Human disturbance and birds of the Northeast:

What makes some species decline, while others are just fine?

A Dissertation Presented

by

Leone M. Brown

to

The Graduate School

in Partial Fulfillment of the

Requirements

for the Degree of

Doctor of Philosophy

in

Ecology and Evolution

Stony Brook University

December 2012

Stony Brook University
The Graduate School

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Abstract of the Dissertation

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Mounting evidence reveals the negative impacts of human activities on wildlife populations. However, studies investigating species' responses to human disturbance often rely on patterns of species' richness or abundance, and may not reflect underlying demographic processes. Is there evidence across geographic regions that humans are causing marked changes in species' survival, reproduction, and population growth? Do species' traits influence vulnerability? Can existing theories of ecology serve to predict or explain observable responses to human disturbance? I examined evidence of effects of human disturbance on populations of 24 breeding bird species across the northeastern United States. Based on reported literature and theoretical expectations, I developed hypotheses about effects of human disturbance on demographic parameters. I first tested the hypothesis that human disturbance negatively impacts survival, reproduction, and population growth across species, by determining the importance of human disturbance and the direction of its effect in predicting demographic parameters. I found support for negative impacts of humans on bird populations, but not consistently across species. Next, I tested hypotheses about characteristics that make species vulnerable to human disturbance, by comparing their relationship to each other and the direction of their effect on demographic parameters in the absence and presence of disturbance. Some expected characteristics revealed vulnerability to human disturbance, but the effect was not always consistent across demographic parameters. Lastly, I tested for evidence of a cost of reproduction on survival or future reproduction across species, and asked if human disturbance enhanced costs. A cost of reproduction expected by life history theory was evident across species, but not consistently across different levels of human disturbance. While populations of numerous bird species are declining locally and globally, the extent to which effects of human disturbance are species-specific versus generalizable is not well understood. Mitigating the problem is limited without multi-species analyses of the demographic parameters driving persistence. My results contribute

to the body of research measuring human impacts on wildlife populations, demonstrate the value of theoretical and empirical knowledge for predicting and understanding species' responses, and underscore the importance of long-term, large-scale population monitoring programs to collect data integral to addressing these questions.

For John W. Taylor,
Friend and lover of nature
Whose decades of voluntary contribution
To the Monitoring Avian Productivity and Survivorship program,
In part made this dissertation possible.

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Acknowledgements

I am greatly indebted to a huge number of people that have helped me to complete this dissertation, and provided intellectual, moral, and financial support. First, I wish to thank my committee for their ongoing support: my advisor Catherine Graham, the Chair of my committee Resit Akçakaya, Jeffrey Levinton, and my outside committee member Anna Pidgeon.

Catherine Graham and I met early in both of our careers, hers as a newly minted faculty member and mine as a graduate student. When I started, Catherine did not yet have an ongoing research program for students to work on, so we were left to our own devices as far as fieldwork and locations. Catherine patiently waited as I stumbled through idea after idea before settling upon the current project, and tried to help me throughout by providing ideas of her own and setting me up with laboratory projects. When my first project went terribly awry, she kept me on as a graduate student who refused to quit even at my wit's end. I would like to think we have learned a lot from each other, and I can only hope she is as proud to have seen me grow as a young scientist, as I am to have watched her grow into the amazing scientist and advisor she has become. I am incredibly grateful for her support and help on this dissertation, as well as her concern, encouragement, and sagacious advise with regard to my future.

Resit Akçakaya's expertise in population biology has been invaluable in completing this dissertation project. He has been incredibly generous with his time and knowledge, and I have thoroughly enjoyed all of our interactions. I have never left his office without my head exploding with information, and I am incredibly indebted to him for this. His critical eye misses nothing as far as I can tell, and he has a will to understand and teach that is beyond admirable. I can only hope to someday become as meticulous and brilliant a scientist as he is, and yet still remain as un-judging and kind.

Jeffrey Levinton's contribution to completion of this dissertation has been both unusual and crucial. I initially chose Jeff as a committee member because of his contributions to work in urban ecology, but the project on which I settled was removed from the taxa on which Jeff normally focuses. This has served to my benefit. While my other committee members could speak directly to my project with regard to bird populations or demographic studies, Jeff brought a fresh, outside perspective, and an abundance of ideas unique to his experiences to the table. He also provided endless statistical suggestions. Jeff's contribution was rounded out with his help on my final chapter on life history trade-offs, on which he has decades of accumulated knowledge and expertise.

Anna Pidgeon was the best outside committee member I could have hoped for. Her work and interests are very closely aligned with mine, and her knowledge of North American birds, their natural history, and impacts of human disturbance on bird populations is tremendous. She has been incredibly responsive, generous with her time, constructively critical, and encouraging.

