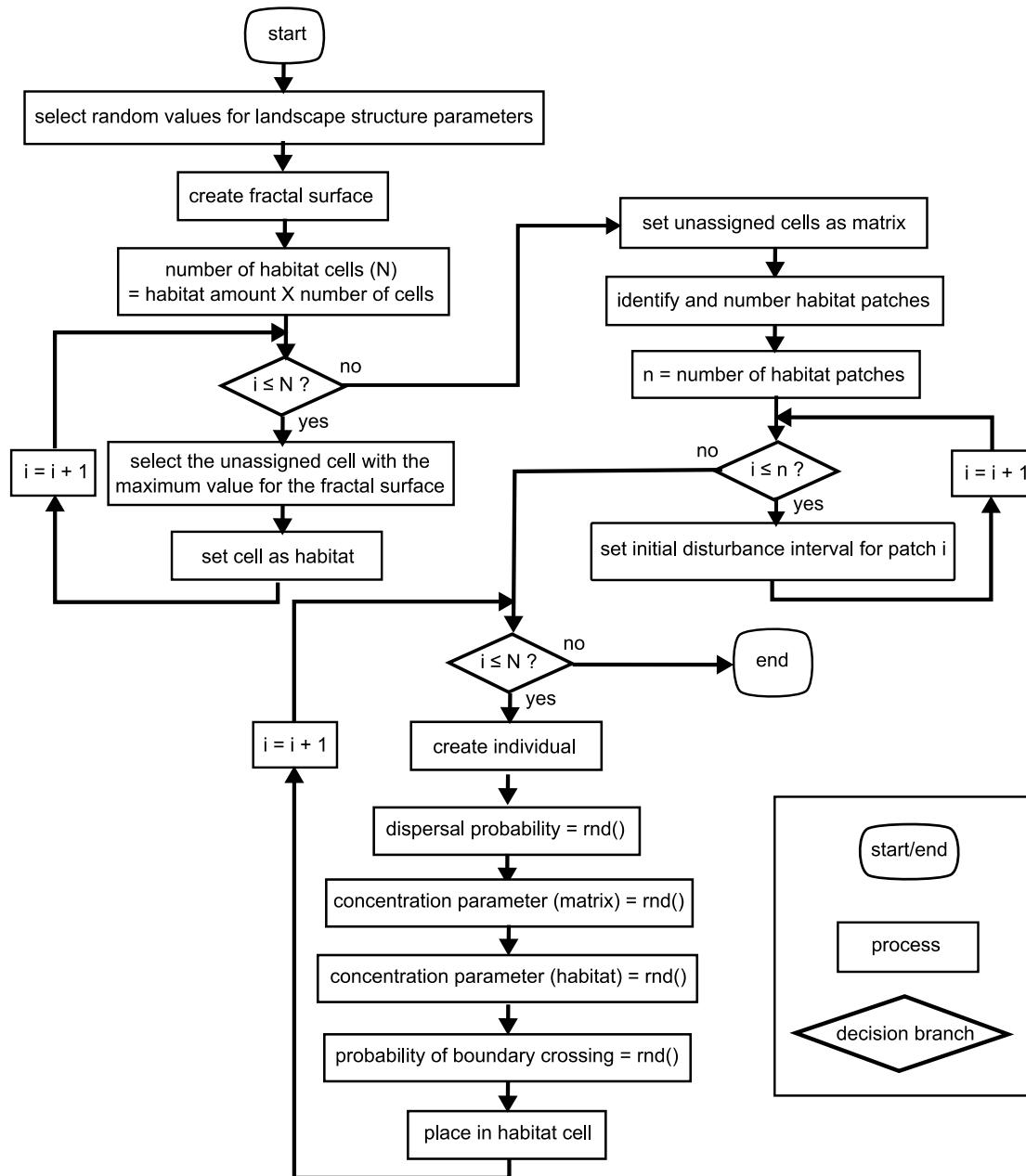


Figure H1. Flow chart for the 'set up' subprocess of the simulation model. See

Figure 4.2 for the model overview. $\text{rnd}()$ = random number between 0 and 1,

drawn from a uniform distribution.

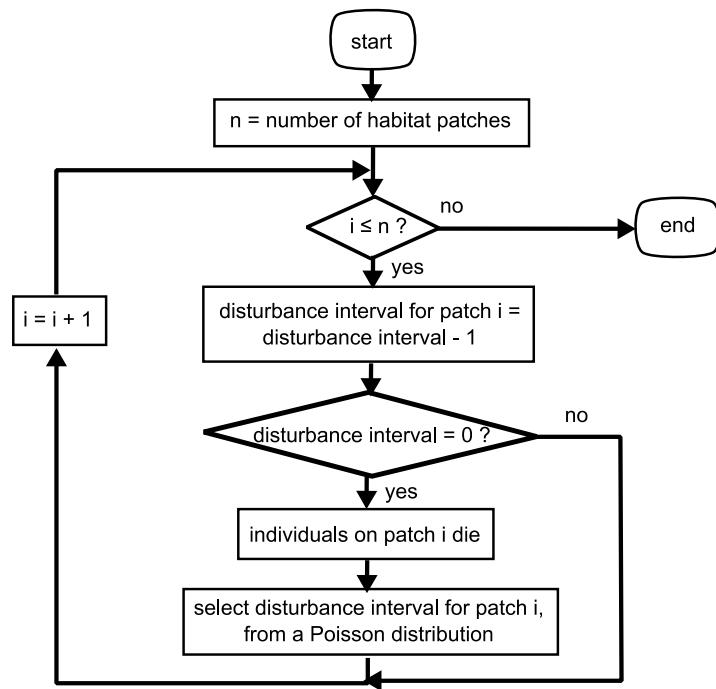


Figure H2. Flow chart for the 'disturbance' subprocess of the simulation model.

See Figure 4.2 for the model overview and Figure H1 for the flow chart legend.

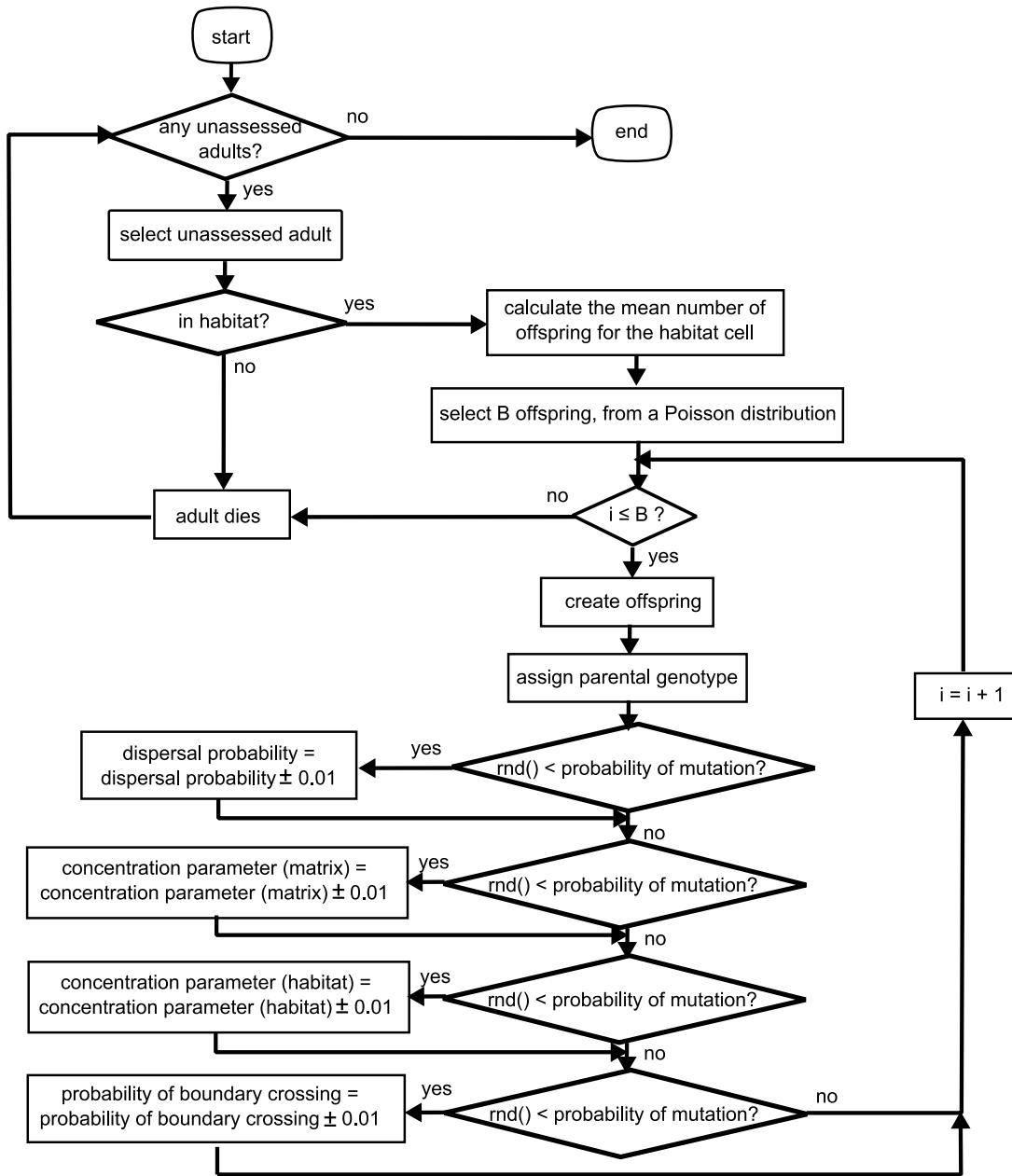


Figure H3. Flow chart for the ‘reproduction’ subprocess of the simulation model.

See Figure 4.2 for the model overview and Figure H1 for the flow chart legend.

`rnd()` = random number between 0 and 1, drawn from a uniform distribution.