I wish to thank the Institute for Bird Populations for generously providing me with these data that I have used to complete my dissertation, and for all of their hard work and dedication in making the Monitoring Avian Productivity and Survivorship (MAPS) program run smoothly and successful for over two decades. With this, I also owe enormous gratitude to the many current and past volunteers at the banding locations across the northeastern United States. Among these, I thank Lorraine Bondi-Goldsmith and Aaron Virgin for allowing me volunteer with them at the Hoffman Center in Oyster Bay, NY, and John Taylor for allowing me to band with him for several years on his property in Cold Spring Harbor, NY. Working at these MAPS locations both improved my bird banding, handling and monitoring skills, as well as gave me a good

understanding of how the data are collected for the MAPS program and any issues that may arise. In addition, John and his wife Joy have become good friends over the years, and I feel very lucky to have such amazing people in my life. I have learned a ton from John in working with him, and he is the epitomy of kindness, dedication, and love of birds and nature.

Several others have provided intellectual support and guidance, including Stephan Munch, Jim Rohlf, Heather Lynch, Jan Gogarten, Kevin Shoemaker, Matthew Aiello-Lammens, Jessie Stanton, Matthew Sisk, John Wiens, Ramona Walls, Shea Lambert, Antonin Machac, and the entire Graham lab past and present, especially Jorge Velasquez, Juan Parra, Boris Tinoco, Ben Weinstein, Melissa Mark, Jessie Knowlton, and Norah Warchola.

I have also had a huge amount of support from my family, and the best friends of my life. Those that have uplifted me in the darkest hours and provided shoulders on which to laugh and cry include some of the best friends of my life: Melissa Mark, Norah Warchola, Ramona Walls and John Wiens, J. Matt Hoch, Paul Bourdeau, Dan Moen, Jan Gogarten, Matthew Aiello-Lammens, Roberta Salmi, James Herrera, Jorge Velasquez, Jessie Stanton, Matthew Sisk, Juan Parra, Boris Tinoco, and Jessie Knowlton. Other close friends that have provided great moral support include André Levy, Mike Alessi, Janet Morrison, Andreas Koenig and Carola Borries. My family has of course provided immense support both financially and in unconditional love. I am also greatly indebted to Julian Pessier at the University Counseling Center who, over the last two years of my graduate career, was an awesome cheerleader, provided endless support, and taught me a ton about myself, helping me to learn and grow with confidence. Finally, I thank the Long Island Shetland Sheepdog Rescue for providing me with my lovely dog, Ebby, who has been an enduring and excellent companion over the past three and a half years, and has made me laugh endlessly with her quirks, as well as brought smiles to the faces of many, many others.

Last, but not least, I thank the Department of Ecology and Evolution for allowing me to be a part of their family, and for providing me with financial, administrative, and moral support throughout this journey.

Chapter 1:
Background and Aims

The “footprint” of humans on wildlife

The human population doubled in the last half of the 20th century, and is expected to reach nearly 9 billion by the year 2050 (Cohen 2003). While the rate of human population growth has slowed (Cohen 2003), the proportion of the population living in urban areas continues to increase (Marzluff 2001, McKinney 2006). Whether urban centers are large or small, their surrounding sprawl is a trademark of urbanization. This urban sprawl is especially prominent in the conterminous United States, where the trend over recent decades of nuclear family households, facilitated by increases in economic status, creates a mosaic of altered landscapes interrupted by roads (Forman and Alexander 1998, Brown et al. 2005). Even in rural areas where human population densities are low, sprawl has rapidly and drastically altered land cover (Brown et al. 2005, Radeloff et al. 2005). As governmental policies have traditionally facilitated rather than minimized the spread of human-altered landscapes (Lawrence 2005, Alberti et al. 2008), impacts of human disturbance on ecosystems and wildlife populations have been an increasingly important focus of research.

Urbanization, defined as an increase in human population density and land use intensity (Marzluff 2001), can have several negative impacts on wildlife. First, urbanization causes both habitat fragmentation and destruction, leading to biodiversity loss (Johnson and Klemens 2005). In addition, urbanized areas often have a greater influx of invasive species that may fill in where native populations have been extirpated, outcompete remaining natives, and exacerbate habitat and biodiversity loss (Vitousek et al. 1997). Independent of habitat loss or competition with invasive species, the very nature of urbanization tends to favor simplified vegetation structure (McKinney 2008), which does not promote biological diversity. Further, urbanization may alter pathogen dynamics and make wildlife populations more susceptible to disease by altering immune function and introducing novel pathogens via invasive species (Bradley and Altizer 2007, Martin et al. 2010). All of these negative impacts ultimately can make urbanization a major cause of population declines, and in some cases extinctions, while increasing biotic homogenization (McKinney 2006). Whereas some threats to species such as hunting or disease may be mitigated via environmental policies or targeted control strategies, urban areas are unique among human disturbances in that they are rarely reversed (McKinney 2002). This underscores the need for continued research to fully understand how human-disturbed landscapes affect wildlife populations.

Assessing impacts of human disturbance

Mitigating the effect of human-induced disturbances on natural populations requires a quantitative assessment of potential causes of population declines, and the role of human disturbance. However, since populations naturally fluctuate over time and space, a snapshot of the status of wildlife populations in a single year at a single location is not sufficient to evaluate their status. Conservation biologists and government regulators rely on long-term and large-scale monitoring programs to evaluate population trajectories and guide conservation and land management.

Birds are well-loved, and hence commonly one of the first observed indicators of human disturbance. They are also one of the most well-studied taxa long term. As early as 1900, the Christmas bird count was established by Frank M. Chapman as a retort to a Christmas bird hunting tradition (Audubon 2012). Just over half a century later, Rachel Carson's cries about the impacts of DDT on bird populations (Carson 1962) catalyzed establishment of the Breeding Bird Survey (BBS) in 1966. These programs, as well as state atlases and local monitoring by individuals, have produced a huge database on which much of our knowledge about species' responses to urbanization has been obtained. Specifically, these data have revealed declines in species richness in urban areas (Marzluff 2001, Chace and Walsh 2006, Shochat et al. 2006, but see Minor and Urban 2010), changes in species abundance from rural to urban gradients (Blair 1996, Tratalos et al. 2007), biotic homogenization and exploitation by synanthropic species, i.e., those able to co-exist with humans (McKinney 2006, Blair and Johnson 2008), and inferences about the types of species likely to decline versus increase (e.g., generalists versus specialists; Devictor et. al. 2008).

More recently, it has been recognized that observed differences in patterns of species richness and abundance may get at the urgency of the problem, but miss underlying mechanisms driving patterns, and fail to detect trends in population viability (e.g., Brawn and Robinson 1996). Declines in species richness and altered patterns of abundance are ultimately driven by differences in annual survival and productivity (Saracco et al. 2008). Using only abundance or richness data does not reveal how populations are fairing or their level of tolerance. These data do not reveal if individuals in more urbanized areas are thriving or have decreased survival relative to those in less urban areas. Nor do they reveal if individuals persisting in an area are unique in their ability to use an area, or outcasts from higher quality sites. Richness or abundance data may yield some information about habitat quality, but demographic data are necessary to reveal source or sink habitats and yield insight into population persistence (Pulliam 1988, Blair 1996).

In response to concerns about the lack of a mechanistic approach to understanding effects of urbanization (Shochat et al. 2006), more recent studies have assessed reproductive success across rural to urban gradients. These studies have revealed some generalizations, but have often differed depending on how reproductive success is measured (Chamberlain et al. 2009). A few studies have evaluated adult survival and found higher survival in urban areas for urban-adapted species, higher population growth in suburban and rural areas, or no relationship between survival and urbanization (Marzluff et al. 2001, Rodewald and Shustack 2008). How other birds respond to urbanization is largely unknown.

What current approaches lack

Although the above research has contributed greatly to our understanding of population responses to human disturbance, it has also highlighted gaps in our knowledge. First, using only reproductive success or adult survival is likely not a good estimate of population persistence if the relationship between adult survival and reproduction is unknown (Wiens and Reynolds 2005, Arlt et al. 2008). A few studies have simultaneously evaluated reproductive success and survival to estimate population persistence, but these generally use estimates of survival from the literature (Hansen and Rotella 2002, Lloyd et al. 2005, but see Rodewald and Shustack 2008). Using literature estimates ignores the possibility of variation in survival across gradients of disturbance. Further, it is not enough to know only that reproductive success or adult survival is compromised in a region because the management options may differ if the goal is to increase reproduction (e.g., by providing or protecting nest sites) versus to minimize mortality (e.g., by mediating human sources of mortality such as window collisions). A complete picture of species' responses to human disturbance requires simultaneous analysis of multiple demographic parameters.

Second, the effects of human disturbance on populations need to be evaluated across several species within studies. Knowing how one or two particular species are affected by human disturbance is useful for those species, but does not facilitate more than speculation about threats to populations of other species, and may be insufficient to understand the extent of threats of human disturbance. This can also be detrimental if management practices are altered based on analyses of a single species, but are harmful to other species (e.g., restoration of a particular vegetation type that is useful for one species but decreases habitat for another species). While multi-species studies have been used to evaluate patterns of species abundance or diversity with human disturbance, studies of changes in demographic parameters (e.g., survival and reproduction) across multiple species are also needed. Species responses to human disturbance should be simultaneously evaluated using similar methods to reduce speculation and to assist in making management decisions.

Third, to obtain a more holistic assessment of species responses to human disturbance, trait-levels analyses are needed in addition to species-level analyses. In some cases, only one or a few specific species may be affected by disturbance, or several species may be affected in different ways. In other cases, however, it may be possible to make generalizations about species' responses to human disturbance based on their life history characteristics. Analyses taking both species- and trait-level approaches would help conservation biologists and managers to distinguish between species- versus trait-level responses. This distinction is important because some management practices could help to conserve many species based on trait-level responses to disturbance, while others may need to be species-specific. This approach, again, has been taken using species abundance or diversity as response variables, but not the demographic parameters expected to drive patterns of abundance or diversity.