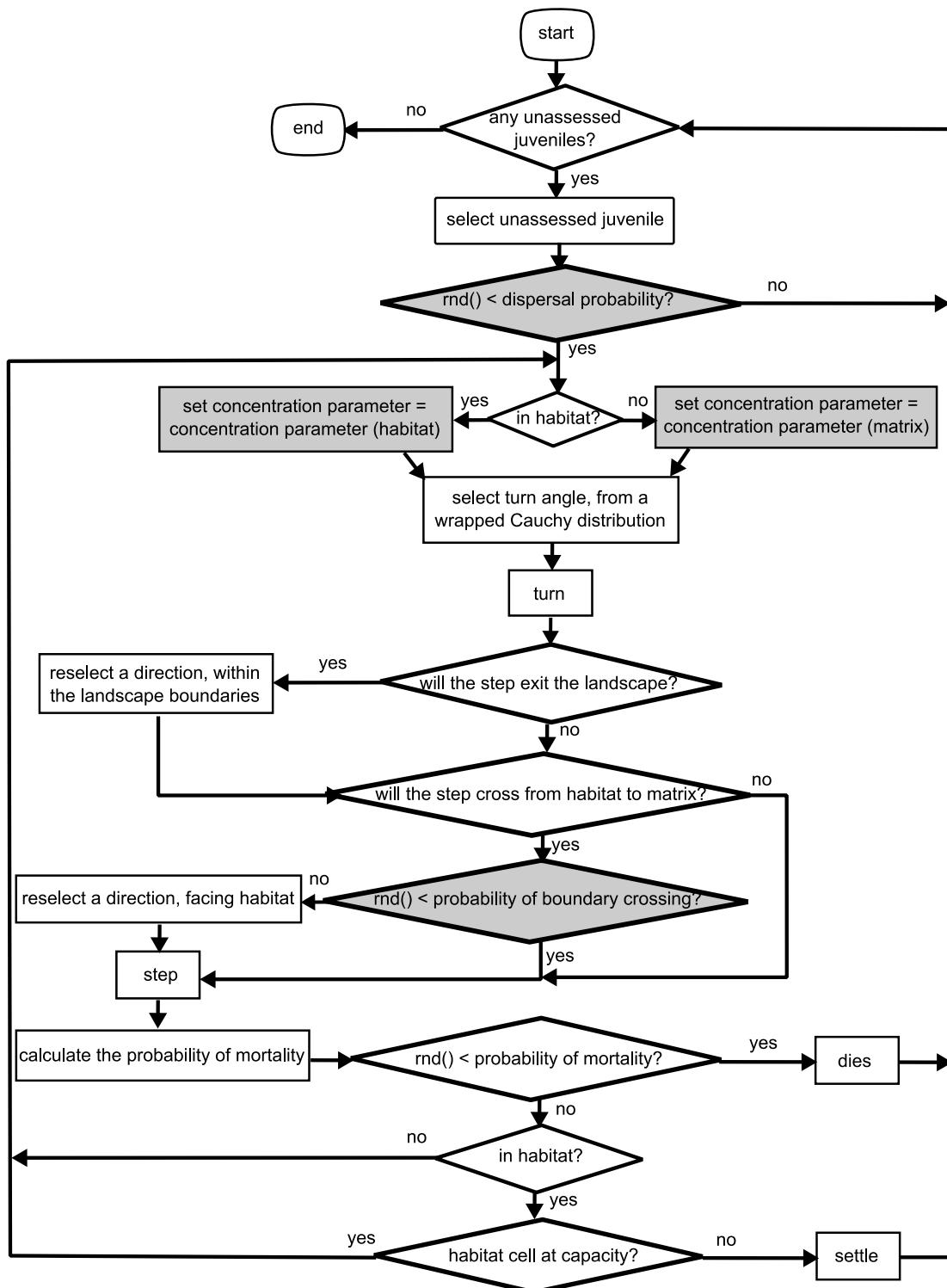


Figure H4. Flow chart for the 'dispersal' subprocess of the simulation model.

(continued on the following page)

See Figure 4.2 for the model overview and Figure H1 for the flow chart legend.

`rnd()` = random number between 0 and 1, drawn from a uniform distribution.

Shading indicates processes or decision branches that depend on the individual's heritable mobility-related characteristics.

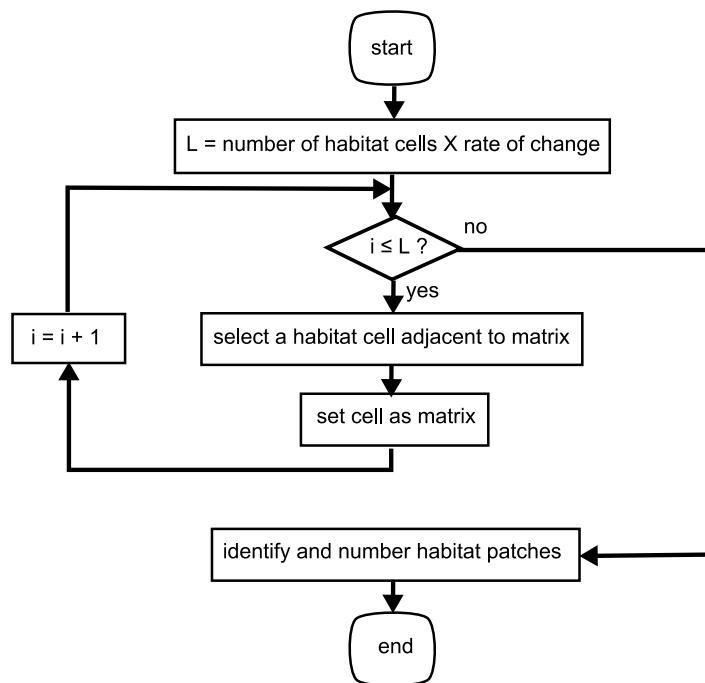


Figure H5. Flow chart for the 'habitat loss' subprocess of the simulation model.

See Figure 4.2 for the model overview and Figure H1 for the flow chart legend.

Appendix I Positive relationships between local extinction and emigration, and between recolonization and immigration in human-altered landscapes.

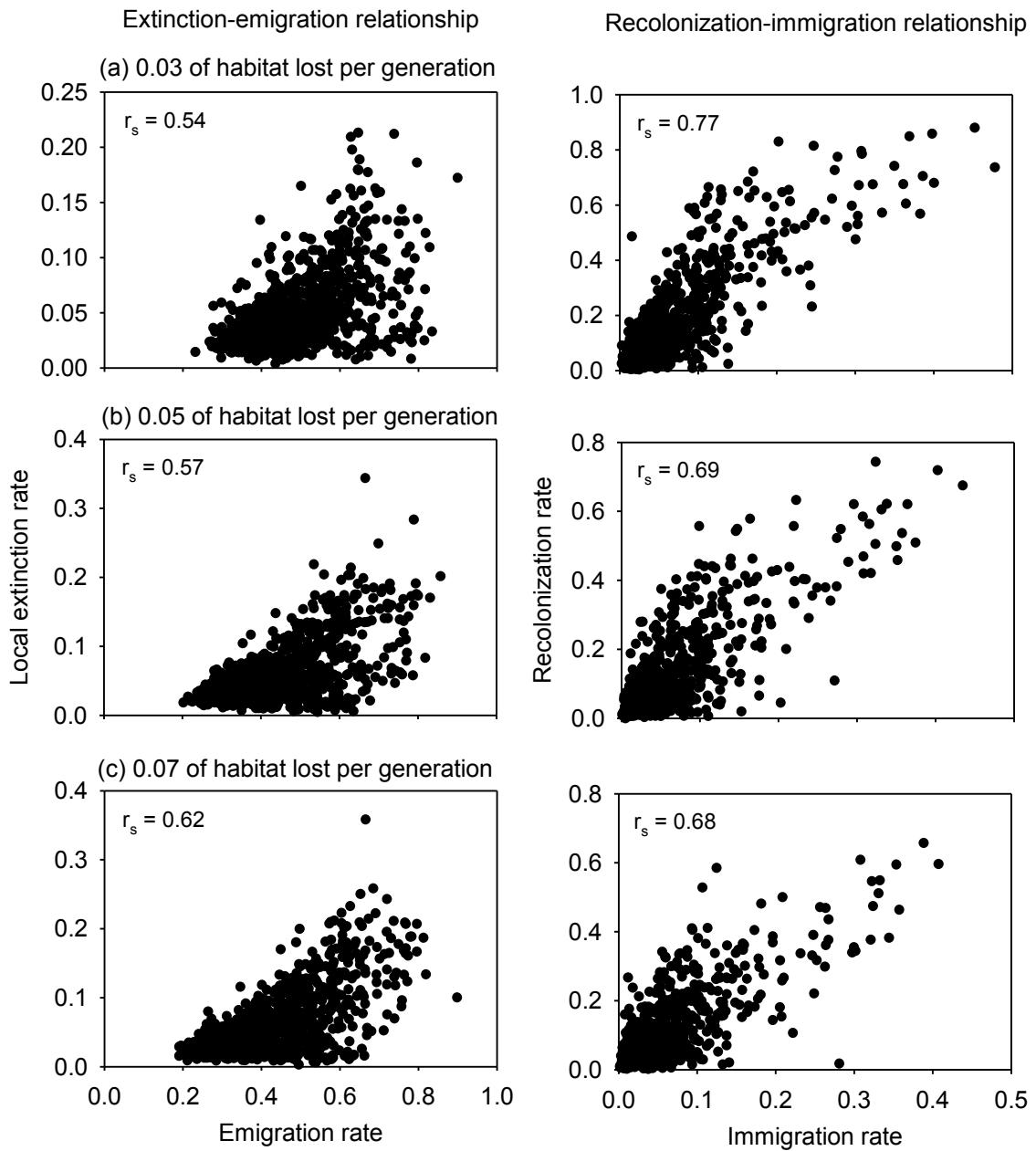


Figure I1. Spearman rank correlations (r_s) between the local extinction rate and
(continued on the following page)

emigration rate (left panel) and between the recolonization rate and immigration rate (right panel) during habitat loss, for the 1000 simulated populations at each of three rates of habitat loss: 0.03, 0.05, and 0.07 of habitat lost per generation.

Local extinction rate = proportion of occupied habitat patches that became unoccupied each generation. Emigration rate = proportion of the population that left their initial habitat cell and did not return, per generation. Recolonization rate = proportion of unoccupied habitat patches that became occupied each generation. Immigration rate = proportion of the population that settled in a different habitat patch, per generation. Each rate was averaged over the 100 generations during habitat loss, or over all generations until the population went extinct.

Appendix J Typical dispersal distances estimated by the population synchrony dispersal index.

Table J1. Typical dispersal distances (km) estimated by the population synchrony dispersal index (PSDI). I include the number of distance classes with at least 10 paired sample locations (n), and the PSDI at each of four α -levels. Distances were estimated for species with at least one distance class with significantly more positive, one-year-lagged correlations than expected by chance at a given α -level. If there were significant proportions of positive, time-lagged correlations at multiple distance classes, the PSDI was estimated as the median of the range of the significant distance classes (range in brackets).

Scientific name	Common name	n	Population synchrony dispersal index			
			$\alpha = 0.005$	$\alpha = 0.01$	$\alpha = 0.05$	$\alpha = 0.1$
<i>Acrocephalus schoenobaenus</i>	sedge warbler	20	105	105	100 (90-110)	100 (90-110)
<i>Acrocephalus scirpaceus</i>	reed warbler	20	---	---	65	65
<i>Actitis hypoleucos</i>	common sandpiper	18	---	---	165	165
<i>Aegithalos caudatus</i>	long-tailed tit	20	---	---	---	130 (80-180)

(continued on the following page)

Table J1 continued.

Scientific name	Common name	n	Population synchrony dispersal index			
			$\alpha = 0.005$	$\alpha = 0.01$	$\alpha = 0.05$	$\alpha = 0.1$
<i>Alauda arvensis</i>	skylark	20	25	25	80 (20-140)	80 (20-140)
<i>Alectoris rufa</i>	red-legged partridge	20	---	---	95 (30-160)	95 (30-160)
<i>Anas platyrhynchos</i>	mallard	20	---	---	155	135
<i>Anas strepera</i>	gadwall	16	---	---	---	115
<i>Anser anser</i>	greylag goose	19	---	---	---	155
<i>Anthus pratensis</i>	meadow pipit	20	---	---	15	15 (0 - 30)
<i>Anthus trivialis</i>	tree pipit	20	---	---	70 (10-130)	70 (10-130)
<i>Apus apus</i>	swift	20	125	125	125	125
<i>Ardea cinerea</i>	grey heron	20	---	---	135	135
<i>Athene noctua</i>	little owl	19	---	---	65	60 (50-70)
<i>Aythya fuligula</i>	tufted duck	20	5	5	5	20 (0-40)
<i>Branta canadensis</i>	Canada goose	20	---	---	---	95

(continued on the following page)

Table J1 continued.

Scientific name	Common name	n	Population synchrony dispersal index			
			$\alpha = 0.005$	$\alpha = 0.01$	$\alpha = 0.05$	$\alpha = 0.1$
<i>Buteo buteo</i>	buzzard	20	---	---	---	70 (60-80)
<i>Carduelis cannabina</i>	linnet	20	---	45	30 (10-50)	100 (10-190)
<i>Carduelis carduelis</i>	goldfinch	20	25 (10-40)	30 (10-50)	60 (0-120)	65 (0-130)
<i>Carduelis chloris</i>	greenfinch	20	15 (0-30)	15 (0-30)	25 (0-50)	25 (0-50)
<i>Carduelis cabaret</i> *	lesser redpoll	20	---	---	---	155
<i>Carduelis spinus</i>	siskin	20	---	---	130 (100-160)	130 (100-160)
<i>Columba livia</i>	feral pigeon	20	---	---	---	130
<i>Columba oenas</i>	stock dove	20	---	---	100 (10-190)	100 (10-190)
<i>Columba palumbus</i>	woodpigeon	20	10 (0-20)	15 (0-30)	15 (0-30)	75 (0-150)
<i>Corvus corax</i>	raven	20	---	75	75	75
<i>Corvus corone</i>	carrion crow	20	---	25	55 (20-90)	70 (20-120)
<i>Corvus cornix</i> **	hooded crow	18	---	---	75	45 (10-80)

(continued on the following page)

Table J1 continued.

Scientific name	Common name	n	Population synchrony dispersal index			
			$\alpha = 0.005$	$\alpha = 0.01$	$\alpha = 0.05$	$\alpha = 0.1$
<i>Corvus monedula</i>	jackdaw	20	30 (20-40)	45 (20-70)	45 (20-70)	35 (0-70)
<i>Cuculus canorus</i>	cuckoo	20	175	175	175	95 (0-190)
<i>Cygnus olor</i>	mute swan	20	---	---	15	100 (10-190)
<i>Delichon urbicum</i>	house martin	20	---	---	50 (30-70)	100 (30-170)
<i>Dendrocopos major</i>	great spotted woodpecker	20	---	---	---	5
<i>Emberiza citrinella</i>	yellowhammer	20	---	---	25	105 (20-190)
<i>Emberiza schoeniclus</i>	reed bunting	20	---	---	25 (10-40)	35 (0-70)
<i>Erithacus rubecula</i>	robin	20	5	5	80 (0-160)	80 (0-160)
<i>Falco tinnunculus</i>	kestrel	20	---	---	---	95
<i>Ficedula hypoleuca</i>	pied flycatcher	11	---	---	---	85
<i>Fringilla coelebs</i>	chaffinch	20	20 (0-40)	20 (0-40)	35 (0-70)	35 (0-70)
<i>Fulica atra</i>	coot	20	---	145	140 (130-150)	140 (130-150)

(continued on the following page)

Table J1 continued.

Scientific name	Common name	n	Population synchrony dispersal index			
			$\alpha = 0.005$	$\alpha = 0.01$	$\alpha = 0.05$	$\alpha = 0.1$
<i>Gallinago gallinago</i>	snipe	20	---	---	---	195
<i>Gallinula chloropus</i>	moorhen	20	15	15	15	35 (10-60)
<i>Garrulus glandarius</i>	jay	20	---	---	---	145
<i>Haematopus ostralegus</i>	oystercatcher	20	---	---	120 (40-200)	100 (0-200)
<i>Hirundo rustica</i>	swallow	20	---	---	---	55
<i>Lagopus lagopus</i>	red grouse	20	---	---	45	45
<i>Larus argentatus</i>	herring gull	20	75	75	100 (70-130)	90 (50-130)
<i>Larus fuscus</i>	lesser black-backed gull	20	---	---	95	95
<i>Larus ridibundus</i>	black-headed gull	20	---	---	175	115 (50-180)
<i>Luscinia megarhynchos</i>	nightingale	15	---	---	55	55
<i>Miliaria calandra</i>	corn bunting	20	---	---	---	135
<i>Motacilla alba</i>	pied/white wagtail	20	---	---	---	25

(continued on the following page)

Table J1 continued.

Scientific name	Common name	n	Population synchrony dispersal index			
			$\alpha = 0.005$	$\alpha = 0.01$	$\alpha = 0.05$	$\alpha = 0.1$
<i>Motacilla cinerea</i>	grey wagtail	20	---	---	---	95 (50-140)
<i>Motacilla flava</i>	yellow wagtail	20	---	---	65	65
<i>Muscicapa striata</i>	spotted flycatcher	20	---	---	135	125 (110-140)
<i>Numenius arquata</i>	curlew	20	---	145	125 (100-150)	75 (0-150)
<i>Oenanthe oenanthe</i>	wheatear	20	---	---	---	175
<i>Parus ater</i>	coal tit	20	---	---	95	65 (30-100)
<i>Parus caeruleus</i>	blue tit	20	15	15	95 (10-180)	105 (10-200)
<i>Parus major</i>	great tit	20	---	---	5	5
<i>Parus palustris</i>	marsh tit	20	---	---	75	75
<i>Passer domesticus</i>	house sparrow	20	30 (0-60)	30 (0-60)	35 (0-70)	50 (0-100)
<i>Passer montanus</i>	tree sparrow	20	---	---	40 (10-70)	105 (10-200)
<i>Perdix perdix</i>	grey partridge	20	---	---	135	90 (40-140)

(continued on the following page)

Table J1 continued.

Scientific name	Common name	n	Population synchrony dispersal index			
			$\alpha = 0.005$	$\alpha = 0.01$	$\alpha = 0.05$	$\alpha = 0.1$
<i>Phalacrocorax carbo</i>	cormorant	20	---	---	65	105 (60-150)
<i>Phasianus colchicus</i>	pheasant	20	35	35	20 (5-35)	30 (0-60)
<i>Phoenicurus phoenicurus</i>	redstart	20	---	115	115	100 (40-160)
<i>Phylloscopus collybita</i>	chiffchaff	20	155	155	145 (130-160)	105 (20-290)
<i>Phylloscopus sibilatrix</i>	wood warbler	15	---	---	---	85
<i>Phylloscopus trochilus</i>	willow warbler	20	---	55	60 (10-110)	60 (10-110)
<i>Pica pica</i>	magpie	20	---	---	115 (40-190)	115 (40-190)
<i>Picus viridis</i>	green woodpecker	20	5	5	5	40 (0-80)
<i>Pluvialis apricaria</i>	golden plover	20	---	---	15	15
<i>Podiceps cristatus</i>	great crested grebe	20	---	---	135	120 (100-140)
<i>Prunella modularis</i>	dunnock	20	---	---	5	20 (0-40)
<i>Pyrrhula pyrrhula</i>	bullfinch	20	15	15	25 (10-40)	75 (10-140)

(continued on the following page)

Table J1 continued.

Scientific name	Common name	n	Population synchrony dispersal index			
			$\alpha = 0.005$	$\alpha = 0.01$	$\alpha = 0.05$	$\alpha = 0.1$
<i>Regulus regulus</i>	goldcrest	20	---	15	70 (0-140)	70 (0-140)
<i>Saxicola torquatus</i>	stonechat	20	---	---	---	70 (50-90)
<i>Streptopelia decaocto</i>	collared dove	20	---	25	40 (10-70)	45 (10-80)
<i>Streptopelia turtur</i>	turtle dove	20	---	---	80 (20-140)	85 (20-150)
<i>Strix aluco</i>	tawny owl	17	---	---	65	65
<i>Sturnus vulgaris</i>	starling	20	15 (0-30)	15 (0-30)	55 (0-110)	90 (0-180)
<i>Sylvia atricapilla</i>	blackcap	20	---	---	---	45
<i>Sylvia borin</i>	garden warbler	20	---	---	---	145 (120-170)
<i>Sylvia communis</i>	whitethroat	20	55	55	60 (50-70)	60 (50-70)
<i>Sylvia curruca</i>	lesser whitethroat	20	---	---	85 (10-160)	85 (10-160)
<i>Tachybaptus ruficollis</i>	little grebe	19	---	---	105	105
<i>Tadorna tadorna</i>	shelduck	20	---	---	35	35

(continued on the following page)

Table J1 continued.

Scientific name	Common name	n	Population synchrony dispersal index			
			$\alpha = 0.005$	$\alpha = 0.01$	$\alpha = 0.05$	$\alpha = 0.1$
<i>Tringa totanus</i>	redshank	19	---	---	115	70 (20-120)
<i>Turdus merula</i>	blackbird	20	5	5	10 (0-20)	70 (0-140)
<i>Turdus philomelos</i>	song thrush	20	35	35	30 (20-40)	70 (10-130)
<i>Turdus viscivorus</i>	mistle thrush	20	45	45	80 (40-120)	85 (40-130)

* For phylogenetic trees I substituted *Carduelis flammea* (common redpoll) for *Carduelis cabaret* (lesser redpoll), because *Carduelis cabaret* was not included in the phylogeny produced by Jetz et al. (2012). *Carduelis cabaret* was previously classified as a subspecies of *Carduelis flammea*.

** *Corvus cornix* (hooded crow) was not included in the phylogeny produced by Jetz et al. (2012). *Corvus cornix* is most closely related to *Corvus corone* (carrion crow). I did not include *Corvus cornix* in my analyses because I estimated dispersal distances for both these species, and could not include them both as the same species in my analyses.