Lastly, a more holistic approach should also allow us to use existing theories of ecology to understand species' responses to human disturbance. Some authors have argued for theories of urban ecology (e.g., Pickett et al. 2008), while others argue that current theories, if robust, should be applicable across environments (e.g., Niemelä 1999). Studies of species' responses to human disturbance have already attempted to invoke some fundamental theories. For instance, the intermediate disturbance hypothesis has been used to explain why species diversity is often greatest not in the least nor the most human-disturbed areas, but in areas of moderate human disturbance (e.g., Blair 1996, Marzluff 2005, Lepczyk et al. 2008). In addition, theories of island biogeography, metapopulations, source-sink dynamics and ecological traps have been used to understand extinction and colonization dynamics in urbanizing regions (Davis and Glick 1978, Tilghman 1987, Soulé et al. 1988, Donovan and Thompson 2001, Marzluff 2005). A more holistic approach to assessing species' responses to human disturbance should expand on these to include application and investigation of other fundamental theories of ecology an evolution in urbanizing areas to understand the processes affecting populations.

How can we address gaps in current understanding?

Fortunately, as with the efforts of the Christmas Bird Count (CBC) and Breeding Bird Survey (BBS), long-term data are becoming available from which multiple demographic parameters can be estimated simultaneously across multiple species. Further, these data facilitate investigation of species- and trait-level processes in human disturbed areas, and application of fundamental theories in ecology and evolution. Among these data, the most extensive is likely the Monitoring Avian Productivity and Survivorship (MAPS) program initiated by the Institute for Bird Populations in 1989, which coordinates collection of mark-recapture data for species across the continental United States (DeSante et al. 1995). This program was established with the goal of collecting information about the ecology and population demographics of bird populations, specifically parameters underlying population trends, to aid species' conservation and management (DeSante et al. 1995). As with the CBC and BBS data, MAPS data are collected almost entirely by volunteer operators of bird banding stations. Stations are established in ~20 hectares or larger areas that are expected to remain relatively unchanged so as to facilitate long term monitoring (DeSante et al. 2012). Stations are operated during the breeding season of North American birds, once per 8-10 consecutive ten-day periods, the number of periods depending on the latitude of a location (DeSante et al. 2012). A standard-effort protocol is maintained across stations to minimize sources of error between stations. These data can be made available upon written request in the form of a project proposal, and can be used to address many of the gaps in our knowledge.

Aims of the dissertation

In this dissertation, I used MAPS data to assess the effect of human disturbance on three interrelated aspects of bird populations: species-level responses, trait-level responses, and life history trade-offs. In doing so, I aimed to address three gaps the literature: 1) a lack of multi-species studies assessing responses to human disturbance using multiple demographic parameters, 2) uncertainties and conflicting results regarding generalizations that can be made about species responses to human disturbance, and 3) few studies applying fundamental theories in ecology and evolution to predict and understand processes occurring in urbanized regions. I used MAPS data from the northeastern United States because this region has several urban centers with extensive urban sprawl, large swaths of relatively undisturbed land, and housing sprinkled throughout. Further, demographic parameters in this region are expected to be lower relative to other regions of the United States as a result of human disturbance (Clark and Martin 2007).

In my dissertation, I addressed the following questions:

1. **Is there evidence across a range of species for a general negative response to human disturbance?** I evaluated the response of demographic parameters to disturbance across a quantitative gradient in 22 bird species of the northeastern United States. Using multimodel inference, I tested a series of hypotheses about the influence of human disturbance on survival, reproduction, and population growth. I evaluated the importance of human disturbance alone, as well as in combination with environmental variables expected to affect breeding bird populations, to ask which combinations of human disturbance and other environmental variables were important in predicting demographic parameters fore each species. I also compared how often human disturbance had a negative versus positive effect on demographic parameters, and the sensitivity of population growth to survival versus reproduction across species.

2. **Can we make generalizations about species' responses based on life history characteristics?** Addressing the previous question yielded insight into how individual species were responding to human disturbance, but not with enough power to say which life history

characteristics were important in influencing the combination of disturbance and environmental variables that can predict population persistence. In my second chapter, I ignored specific-species responses to disturbance to focus on the overall effect of different life history characteristics on demographic parameters in 24 bird species. I used mixed effect models to test hypotheses about the characteristics that would make species most vulnerable, and asked if disturbance changes which life history characteristics have the greatest influence on population parameters. I compared the overall effect of species characteristics on survival, reproduction, and population growth (e.g., the effect of nest location versus food preference), and then compared the strength and direction of the response to human disturbance within species characteristics (e.g., the effect of being a cavity-nesting versus a ground-nesting species) and demographic parameters.

3. **Does disturbance mediate or exacerbate costs of reproduction?** My first two questions allowed me to explore the effects of disturbance and life history characteristics on demographic parameters both within and across species. To address my last question, I tested for an effect of human disturbance on the relationship between demographic parameters. Combining life history theory and expected responses to urbanization, I generated hypotheses about expected trade-offs between demographic parameters in more and less disturbed environments. I used phylogenetic regression and mixed effect models to test for an effect of disturbance on the trade-off between reproduction and survival across 24 species. I then tested within species for trade-offs between reproduction and survival across environments, between current reproduction and future survival, and between current and future reproduction.

My goal in addressing the above questions was to create a cohesive body of work addressing the impact of human disturbance on wildlife populations, taking both applied conservation and theoretical ecology points of view. I hope these results can provide a useful contribution to the literature and encourage further collection and use of long-term demographic data to assess and mitigate impacts of human disturbance

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Chapter 2:
The influence of anthropogenic disturbance on survival, reproduction and population growth of birds in the northeastern United States

Abstract

Human disturbance, specifically human-developed land cover, influences species abundance and richness worldwide. How negative effects of human disturbance on abundance and richness are reflected in simultaneous measures of survival, reproduction, and population growth across species has yet to be investigated. I estimated survival, reproduction, and population growth from bird banding data collected for 22 breeding species across the northeastern United States. I used a multimodel inference and model selection approach to determine the importance of human disturbance derived from land cover data in predicting demographic parameters, alone or in combination with other land cover or climate variables. Human disturbance predicted survival, reproduction, or population growth in 16 of 22 species, and predicted survival in more species than it predicted other parameters. The direction of the effect of human disturbance on demographic parameters was not uniform across species, suggesting that species do not have a uniformly negative response to human disturbance. However, populations for most species were declining at more locations across the northeastern United States than they were increasing. Investigating the effects of human disturbance on more than one demographic parameter may yield insight into the underlying mechanisms driving population growth or decline.

Introduction

Human disturbances, such as altered land cover and increasing urbanization, are changing patterns of species richness and abundance worldwide (Blair 1996, Clergeau et al. 1998, Marzluff 2001, Donnelly and Marzluff 2006, McKinney 2008). Scientists are challenged to evaluate how these emerging changes and novel environments may influence species' persistence. While many studies have focused on the effects of human disturbance on species abundance, richness, fledgling survival and nest success independently, few studies have simultaneously examined the effects of disturbance on multiple population parameters that lead to altered patterns of abundance and richness. Demographic information is crucial for understanding the future trajectory of populations and for providing information on how survival, reproduction, and, ultimately, population growth, vary across species. Knowledge of variation in demographic responses across species is also useful for determining the best strategies to mitigate negative effects of human disturbance (e.g., LeClerc et al. 2005), or minimize causes of adult mortality (Klem 1989). To address this knowledge gap, I evaluated the effect of human disturbance on survival, reproduction and population growth of North American birds across landscapes of differing land cover and degrees of urbanization.

The effects of land use and urbanization on multiple demographic parameters have not been widely or simultaneously evaluated. While many studies have quantified reproductive success along gradients of human disturbance, those that include survival have generally only evaluated fledgling success or survival, and nest predation (e.g., Thorington and Bowman 2003, Reale and Blair 2005, Ryder et al. 2010, Balogh et al. 2011), but not adult survival. If the relationship between survival and reproduction is unknown, or varies greatly between individuals, then there are several reasons why using only reproductive success or nestling survival may not be a good proxy for measuring population persistence (Wiens and Reynolds 2005, Arlt et al. 2008). Measures of reproductive success may lead to classifying some sites as unfavorable sinks, but these may be useful sites for populations if fledglings or adults are dispersing to them for alternative sources of food, and thus improving chances of survival. Alternatively, some habitats that appear productive may become unfavorable sinks if survival at these sites is low or if disturbance causes high dispersal (Balogh et al. 2011). As a result, measures of reproductive success alone may not capture variation in population growth and persistence. Studies using estimates of reproduction, e.g., breeding success or production of young, often assume that differences in reproductive parameters will be reflected in local population growth rates (Arlt et al. 2008). However, if survival is negatively correlated with reproduction or contributes more to population growth than reproduction, then this assumption may be not true (Arlt et al. 2008). Further, if adults alter their behavior to buffer their offspring from the negative effects of disturbance, these behavioral changes may compromise parental survival (Kight and Swaddle 2007) and could decrease overall population growth. These insights cannot be gleaned from examining only reproductive success or only survival. Only by evaluating demographic metrics in combination can the effects of disturbance on bird populations be fully understood.

Studies attempting to simultaneously evaluate reproductive success and survival to estimate population growth across regions of different land cover or urbanization have generally used estimates of adult survival from the literature (Hansen and Rotella 2002, Lloyd et al. 2005, but see Rodewald and Shustack 2008). Using literature estimates for survival does not account for the possibility of variation in survival across sites with different levels of human disturbance. The few studies that have empirically measured adult survival in response to human disturbance have found increased survival in urban areas for urban-adapted species, or no relationship between survival and urbanization (Marzluff et al. 2001, Rodewald and Shustack 2008). However, population growth may still be greater in suburban and rural areas, even for birds with higher adult survival in urban areas (Marzluff et al. 2001). It is unknown if birds that exist along gradients of human disturbance vary in the direction of their response to disturbance, or if some species are just tolerant and able to persist, but not necessarily with higher survival or reproductive success than in less disturbed areas (Blair and Johnson 2008).