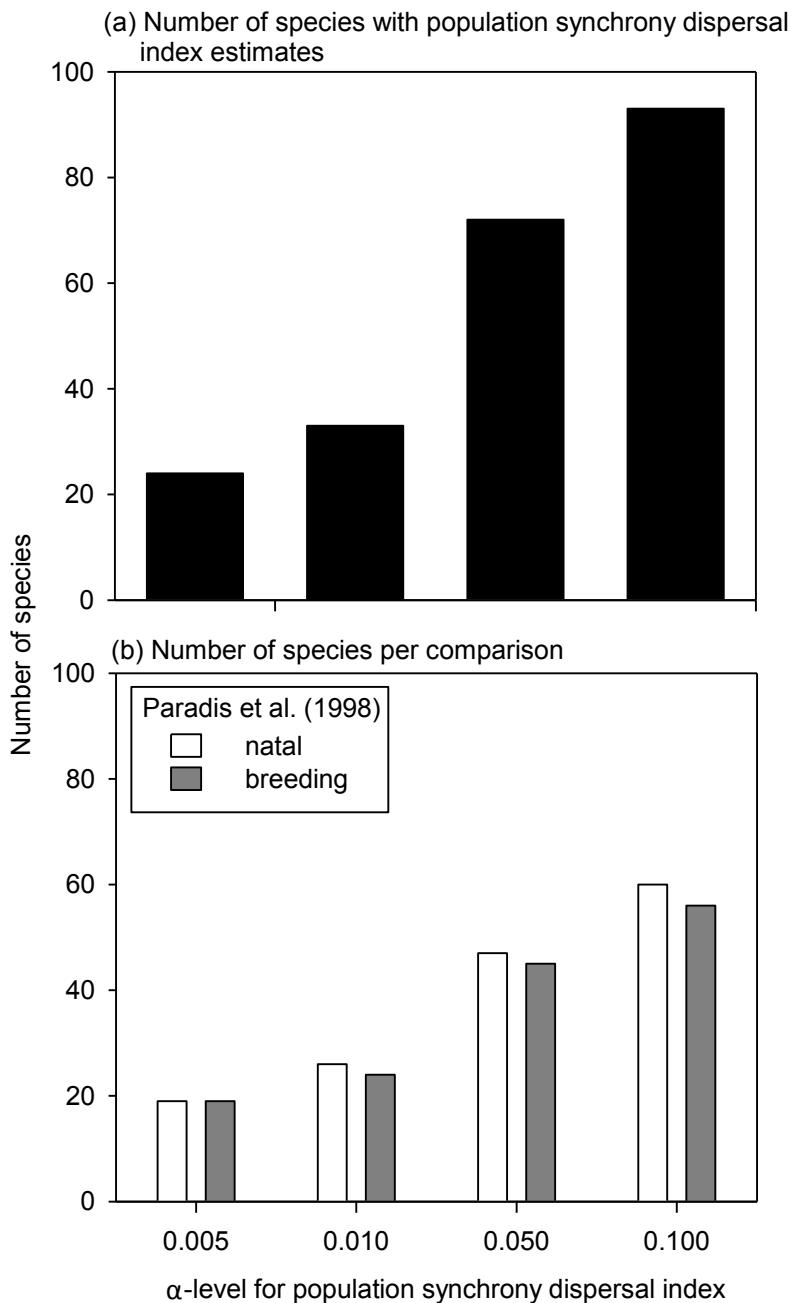


Figure J1. (a) Number of species with an estimated population synchrony dispersal index (PSDI), and (b) number of species for comparisons of the PSDI to natal and breeding dispersal distance estimates from Paradis et al. (1998), at
(continued on the following page)

each of the four tested α . Only species with both an estimated PSDI and a dispersal distance estimate in Paradis et al. (1998) could be used in comparisons.

Appendix K Lack of relationship between the population synchrony dispersal index and species' habitat.

Methods

To test whether there was a relationship between the population synchrony dispersal index (PSDI) and the species' habitat, I modelled the relationship between the PSDI, estimated at each of four α (0.005, 0.01, 0.05, and 0.1), and eight habitat types: aquatic, coastal, developed, farm, forest, scrub, grass, and wetland.

Habitat classifications were derived from published habitat assessments (Robinson 2005), which were available for 83 of the 91 study species. Habitat assessments were based on data collected in 2000, 2002, and 2003 for the United Kingdom Breeding Bird Survey (UK BBS). The UK BBS is an annual breeding bird monitoring scheme, with standardized bird counts at approximately 3000, 1 km squares (Gregory et al. 2004). Volunteers record counts of all birds seen or heard along two, 1 km transects within the sampling square, and classify land cover for five, 0.2 km sections along each transect, according to Crick (1992). Robinson (2005) reduced these land cover classifications to 19 land cover classes (Table K1), and calculated the proportion of all transect sections in each land cover class that was occupied by each species in a given sampling year. These proportions were then scaled so that values ranged from 0 (absent) to 1 (most frequently occupied), and averaged for the three sample years. To identify habitat for each species, I created a binary variable, classifying a land

Table K1. Land cover classifications, showing how Level 1 and 2 land cover classifications from the United Kingdom Breeding Bird Survey (land cover code in brackets), classified according to Crick (1992), were combined to produce the 19 land cover classes used in Robinson (2005), and the eight land cover classes in this study.

Land cover class	Robinson (2005)	Crick (1992)
aquatic	along streams	stream (G6)
		ditch with water (G8)
	along rivers	river (G7)
		small canal (G9)
		large canal (G10)
	lakes	lake/unlined reservoir (G3)
		lined reservoir (G4)
	ponds	pond (G1)
		small waterbody (G2)
		gravel pit/sand pit (G5)
coastal	coastal habitat	saltmarsh (C9)
		marine-open shore (H1)
		marine shore-inlet/cove/loch (H2)
		estuarine (H3)
		brackish lagoon (H4)
		open sea (H5)

(continued on the following page)

Table K1 continued.

Land cover class	Robinson (2005)	Crick (1992)
coastal	open shore	marine-open shore (H1) marine shore-inlet/cove/loch (H2) open sea (H5)
	estuaries	saltmarsh (C9) estuarine (H3) brackish lagoon (H4)
developed	towns	urban (F1) suburban (F2)
	villages	rural (F3)
farm	arable farmland	improved (E1)
	pasture farmland	unimproved (E2)
forest	deciduous wood	broadleaved (A1) broadleaved water-logged (A4)
	coniferous wood	coniferous (A2) coniferous water-logged (A5)
grass	grass/heath	chalk downland (C1) machair (C4) other dry grassland (C5) dry heath (D1) breckland (D5)

(continued on the following page)

Table K1 continued.

Land cover class	Robinson (2005)	Crick (1992)
grass	moorland	grass moor (C2) grass moor mixed with heather (C3)
scrub	scrub	regenerating natural or semi-natural woodland (B1) downland (B2) heath scrub (B3) young coppice (B4) new plantation (B5) clear-felled with or without new saplings (B6) other (B7)
wetland	bog	bog (D4) drained bog (D6) bare peat (D7)
	marsh	water-meadow/grazing marsh (C6) other open marsh (C8) wet heath (D2)
	reedbed	reed swamp (C7)

cover class as habitat if its scaled proportional occupancy was ≥ 0.7 , or non-habitat if its scaled proportional occupancy was < 0.7 . To create a manageable number of variables for multimodel analysis (see below), I further reduced the 19 land cover classes from Robinson (2005) to eight (Table K1).

I used multimodel inference, based on the small-samples Akaike Information Criterion (AICc), to model the relationships between the PSDI and subsets of the global model (aquatic + coastal + developed + farm + forest + grass + scrub + wetland), repeated using each of the four PSDI estimates. To ensure adequate sample sizes for each candidate model, I limited the subset of models to those with at least 10 data points per land cover class. This resulted in a maximum of two predictors per model when PSDI was estimated at $\alpha = 0.005$ ($n = 23$), three predictors per model when PSDI was estimated at $\alpha = 0.01$ ($n = 32$), six predictors per model when PSDI was estimated at $\alpha = 0.05$ ($n = 66$), and eight predictors per model when PSDI was estimated at $\alpha = 0.1$ ($n = 83$). To ensure adequate representation of each habitat, I included only land cover classes classified as habitat for at least five species. This resulted in removal of models with aquatic, coastal, or grass land cover classes when PSDI was estimated at $\alpha = 0.005$ or 0.01 . I controlled for non-independence of observations caused by the phylogenetic relatedness of my sampled species by modelling relationships using a generalized least squares model, including a covariance matrix where covariance between a given pair of species was based on a phylogenetic tree and a Brownian model of evolution (Martins and Hansen 1997). To account for uncertainty in the phylogenetic relationships among species, I

used a random sample of 5000 phylogenetic trees, chosen from the pseudoposterior distribution of trees with a Hackett backbone (Jetz et al. 2012). I then fit the above set of candidate models 5000 times, each with a different phylogeny. To determine the support for a relationship between the PSDI and species' habitat, I predicted the median model-averaged PSDI and median 95% unconditional confidence interval for species using each land cover class as habitat, from the 5000 analyses. A relationship between the PSDI and species' habitat would be supported if there was no overlap in the 95% confidence intervals for PSDI predicted for species with different habitats.

Data analyses were conducted in R (R Core Team 2014), using the 'ape' (Paradis et al. 2004), 'nlme' (Pinheiro et al. 2014), and 'MuMIn' (Barton 2014) packages.

Results

There was little support for a relationship between the PSDI and species' habitat. The 95% confidence intervals for PSDI predicted for species with different habitats generally overlapped, suggesting no difference in PSDI for species with different habitat requirements (Figure K1). The only exception was that PSDI estimated at $\alpha = 0.1$ were lower for species using developed areas as habitat than for species with aquatic, farm, or forest habitats (Figure K1).