Evaluating the effects of human disturbance on multiple demographic parameters across many species requires a large spatial and temporal effort and training of field assistants to build appropriate datasets. The Monitoring Avian Productivity and Survivorship (MAPS) program is a continent-wide bird-banding effort from which long-term survival and reproductive effort can be estimated, respectively, from recaptures and from ratios of relative juvenile to adult abundances (Desante et al. 1995). In combination with land cover data, it is possible to evaluate the potential influence of natural land cover and anthropogenic disturbance, as measured by housing density, on survival, reproduction (hereafter referred to as maternity), and population growth (hereafter referred to as lambda). I investigated the effect of human disturbance on survival, maternity and lambda in 22 breeding bird species of the northeastern United States. I developed a series of models based on *a priori* hypotheses to test the relationship between human disturbance and demographic parameters, both alone and in combination with environmental variables that may also predict demographic parameters or interact with human disturbance. I evaluated these hypotheses for each species across all sites at which each species was found.

Increased urbanization confers a series of threats to birds including: decreased food availability (where not provided by humans for certain species), increased predation by cats and urban-adapted raptors (but see Newhouse et al. 2010), increased potential for disease outbreaks due to large densities of individuals and common resource use (e.g., bird feeders), and collisions with buildings and vehicles (Klem 1989, Lepczyk et al. 2004a, Lepczyk et al. 2004b, Hotchkiss et al. 2005, Chace and Walsh 2006). Based on these threats, I hypothesized that human disturbance would have a negative effect on species, caused by either, a) more developed areas directly causing a decline in survival, maternity, or lambda, b) dominant birds choosing higher quality habitat, excluding subordinates that already have lower survival and productivity and relegating them to lower quality habitat (Fretwell 1969), which I hypothesized are the more developed areas, or c) birds not returning to these habitats, i.e., there is low site-fidelity, resulting in lower apparent survival (Blums et al. 2002). Because natural land cover should be important for choosing breeding sites and providing refuge from disturbance events, I expected that both human disturbance and natural land cover together may be important for predicting demographic parameters, and may even interact. For instance, a disturbed area with a high proportion of an appropriate natural land cover type, such as forest for forest-dwelling species, might confer higher survival or maternity than a similarly disturbed area with a lower proportion of appropriate natural land cover. I also expected that climate might be important in combination with the effect of human disturbance on demographic metrics. In some species there may even be an interaction between human disturbance and climate, whereby the negative effects of colder winter or early spring temperatures may be mediated by additional food sources found in a human-disturbed environment. For instance, residents in extremely cold urban regions may have higher survival and subsequent reproductive success due to the presence of bird feeders (Robb et al. 2008), or an urban heat island effect that shields these regions from the most extreme temperatures (Jin et al. 2005). I tested these hypotheses by regressing survival, maternity and lambda for each of 22 bird species on combinations of human disturbance, natural land cover, climate variables, and interactions between human disturbance and natural land cover, and between human disturbance and minimum temperature across multiple locations in the northeastern United States.

Methods

Bird banding data and locations

I obtained MAPS banding data from the Institute for Bird Populations for 98 locations in the northeastern United States (Maine, Vermont, New Hampshire, Massachusetts, Connecticut, Rhode Island, New York, Pennsylvania, New Jersey, Delaware), ranging from 4-19 years of data spanning 1989-2007 (www.birdpop.org; Figure 2.1). Each banding site spans an approximately 20-hectare area in which mist nets are placed and birds are banded according to a standard-effort protocol (DeSante et al. 1995, DeSante et al. 2012). These sites are typically located in wooded or semi-wooded areas that are expected to remain relatively unchanged so as to facilitate long-term monitoring.

I checked the recorded latitude and longitude for each banding site using Google Earth (version 5.2, build date Sep 1, 2010). I verified locations of the 98 sites based on the overall vegetation structure of the banding sites as recorded by the operators, and site location names compared with similarly named locations (e.g., parks or landmarks) on Google Earth. I located each banding site and compared the vegetation within which it was found, which I could distinguish on Google Earth, with the vegetation recorded by operators and the site name. I moved locations of twelve of the 98 stations, all by less than one kilometer. I have worked at two of these sites personally and so was aware of their exact location. Prior to adjusting their location, three sites were located in water and two were located on city streets, according to Google Earth. These five sites and three additional sites were all named based on their occurrence in national or state parks. I moved these sites within the boundaries of the parks to the closest area with vegetation consistent with that recorded by station operators (e.g., deciduous forest, as opposed to water or city blocks). Two additional sites were recorded as being in wooded areas, but the recorded latitude and longitude land cover were fields next to a wooded area, so I adjusted their geographic coordinates to occur just within the wooded area. I created a 1-km buffer around each site to further account for error or variation in GPS records, and to encompass variation in human developed land cover surrounding the sites. For stations located less than 1-km apart in which buffers overlapped by more than 10%, I combined the buffers and station data. Only two pairs of stations that overlapped were not combined, and the buffers for these stations overlapped by only 2% and <6%, respectively. Fifteen of the 98 stations were combined, 12 into pairs and 3 into one group. The 22 species studied here occurred in 84 of the final sites.