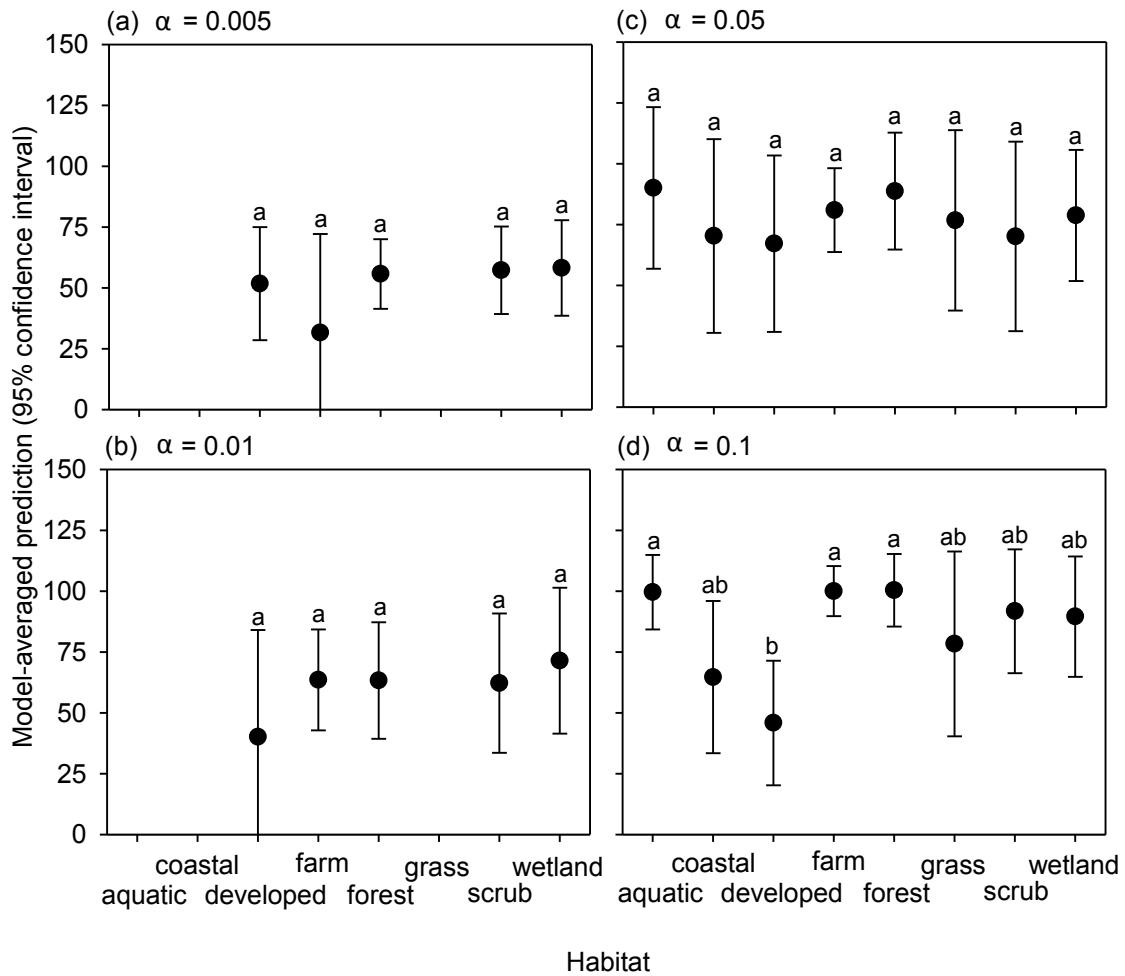


Figure K1. Model-averaged predictions from multimodel inference, modelling the relationship between the population synchrony dispersal index (PSDI) and species' habitat requirements, with PSDI estimated at (a) $\alpha = 0.005$, (b) $\alpha = 0.01$, (c) $\alpha = 0.05$, and (d) $\alpha = 0.1$. Relationships were modelled using generalized least squares, with a covariance matrix to account for phylogenetic relationships among species. Presented are the medians from the set of 5000 analyses, each conducted with a different phylogenetic tree. No PSDI were estimated for (continued on the following page)

aquatic, coastal, or grass land cover classes when $\alpha = 0.005$ or 0.01 , because there were less than five species using each land cover as habitat. Letters indicate which of the predictions had overlapping confidence intervals.

Appendix L Lack of relationship between the population synchrony dispersal index and species' diet.

Methods

To test whether there was a relationship between the population synchrony dispersal index (PSDI) and the species' diet, I modelled the relationship between the PSDI, estimated at each of four α (0.005, 0.01, 0.05, and 0.1), and six food types: fish/bivalve, fruit, invertebrate, plant (including leaves and roots), seed, and vertebrate (including mammals, birds, reptiles, and amphibians). Each food type was a binary variable, classified as a species' diet, or not. Species diet classifications were taken from Robinson (2005), and included only the main foods for each species.

I used multimodel inference, based on the small-samples Akaike Information Criterion (AICc), to model the relationships between the PSDI and subsets of the global model (fish/bivalve + fruit + invertebrate + plant + seed + vertebrate), repeated using each of the four PSDI estimates. To ensure adequate sample sizes for each candidate model, I limited the subset of models to those with at least 10 data points per food type. This resulted in a maximum of two predictors per model when PSDI was estimated at $\alpha = 0.005$ ($n = 24$), three predictors per model when PSDI was estimated at $\alpha = 0.01$ ($n = 33$), and six predictors per model when PSDI was estimated at $\alpha = 0.05$ ($n = 70$) or $\alpha = 0.1$ ($n = 91$). To ensure adequate representation of each diet, I included only the food types that were diets for at least five species. This resulted in removal of models

with fish/bivalve or vertebrate food types when PSDI was estimated at $\alpha = 0.005$ or 0.01. I controlled for non-independence of observations caused by the phylogenetic relatedness of my sampled species by modelling relationships using a generalized least squares model, including a covariance matrix where covariance between a given pair of species was based on a phylogenetic tree and a Brownian model of evolution (Martins and Hansen 1997). To account for uncertainty in the phylogenetic relationships among species, I used a random sample of 5000 phylogenetic trees for my species, chosen from the pseudoposterior distribution of trees with a Hackett backbone (Jetz et al. 2012). I then fit the above set of candidate models 5000 times, each with a different phylogeny. To determine the support for a relationship between the PSDI and diet, I predicted the median model-averaged PSDI and median 95% unconditional confidence interval for species with each diet, from the 5000 analyses. A relationship between the PSDI and the species' diet would be supported if there was no overlap in the 95% confidence intervals for PSDI predicted for species with different diets.

Data analyses were conducted in R (R Core Team 2014), using the 'ape' (Paradis et al. 2004), 'nlme' (Pinheiro et al. 2014), and 'MuMIn' (Barton 2014) packages.

Results

There was little support for a relationship between the PSDI and species' diet. The 95% confidence intervals for different food types generally overlapped,

suggesting no difference in PSDI for species with different diets (Figure L1). The only exception was that PSDI estimated at $\alpha = 0.05$ were lower for species eating fish or bivalves than for species eating invertebrates, plants, seeds, or vertebrates (Figure L1).

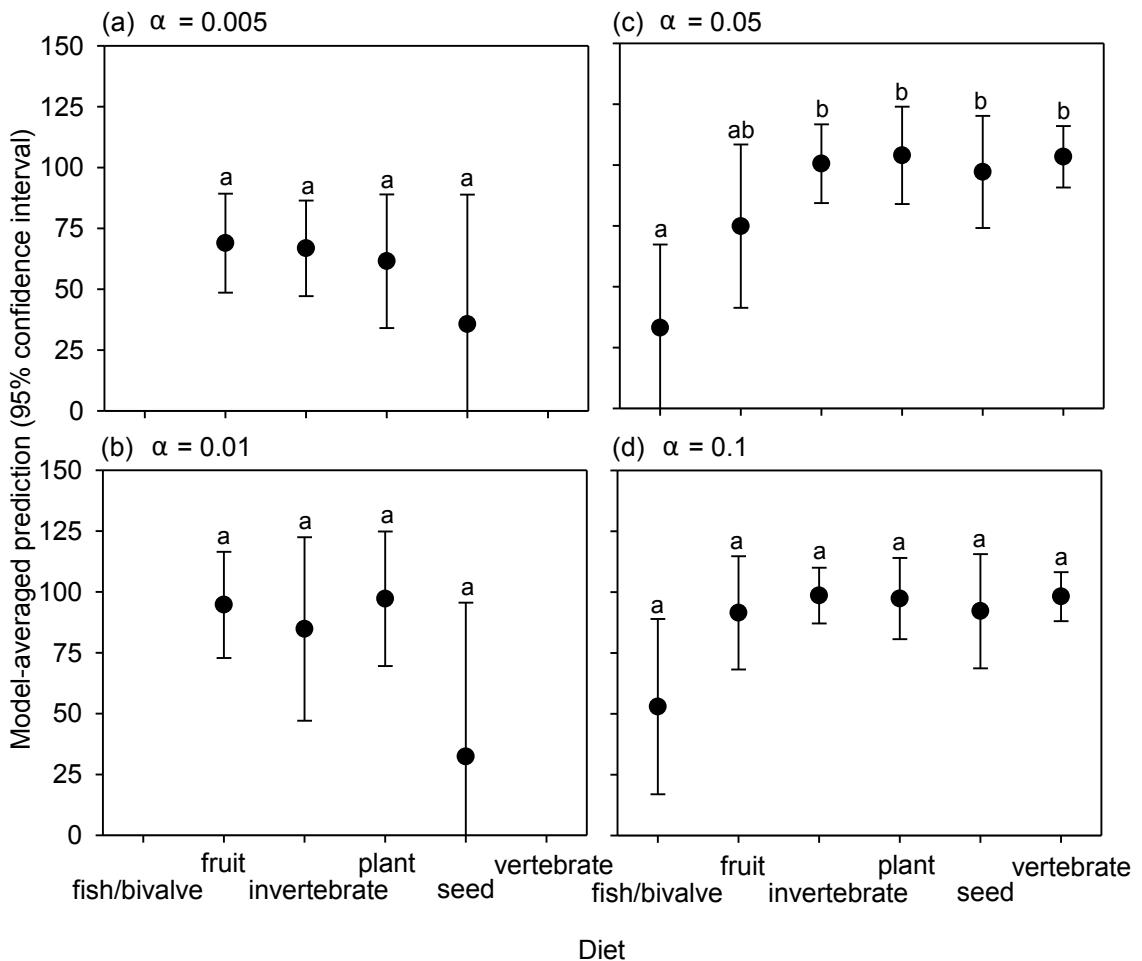


Figure L1. Model-averaged predictions from multimodel inference, modelling the relationship between the population synchrony dispersal index (PSDI) and species' diet, with PSDI estimated at (a) $\alpha = 0.005$, (b) $\alpha = 0.01$, (c) $\alpha = 0.05$, and (d) $\alpha = 0.1$. Relationships were modelled using generalized least squares, with a covariance matrix to account for phylogenetic relationships among species. Presented are the medians from the set of 5000 analyses, each conducted with a different phylogenetic tree. No estimates were made for fish/bivalve or vertebrate

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diets when $\alpha = 0.005$ or 0.01 , because there were less than five species with these diets. Letters indicate which of the predictions had overlapping confidence intervals.

Appendix M Positive correlations between population synchrony dispersal indices estimated at different α .

Methods

To test whether population synchrony dispersal indices (PSDI) estimated at different α predict similar relative dispersal distances, I calculated the Spearman rank correlation (r_s) between all pairings of the four PSDI, each estimated at a different α -level (0.005, 0.01, 0.05, or 0.1), for a total of six comparisons. For each comparison I transformed the estimated distances into phylogenetically independent contrasts (Felsenstein 1985), to account for phylogenetic non-independence. To account for uncertainty in the phylogenetic relationships among species, I obtained a random sample of 5000 phylogenetic trees for my species, chosen from the pseudoposterior distribution of trees with a Hackett backbone (Jetz et al. 2012). I then conducted the above analyses 5000 times, each with a different phylogeny. To determine whether there were significant, positive correlations between PSDI, I calculated the median statistical test results (i.e. median r_s and median p-value) for the 5000 analyses. Significant, positive correlations would suggest that PSDI estimated at the different α predict similar relative dispersal distances.