Land cover data and nonmetric multidimensional scaling

I obtained land cover data for the northeastern United States from the 30-m resolution National Landcover database (NLCD 2001, version 2, http://www.mrlc.gov/; Figure 2.1). Within each banding site's 1-km buffer, I created a point shapefile with a 30-m cell size to match the cell size of the land cover map. I extracted land cover values for the points within the buffers around each station using ArcMap 9.3 (ESRI cite). I calculated the proportion of each land use type surrounding each banding site by counting the number of points representing each land use type, using R, version 2.13.1 (R Development Core Team 2012).

Of the 15 land cover types included in the NLCD data, I dropped open water and barren rock (following Lloyd et al. 2005). To minimize number of land cover types being analyzed and focus on classifications that may be more broadly important for birds at a landscape level, I combined six of the remaining 13 land cover types that seemed most similar based on the land cover type descriptions (Homer et al. 2004). The final 8 land cover types were: 1) forest (deciduous, mixed, and evergreen forest), 2) shrub/scrub, 3) developed open space to low intensity development (combination of these two land cover types represents land that is <50% developed), 4) medium to high developed (combination of developed medium to high intensity, represents land that is >50% developed), 5) grassland/herbaceous and pasture/hay (both not highly disturbed or tilled), 6) cultivated crop (considered disturbed), 7) emergent herbaceous wetland, and 8) woody wetlands.

I analyzed the proportions of each of these 8 land cover types across sites using nonmetric multidimensional scaling (NMDS, 100 iterations; R package 'ecodist', Goslee and Urban 2007). I partitioned the variance in percentage cover of the set of 8 land cover types into loadings onto two axes as indices of land cover across sites. I determined the direction of relationship between the proportion of each land cover type and the two NMDS axes to evaluate how land cover variables were being partitioned across these two axes. The two NMDS axes explained on average 88.3% of the variation in overall land cover between sites. There was a clear negative relationship between NMDS axis 1 and forest, grassland/herbaceous and pasture/hay, and cultivated crop. There was a clear positive relationship between NMDS axis 1 and developed open to low, developed medium to high, and emergent herbaceous wetlands.

There was a clear positive relationship between NMDS axis 2 and forest, and a negative relationship between NMDS axis 2 and grassland/herbaceous and pasture/hay, woody wetland, and emergent herbaceous wetland (Table 2.1). These results indicated that the NMDS axis 1 separated human disturbance from other types of land cover, with the possible exception of the emergent herbaceous wetland and shrub/scrub land cover types. NMDS axis 2 separated forested from non-forested natural (i.e., undeveloped) land cover. Lower to higher values of NMDS axis 1 represented lower to higher proportions of disturbed land use, and lower to higher values of NMDS axis 2 represented the gradient from more open to more closed (e.g., forest) land cover types (Figure 2.2). I confirmed the use of NMDS axis 1 as an index of human disturbance by correlating this axis with an independent measure of housing density obtained from 1-km resolution housing density estimates for the year 2000 (close to the date for the land cover layers; Hammer et al. 2004). A single site may fall within different levels of housing density, so I calculated a weighted average housing density based on the number of pixels within each station's buffer that fell within each housing density value. I assumed a high correlation between housing density and human population (Lepczyk et al. 2008), and so did not use population census data. Housing density was highly correlated with the first NMDS axis (t=9.52, df=76, r=0.737, p<0.0001; Figure 2.3), indicating that NMDS axis 1 likely reflects human disturbance and land-use intensity. I used the NMDS axes to evaluate the relationship between human disturbance and species demographic parameters because the land cover data are finer resolution the than housing density data (30-m vs. 1-km resolution, respectively).

Climate data

I obtained 800-m resolution 1971-2000 means for average April, May, July, and August precipitation, average annual precipitation, and minimum annual temperature from the PRISM Climate group (Daly et al. 2002). I averaged April-May and July-August precipitation values as potentially important periods for breeding birds because, assuming food abundance is related to precipitation, these periods may be important for birds recovering from migration and establishing territories, as well as for obtaining enough food to feed offspring and fatten for migration. For all climate values, I calculated a weighted mean for each site based on the number of pixels within the buffer area and the climate values assigned to each of these pixels. April-May and July-August values were correlated with each other and with average annual precipitation, so I used only average annual precipitation.