Data analyses were conducted in R (R Core Team 2014), using the ‘ape’ (Paradis et al. 2004) and ‘picante’ (Kembel et al. 2014) packages.

Results

The number of species that I could calculate a PSDI for depended on the stringency of the α -level, with more PSDI calculated as α increased. This resulted in variation in the number of species per comparison. The number of species per comparison was 24 when comparing the PSDI at $\alpha = 0.005$ to PSDI at $\alpha = 0.01$, 0.05, or 0.1, 33 when comparing the PSDI at $\alpha = 0.01$ to PSDI at $\alpha = 0.05$ or 0.1, and 70 when comparing the PSDI at $\alpha = 0.05$ to PSDI at $\alpha = 0.1$.

There were strong, positive correlations between PSDI estimated at different α (Figure M1). All comparisons produced significant, positive correlations (all $p < 0.002$).

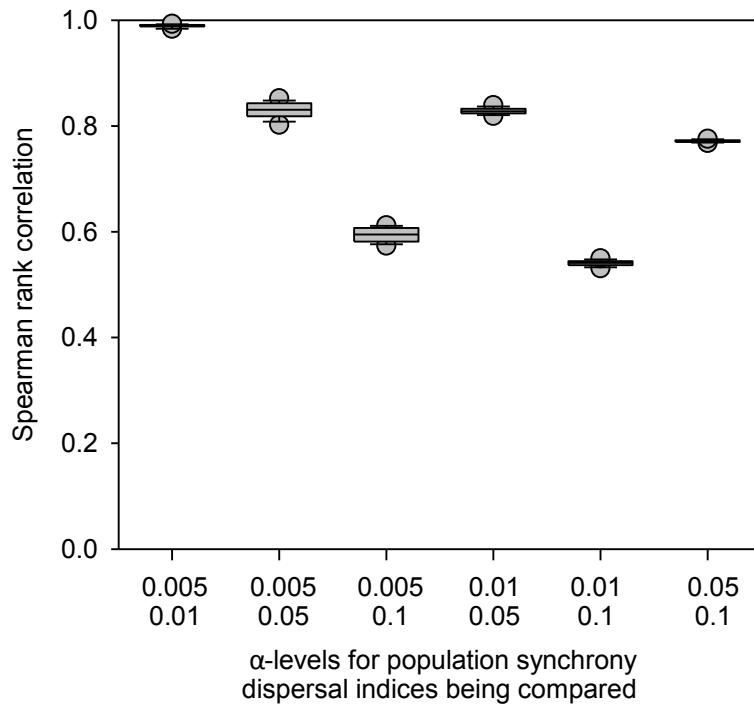


Figure M1. Spearman rank correlations between population synchrony dispersal indices calculated using different α , after controlling for phylogenetic non-independence. Variability in correlations results from uncertainty in the phylogenetic relationships among species ($n = 5000$ possible phylogenies).

Appendix N Calibration of population synchrony dispersal indices using independent estimates of mean dispersal distances.

Methods

To show how independent distance estimates can be used to calibrate population synchrony dispersal indices (PSDI), and produce more realistic estimates of mean dispersal distances, I calibrated my PSDI, estimated at $\alpha = 0.05$, to dispersal distance estimates from Paradis et al. (1998). If there are independent dispersal distance estimates for a subset of your species of interest, you should be able to relate these to the PSDI estimates, and predict the dispersal distances for the rest of the species.

I modelled each set of dispersal distance estimates from Paradis et al. (1998; natal and breeding dispersal) as a function of the PSDI, using a generalized least squares model, with a covariance matrix where covariance between a given pair of species was based on a phylogenetic tree and a Brownian model of evolution (Martins and Hansen 1997). To fit with model assumptions, I removed four outliers from the model relating natal dispersal distances to PSDI. The models were then used to predict PSDI calibrated to natal dispersal distances ($PSDI_n$) and PSDI calibrated to breeding dispersal distances ($PSDI_b$). To account for uncertainty in the phylogenetic relationships among species, I used a random sample of 5000 phylogenetic trees for my species, chosen from the pseudoposterior distribution of trees with a Hackett backbone (Jetz et al. 2012), and repeated the analysis above 5000 times. $PSDI_n$

and PSDI_b were each estimated as the median prediction for a given species for the 5000 analyses.

All data analyses were conducted in R (R Core Team 2014), using the ‘ape’ (Paradis et al. 2004) and ‘nlme’ (Pinheiro et al. 2014) packages.

Results

I related 43 PSDI to natal dispersal distance estimates from Paradis et al. (1998), and used this to predict PSDI_n for 23 additional species, and related 45 PSDI to breeding dispersal distance estimates from Paradis et al. (1998), and used this to predict PSDI_b for 25 additional species (Table N1).

Table N1. Mean natal and breeding dispersal distance estimates (km), estimated by calibrating the population synchrony dispersal index (PSDI) to mean dispersal distance estimates from Paradis et al. (1998).

Scientific name	Common name	Natal	Breeding
<i>Acrocephalus schoenobaenus</i>	sedge warbler	4.64	2.94
<i>Acrocephalus scirpaceus</i>	reed warbler	3.24	2.27
<i>Actitis hypoleucos</i>	common sandpiper	7.24*	4.18*
<i>Alauda arvensis</i>	skylark	3.84	2.55
<i>Alectoris rufa</i>	red-legged partridge	4.44*	2.84*
<i>Anas platyrhynchos</i>	mallard	6.84	3.99
<i>Anthus pratensis</i>	meadow pipit	1.24*	1.31*
<i>Anthus trivialis</i>	tree pipit	3.44*	2.36*
<i>Apus apus</i>	swift	5.64	3.42
<i>Ardea cinerea</i>	grey heron	6.04**	3.61
<i>Athene noctua</i>	little owl	3.24	2.27
<i>Aythya fuligula</i>	tufted duck	0.84*	1.12*
<i>Carduelis cannabina</i>	linnet	1.84	1.60
<i>Carduelis carduelis</i>	goldfinch	3.04	2.17
<i>Carduelis chloris</i>	greenfinch	1.64	1.50
<i>Carduelis spinus</i>	siskin	5.84*	3.51*
<i>Columba oenas</i>	stock dove	4.64	2.94
<i>Columba palumbus</i>	woodpigeon	1.24	1.31

(continued on the following page)

Table N1 continued.

Scientific name	Common name	Natal	Breeding
<i>Corvus corax</i>	raven	3.64**	2.46*
<i>Corvus corone</i>	carrion crow	2.84	2.08
<i>Corvus monedula</i>	jackdaw	2.44	1.88
<i>Cuculus canorus</i>	cuckoo	7.64*	4.37*
<i>Cygnus olor</i>	mute swan	1.24**	1.31
<i>Delichon urbicum</i>	house martin	2.64	1.98
<i>Emberiza citrinella</i>	yellowhammer	1.64	1.50
<i>Emberiza schoeniclus</i>	reed bunting	1.64	1.50
<i>Erythacus rubecula</i>	robin	3.84	2.55
<i>Fringilla coelebs</i>	chaffinch	2.04	1.69
<i>Fulica atra</i>	coot	6.24	3.70
<i>Gallinula chloropus</i>	moorhen	1.24	1.31
<i>Haematopus ostralegus</i>	oystercatcher	5.44*	3.32*
<i>Lagopus lagopus</i>	red grouse	2.44*	1.88*
<i>Larus argentatus</i>	herring gull	4.64*	2.94*
<i>Larus fuscus</i>	lesser black-backed gull	4.44	2.84
<i>Larus ridibundus</i>	black-headed gull	7.64	4.37
<i>Luscinia megarhynchos</i>	nightingale	2.84*	2.08*
<i>Motacilla flava</i>	yellow wagtail	3.24	2.27
<i>Muscicapa striata</i>	spotted flycatcher	6.04	3.61

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Table N1 continued.

Scientific name	Common name	Natal	Breeding
<i>Numenius arquata</i>	curlew	5.64*	3.42*
<i>Parus ater</i>	coal tit	4.44	2.84
<i>Parus caeruleus</i>	blue tit	4.44	2.84
<i>Parus major</i>	great tit	0.84	1.12
<i>Parus palustris</i>	marsh tit	3.64*	2.46*
<i>Passer domesticus</i>	house sparrow	2.04	1.69
<i>Passer montanus</i>	tree sparrow	2.24	1.79
<i>Perdix perdix</i>	grey partridge	6.04*	3.61*
<i>Phalacrocorax carbo</i>	cormorant	3.24*	2.27*
<i>Phasianus colchicus</i>	pheasant	1.44*	1.41*
<i>Phoenicurus phoenicurus</i>	redstart	5.24	3.23*
<i>Phylloscopus collybita</i>	chiffchaff	6.44*	3.80*
<i>Phylloscopus trochilus</i>	willow warbler	3.04	2.17
<i>Pica pica</i>	magpie	5.24	3.23
<i>Picus viridis</i>	green woodpecker	0.84	1.12
<i>Pluvialis apricaria</i>	golden plover	1.24*	1.31*
<i>Podiceps cristatus</i>	great crested grebe	6.04*	3.61*
<i>Prunella modularis</i>	dunnock	0.84	1.12
<i>Pyrrhula pyrrhula</i>	bullfinch	1.64	1.50
<i>Regulus regulus</i>	goldcrest	3.44*	2.36*

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Table N1 continued.

Scientific name	Common name	Natal	Breeding
<i>Streptopelia decaocto</i>	collared dove	2.24	1.79
<i>Streptopelia turtur</i>	turtle dove	3.84	2.55
<i>Strix aluco</i>	tawny owl	3.24	2.27
<i>Sturnus vulgaris</i>	starling	2.84	2.08
<i>Sylvia communis</i>	whitethroat	3.04	2.17
<i>Sylvia curruca</i>	lesser whitethroat	4.04**	2.65
<i>Tachybaptus ruficollis</i>	little grebe	4.84*	3.04*
<i>Tadorna tadorna</i>	shelduck	2.04*	1.69*
<i>Tringa tetanus</i>	redshank	5.24*	3.23*
<i>Turdus merula</i>	blackbird	1.04	1.21
<i>Turdus philomelos</i>	song thrush	1.84	1.60
<i>Turdus viscivorus</i>	mistle thrush	3.84	2.55

* = predicted dispersal distances for species not found in Paradis et al. (1998).

** = dispersal distances from Paradis et al. (1998) not used to calibrate the PSDI.

Appendix O Species specialization indices and population synchrony dispersal indices for North American breeding bird species.

Table O1. Species specialization indices (SSI) and population synchrony dispersal indices (PSDI) of North American breeding bird species. SSI were estimated as the coefficient of variation in the estimated species densities among different land cover classes (Julliard et al. 2006). For SSI, the sample size (n) is the number of routes where the species was observed. PSDI uses one-year-lagged synchrony in species abundance estimates between sampling sites as an indicator of typical species dispersal distances (Tittler et al. 2006, 2009). For PSDI, the sample size (n) is the number of distance classes with at least 10 paired sample locations. PSDI were estimated for species with at least one distance class with significantly more positive, one-year-lagged correlations than expected by chance at $\alpha = 0.05$. If there were significant proportions of positive, time-lagged correlations at multiple distance classes, the PSDI was estimated as the median of the range of the significant distance classes (range in brackets).

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Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Actitis macularius</i>	spotted sandpiper	34	1.31	---	---
<i>Agelaius phoeniceus</i>	red-winged blackbird	577	1.10	19	45 (30-60)
<i>Aimophila cassini</i>	Cassin's sparrow	48	1.75	17	45
<i>Aix sponsa</i>	wood duck	15	1.27	---	---
<i>Ammodramus leconteii</i>	le Conte's sparrow	18	1.61	16	165
<i>Ammodramus savannarum</i>	grasshopper sparrow	140	2.38	---	---
<i>Amphispiza belli</i>	sage sparrow	26	2.71	---	---
<i>Amphispiza bilineata</i>	black-throated sparrow	62	1.73	---	---
<i>Anas americana</i>	American wigeon	17	1.49	---	---
<i>Anas clypeata</i>	northern shoveler	13	1.71	12	185
<i>Anas crecca</i>	green-winged teal	10	2.15	---	---
<i>Anas discors</i>	blue-winged teal	17	2.19	---	---

(continued on the following page)

Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Anas platyrhynchos</i>	mallard	164	0.91	19	45 (20-70)
<i>Anas strepera</i>	gadwall	10	2.58	---	---
<i>Aphelocoma californica</i>	western scrub-jay	28	1.21	---	---
<i>Archilochus colubris</i>	ruby-throated hummingbird	10	1.43	---	---
<i>Ardea herodias</i>	great blue heron	89	1.12	19	145 (130-160)
<i>Baeolophus bicolor</i>	tufted titmouse	290	0.54	19	85 (40-130)
<i>Bartramia longicauda</i>	upland sandpiper	32	2.59	17	85
<i>Bombycilla cedrorum</i>	cedar waxwing	24	2.43	19	15
<i>Bonasa umbellus</i>	ruffed grouse	15	1.16	---	---
<i>Botaurus lentiginosus</i>	American bittern	64	0.94	---	---
<i>Branta canadensis</i>	Canada goose	75	1.31	19	100 (50-150)
<i>Bubo virginianus</i>	great horned owl	240	0.90	---	---

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Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Buteo jamaicensis</i>	red-tailed hawk	35	1.14	18	120 (110-130)
<i>Buteo lineatus</i>	red-shouldered hawk	10	2.24	18	45 (10-80)
<i>Buteo swainsoni</i>	Swainson's hawk	11	2.19	---	---
<i>Butorides virescens</i>	green heron	24	1.24	---	---
<i>Calamospiza melanocorys</i>	lark bunting	47	1.99	17	150 (140-160)
<i>Calcarius ornatus</i>	chestnut-collared longspur	10	1.60	---	---
<i>Callipepla californica</i>	California quail	39	1.34	19	25
<i>Callipepla gambelii</i>	Gambel's quail	33	1.72	---	---
<i>Callipepla squamata</i>	scaled quail	16	1.86	---	---
<i>Campylorhynchus brunneicapillus</i>	cactus wren	18	1.62	16	65
<i>Caprimulgus carolinensis</i>	Chuck-will's-widow	239	0.57	19	95 (30-160)
<i>Caprimulgus vociferus</i>	eastern whip-poor-will	125	1.31	19	185

(continued on the following page)

Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Cardinalis cardinalis</i>	northern cardinal	922	0.69	19	50 (10-90)
<i>Cardinalis sinuatus</i>	pyrrhuloxia	14	1.23	---	---
<i>Carduelis flammea</i>	common redpoll	14	1.66	---	---
<i>Carduelis pinus</i>	pine siskin	20	1.61	---	---
<i>Carduelis psaltria</i>	lesser goldfinch	12	2.29	17	125
<i>Carduelis tristis</i>	American goldfinch	122	0.77	19	45
<i>Carpodacus cassini</i>	Cassin's finch	18	1.48	12	105
<i>Carpodacus mexicanus</i>	house finch	213	1.03	---	---
<i>Carpodacus purpureus</i>	purple finch	40	1.22	19	75
<i>Casmerodius albus</i>	great egret	16	1.66	19	50 (20-80)
<i>Catharus fuscescens</i>	veery	171	1.25	19	50 (20-80)
<i>Catharus guttatus</i>	hermit thrush	174	2.19	19	145

(continued on the following page)

Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Catharus minimus</i>	gray-cheeked thrush	12	1.25	---	---
<i>Catharus ustulatus</i>	Swainson's thrush	167	1.37	---	---
<i>Catoptrophorus semipalmatus</i>	willet	12	2.81	---	---
<i>Certhia americana</i>	brown creeper	21	1.81	---	---
<i>Chaetura pelagica</i>	chimney swift	25	1.22	---	---
<i>Charadrius vociferus</i>	killdeer	405	1.07	19	55
<i>Chondestes grammacus</i>	lark sparrow	145	1.97	---	---
<i>Chordeiles acutipennis</i>	lesser nighthawk	33	1.47	---	---
<i>Chordeiles minor</i>	common nighthawk	390	1.16	---	---
<i>Cistothorus palustris</i>	marsh wren	25	1.87	11	135
<i>Cistothorus platensis</i>	sedge wren	31	1.46	18	35
<i>Coccyzus americanus</i>	yellow-billed cuckoo	151	0.81	19	65 (40-90)

(continued on the following page)

Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Coccyzus erythrophthalmus</i>	black-billed cuckoo	31	1.39	15	175
<i>Colaptes auratus</i>	northern flicker	45	0.80	19	20 (10-30)
<i>Colinus virginianus</i>	northern bobwhite	201	1.19	19	60 (20-100)
<i>Columba livia</i>	rock pigeon	11	1.83	19	105
<i>Contopus cooperi</i>	olive-sided flycatcher	47	1.98	---	---
<i>Contopus sordidulus</i>	western wood-peewee	107	1.00	19	55 (10-100)
<i>Contopus virens</i>	eastern wood-peewee	192	0.83	19	85
<i>Corvus brachyrhynchos</i>	American crow	634	1.21	19	35 (10-60)
<i>Corvus corax</i>	common raven	98	1.13	---	---
<i>Corvus cryptoleucus</i>	chihuahuan raven	13	1.22	---	---
<i>Corvus ossifragus</i>	fish crow	25	1.32	19	105 (30-180)
<i>Cyanocitta cristata</i>	blue jay	236	0.91	19	115

(continued on the following page)

Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Cyanocitta stelleri</i>	Steller's jay	24	1.61	18	195
<i>Dendroica caerulescens</i>	black-throated blue warbler	10	2.28	---	---
<i>Dendroica coronata</i>	yellow-rumped warbler	176	2.00	19	75
<i>Dendroica dominica</i>	yellow-throated warbler	29	2.02	18	45
<i>Dendroica fusca</i>	Blackburnian warbler	19	1.47	---	---
<i>Dendroica magnolia</i>	magnolia warbler	48	1.43	19	85
<i>Dendroica occidentalis</i>	hermit warbler	13	2.53	---	---
<i>Dendroica pensylvanica</i>	chestnut-sided warbler	67	1.43	19	80 (40-120)
<i>Dendroica petechial</i>	yellow warbler	313	0.48	---	---
<i>Dendroica pinus</i>	pine warbler	102	1.15	---	---
<i>Dendroica striata</i>	blackpoll warbler	13	1.43	---	---
<i>Dendroica virens</i>	black-throated green warbler	32	1.61	19	95 (40-150)

(continued on the following page)

Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Dolichonyx oryzivorus</i>	bobolink	65	1.37	19	80 (20-140)
<i>Dryocopus pileatus</i>	pileated woodpecker	10	1.25	19	30 (10-50)
<i>Dumetella carolinensis</i>	gray catbird	392	1.05	19	35 (10-60)
<i>Empidonax alnorum</i>	alder flycatcher	108	0.79	19	185
<i>Empidonax difficilis</i>	Pacific-slope flycatcher	32	1.72	---	---
<i>Empidonax hammondi</i>	Hammond's flycatcher	50	1.38	18	55
<i>Empidonax minimus</i>	least flycatcher	92	1.33	---	---
<i>Empidonax oberholseri</i>	dusky flycatcher	42	1.90	18	115
<i>Empidonax occidentalis</i>	Cordilleran flycatcher	16	3.16	---	---
<i>Empidonax traillii</i>	willow flycatcher	79	0.96	19	145
<i>Empidonax virescens</i>	Acadian flycatcher	45	1.13	19	90 (30-150)
<i>Empidonax wrightii</i>	gray flycatcher	15	2.23	---	---

(continued on the following page)

Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Eremophila alpestris</i>	horned lark	297	1.89	19	25
<i>Euphagus cyanocephalus</i>	Brewer's blackbird	80	1.24	19	195
<i>Falco sparverius</i>	American kestrel	10	2.01	17	45
<i>Fulica americana</i>	American coot	25	2.18	---	---
<i>Gallinago delicata</i>	Wilson's snipe	185	0.84	---	---
<i>Gavia immer</i>	common loon	45	0.71	---	---
<i>Geothlypis trichas</i>	common yellowthroat	555	0.80	19	70 (20-120)
<i>Grus canadensis</i>	sandhill crane	29	0.88	---	---
<i>Haliaeetus leucocephalus</i>	bald eagle	14	1.64	---	---
<i>Helminthorus vermivorum</i>	worm-eating warbler	10	2.02	18	115
<i>Hirundo rustica</i>	barn swallow	221	1.64	19	105 (30-180)
<i>Hylocichla mustelina</i>	wood thrush	356	1.14	19	45 (20-70)

(continued on the following page)

Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Icteria virens</i>	yellow-breasted chat	242	0.93	19	15
<i>Icterus bullockii</i>	Bullock's oriole	53	2.06	---	---
<i>Icterus galbula</i>	Baltimore oriole	85	1.24	---	---
<i>Icterus spurius</i>	orchard oriole	110	0.70	---	---
<i>Junco hyemalis</i>	dark-eyed junco	249	1.54	---	---
<i>Lanius ludovicianus</i>	loggerhead shrike	18	1.91	18	105 (90-120)
<i>Larus argentatus</i>	herring gull	19	2.98	---	---
<i>Larus canus</i>	mew gull	14	1.23	---	---
<i>Larus delawarensis</i>	ring-billed gull	31	1.75	17	175
<i>Limosa fedoa</i>	marbled godwit	15	1.62	---	---
<i>Megaceryle alcyon</i>	belted kingfisher	12	1.94	---	---
<i>Megascops asio</i>	eastern screech-owl	26	1.72	---	---

(continued on the following page)

Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Melanerpes carolinus</i>	red-bellied woodpecker	44	0.71	---	---
<i>Melanerpes erythrocephalus</i>	red-headed woodpecker	18	1.43	---	---
<i>Melanerpes formicivorus</i>	acorn woodpecker	15	2.37	15	115 (70-160)
<i>Meleagris gallopavo</i>	wild turkey	86	1.27	---	---
<i>Melospiza georgiana</i>	swamp sparrow	60	1.02	---	---
<i>Melospiza lincolni</i>	Lincoln's sparrow	73	0.99	18	85
<i>Melospiza melodia</i>	song sparrow	716	0.66	19	20 (10-30)
<i>Mimus polyglottos</i>	northern mockingbird	459	0.98	19	35 (20-50)
<i>Mniotilla varia</i>	black-and-white warbler	32	1.40	19	95
<i>Molothrus ater</i>	brown-headed cowbird	178	0.97	19	45
<i>Myadestes townsendi</i>	Townsend's solitaire	12	2.72	---	---
<i>Myiarchus cinerascens</i>	ash-throated flycatcher	79	1.99	19	135 (90-180)

(continued on the following page)

Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Myiarchus crinitus</i>	great crested flycatcher	220	1.09	---	---
<i>Myiarchus tyrannulus</i>	brown-crested flycatcher	11	1.25	---	---
<i>Numenius americanus</i>	long-billed curlew	21	1.76	---	---
<i>Nycticorax nycticorax</i>	black-crowned night-heron	18	1.48	---	---
<i>Oporornis formosus</i>	Kentucky warbler	14	2.07	18	85
<i>Oporornis philadelphia</i>	mourning warbler	45	1.40	19	65
<i>Oporornis tolmiei</i>	Macgillivray's warbler	55	2.03	---	---
<i>Oreortyx pictus</i>	mountain quail	15	2.03	---	---
<i>Oreoscoptes montanus</i>	sage thrasher	52	1.73	19	125
<i>Parula americana</i>	northern parula	55	1.30	19	15
<i>Parus atricapillus</i>	black-capped chickadee	256	1.01	19	155
<i>Parus carolinensis</i>	Carolina chickadee	53	0.93	19	45

(continued on the following page)

Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Parus gambeli</i>	mountain chickadee	49	1.91	---	---
<i>Parus rufescens</i>	chestnut-backed chickadee	13	1.59	---	---
<i>Passer domesticus</i>	house sparrow	248	1.19	---	---
<i>Passerculus sandwichensis</i>	savannah sparrow	246	1.29	19	105 (20-190)
<i>Passerella iliaca</i>	fox sparrow	43	1.98	---	---
<i>Passerina amoena</i>	lazuli bunting	36	1.46	---	---
<i>Passerina caerulea</i>	blue grosbeak	150	0.77	19	55 (10-100)
<i>Passerina ciris</i>	painted bunting	60	1.44	---	---
<i>Passerina cyanea</i>	indigo bunting	534	0.97	19	50 (40-60)
<i>Perdix perdix</i>	gray partridge	10	2.39	---	---
<i>Perisoreus canadensis</i>	gray jay	10	1.58	---	---
<i>Petrochelidon pyrrhonota</i>	cliff swallow	26	2.04	17	95

(continued on the following page)

Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Phalaenoptilus nuttallii</i>	common poorwill	59	1.33	---	---
<i>Phasianus colchicus</i>	ring-necked pheasant	279	1.96	19	50 (10-90)
<i>Pheucticus ludovicianus</i>	rose-breasted grosbeak	91	0.83	---	---
<i>Pheucticus melanocephalus</i>	black-headed grosbeak	86	1.32	19	120 (60-180)
<i>Pica hudsonia</i>	black-billed magpie	36	2.03	---	---
<i>Picoides pubescens</i>	downy woodpecker	19	1.42	19	165
<i>Pipilo chlorurus</i>	green-tailed towhee	49	1.82	---	---
<i>Pipilo crissalis</i>	California towhee	25	1.20	---	---
<i>Pipilo erythrophthalmus</i>	eastern towhee	316	0.88	19	50 (10-90)
<i>Pipilo fuscus</i>	canyon towhee	19	0.38	---	---
<i>Pipilo maculatus</i>	spotted towhee	147	1.18	19	70 (30-110)
<i>Piranga ludoviciana</i>	western tanager	111	1.45	---	---

(continued on the following page)

Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Piranga olivacea</i>	scarlet tanager	96	2.27	19	65 (30-100)
<i>Piranga rubra</i>	summer tanager	146	1.13	19	45
<i>Podilymbus podiceps</i>	pied-billed grebe	28	1.09	12	135
<i>Polioptila caerulea</i>	blue-gray gnatcatcher	161	0.76	19	55
<i>Pooecetes gramineus</i>	vesper sparrow	224	1.64	19	75
<i>Porzana carolina</i>	sora	41	1.33	17	135
<i>Progne subis</i>	purple martin	138	1.14	---	---
<i>Protonotaria citrea</i>	prothonotary warbler	---	---	17	55
<i>Quiscalus major</i>	boat-tailed grackle	12	2.38	18	105
<i>Quiscalus mexicanus</i>	great-tailed grackle	17	1.53	14	155
<i>Quiscalus quiscula</i>	common grackle	173	1.99	19	55 (10-100)
<i>Regulus calendula</i>	ruby-crowned kinglet	54	1.38	19	105

(continued on the following page)

Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Regulus satrapa</i>	golden-crowned kinglet	50	1.17	---	---
<i>Riparia riparia</i>	bank swallow	10	3.14	---	---
<i>Salpinctes obsoletus</i>	rock wren	46	2.21	18	25
<i>Sayornis nigricans</i>	black phoebe	13	1.56	11	175
<i>Sayornis phoebe</i>	eastern phoebe	412	0.91	19	100 (90-110)
<i>Sayornis saya</i>	Say's phoebe	71	1.73	---	---
<i>Scolopax minor</i>	American woodcock	24	1.12	---	---
<i>Seiurus aurocapilla</i>	ovenbird	153	1.47	19	90 (10-170)
<i>Seiurus motacilla</i>	Louisiana waterthrush	13	2.85	---	---
<i>Seiurus noveboracensis</i>	northern waterthrush	34	1.05	---	---
<i>Setophaga ruticilla</i>	American redstart	87	1.20	---	---
<i>Sialia currucoides</i>	mountain bluebird	56	1.73	---	---

(continued on the following page)

Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Sialia mexicana</i>	western bluebird	36	1.74	13	165
<i>Sialia sialis</i>	eastern bluebird	274	0.82	19	60 (40-80)
<i>Sitta canadensis</i>	red-breasted nuthatch	44	1.55	19	135
<i>Sitta carolinensis</i>	white-breasted nuthatch	30	1.40	19	195
<i>Sitta pusilla</i>	brown-headed nuthatch	---	---	12	175
<i>Sphyrapicus varius</i>	yellow-bellied sapsucker	17	1.21	---	---
<i>Spiza americana</i>	dickcissel	146	1.75	19	95 (70-120)
<i>Spizella arborea</i>	American tree sparrow	10	2.14	---	---
<i>Spizella breweri</i>	Brewer's sparrow	75	2.39	---	---
<i>Spizella pallida</i>	clay-coloured sparrow	86	1.23	---	---
<i>Spizella passerina</i>	chipping sparrow	788	0.72	19	75 (20-130)
<i>Spizella pusilla</i>	field sparrow	164	0.95	19	80 (10-150)

(continued on the following page)

Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Stelgidopteryx serripennis</i>	northern rough-winged swallow	55	0.91	15	195
<i>Streptopelia decaocto</i>	Eurasian collared-dove	18	1.56	---	---
<i>Strix varia</i>	barred owl	155	1.17	---	---
<i>Sturnella magna</i>	eastern meadowlark	250	1.49	19	50 (10-90)
<i>Sturnella neglecta</i>	western meadowlark	342	2.19	19	85 (60-110)
<i>Sturnus vulgaris</i>	European starling	151	1.25	19	25
<i>Tachycineta bicolor</i>	tree swallow	172	0.75	---	---
<i>Tachycineta thalassina</i>	violet-green swallow	77	1.02	18	65
<i>Thryomanes bewickii</i>	Bewick's wren	68	1.34	19	105 (60-150)
<i>Thryothorus ludovicianus</i>	Carolina wren	368	0.87	19	125
<i>Toxostoma curvirostre</i>	curve-billed thrasher	16	2.06	---	---
<i>Toxostoma rufum</i>	brown thrasher	219	0.74	19	85 (10-160)

(continued on the following page)

Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Troglodytes aedon</i>	house wren	285	0.89	19	115
<i>Troglodytes pacificus</i>	Pacific wren	37	1.35	---	---
<i>Troglodytes troglodytes</i>	winter wren	60	1.69	---	---
<i>Turdus migratorius</i>	American robin	1358	0.43	19	80 (10-150)
<i>Tyrannus forficatus</i>	scissor-tailed flycatcher	82	1.16	---	---
<i>Tyrannus tyrannus</i>	eastern kingbird	252	0.80	19	85
<i>Tyrannus verticalis</i>	western kingbird	214	1.60	19	175
<i>Tyrannus vociferans</i>	Cassin's kingbird	21	1.67	10	105
<i>Vermivora celata</i>	orange-crowned warbler	66	0.85	---	---
<i>Vermivora peregrina</i>	Tennessee warbler	16	1.31	12	75
<i>Vermivora pinus</i>	blue-winged warbler	---	---	18	135 (120-150)
<i>Vermivora ruficapilla</i>	Nashville warbler	78	1.39	19	135

(continued on the following page)

Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Vireo bellii</i>	Bell's vireo	12	2.72	---	---
<i>Vireo cassinii</i>	Cassin's vireo	11	1.75	---	---
<i>Vireo flavifrons</i>	yellow-throated vireo	32	1.41	19	165 (140-190)
<i>Vireo gilvus</i>	warbling vireo	169	1.57	19	65
<i>Vireo griseus</i>	white-eyed vireo	33	0.89	19	75
<i>Vireo olivaceus</i>	red-eyed vireo	277	1.24	19	15
<i>Vireo solitarius</i>	blue-headed vireo	19	1.65	---	---
<i>Wilsonia citrina</i>	hooded warbler	27	1.54	19	20 (10-30)
<i>Wilsonia pusilla</i>	Wilson's warbler	48	1.41	17	35
<i>Xanthocephalus xanthocephalus</i>	yellow-headed blackbird	38	2.56	17	105
<i>Zenaida asiatica</i>	white-winged dove	27	1.52	---	---
<i>Zenaida macroura</i>	mourning dove	1290	0.77	19	55 (10-100)

(continued on the following page)

Table O1 continued.

Scientific name	Common name	SSI		PSDI	
		n	Estimate	n	Estimate
<i>Zonotrichia albicollis</i>	white-throated sparrow	179	1.06	19	55
<i>Zonotrichia leucophrys</i>	white-crowned sparrow	81	0.61	18	135
<i>Zoothera naevia</i>	varied thrush	58	0.96	18	75

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