Parameter estimates

I estimated survival for adult birds (after-hatch year, AHY) and juvenile birds (hatch-year, HY) using the Cormack-Jolly-Seber (CJS) model in Program MARK (White and Burnham 1999). The CJS model in Program MARK yields parameters estimates for both survival and recapture by breaking each capture history into an overall probability of survival and recapture, and evaluating the probabilities and their frequency across all capture histories using maximum likelihood. The survival and recapture parameters can each be estimated by time, by group (i.e., by site for this analysis), or as a constant, single value. Program MARK provides an Akaike Information Criterion (AIC) value for each CJS model, varying depending on how each parameter is estimated. The Akaike's Information Criterion varies as a function of the model likelihood and the number of parameters in the model, whereby each additional parameter is penalized by +2. For each species, I estimated survival by site, and recapture by both site and as a constant (a single overall value for all sites, expected if banding is based on a sampling-wide constant-effort protocol). I used the survival estimates for each site from the CJS model with the lowest AIC, whether recapture was allowed to vary by site or was estimated as a single value. This allowed me to account for some variation in recapture rates between sites, e.g., if recapture differs greatly between sites due to differences in effort then these will be accounted for in survival estimates. Survival estimates are ‘apparent survival,’ meaning survival rates include lack of return to a site due to death or due to dispersal. Prior to estimating survival, I deleted unbanded individuals and those recorded as dead or injured from the database of individual capture histories, because these individuals were not likely to be recaptured at later time periods. I only estimated survival for species that had at least 300 individual capture histories, resulting in the 22 species examined here. For each of these 22 species, I did not include data from sites that did not have at least one recapture record during the years of monitoring. The resulting data included species captured at an average of 27 sites (range: 9-54 sites per species) across sites with varying levels of human disturbance (Figure 2.4).

As a cross check for survival estimates, I compared the survival estimates I obtained for each species to values available online from the Institute for Bird Populations (IBP; Michel et al. 2006). The IBP estimated a single regional estimate for survival for birds of the northeastern United States, encompassing an area that includes the sites used in this study, as well a portion of the surrounding area. To compare survival values between my study and the regional analysis done by IBP, I re-estimated survival across all sites as a constant, single value in Program MARK, again allowing recapture to be constant or vary by group and choosing the model with the lowest AIC. My estimates as a constant differed on average by ~0.04 from the IBP estimates, and my estimates were generally lower (Table 2.2). I consider this potential underestimate in interpreting results. For any species that had a recapture at an adjacent location (generally these were within the combined sites mentioned above), I also compared the number of recaptures outside of each site to the number of captures within sites, and compared these values across all stations that were combined due to overlap (Table 2.3). Within the 14 out of 22 species that had recaptures outside of a single location, on average ~5% of recaptures occurred at an adjacent location. Across all species, among pairs of adjacent locations, ~3% of recaptures occurred at an adjacent location. I also consider this dispersal as a potential source of bias when interpreting results, which may have resulted in underestimates of survival and lambda.

I used maternity as a measure of reproductive success for each species at each site. The maternity values I calculated represent a “post-breeding” census because the juveniles are counted in the same year that they were born (Akçakaya et. al 1999). For each species at each site, I calculated maternity using the formula

$$\text{a)}\,\frac{f_1 + f_2 + f_3 + ... + f_n}{N_1 + N_2 + N_3 + ... + N_n}$$

where *f* is the number of juveniles captured in years 1 to *n*, and *N* is the number of adults captured in years 1 to *n*. An alternative way to estimate maternity is

$$\text{b)}\,\frac{\frac{f_1}{N_1} + \frac{f_2}{N_2} + \frac{f_3}{N_3} + ... + \frac{f_n}{N_n}}{n}$$

The values obtained from equation a) are weighted averages (maternity, *f*/*N*, weighted by sample size, N, for each year), and thus take into account variation in effort (as measured by sample size) across time steps, such that estimates of maternity from years with small N contribute less to the time-averaged maternity estimates (H. R. Akçakaya, *pers. comm*). Given that sampling effort varies across years in the MAPS program as new sites are initiated and some sites are not monitored or other factors may interfere with monitoring effort, I used the values from equation a). The values of maternity using equations a) and b) did not differ significantly (paired t-test: t=1.63, df=627, p=0.104).

I calculated population growth as lambda for each species at all sites where each species was found. There were not enough hatch year bird (HY) captures to estimate HY survival across all sites for which an estimate for after hatch year (AHY) survival was available. To estimate the HY survival necessary for calculating lambda for all sites in which each species was found, I calculated the average ratio of AHY:HY survival for each species across all sites for which both parameters could be estimated. I then calculated HY survival for each species across all sites as this proportion of the known AHY survival.

To obtain lambda values for each species at each site, I first estimated fecundity of HY and AHY birds. Because HY birds are counted in the same year as they are born, and not captured again until the following year when they are potentially breeding, fecundity of HY birds is $F_{\mathrm{HY}}=S_{\mathrm{HY}}\cdot m_{\mathrm{HY}}$, where S_{HY} is survival of HY birds, and m_{HY} is maternity of subadult birds, i.e., birds in their first year (following a post-breeding census; Akçakaya et al. 1999). Similarly, fecundity of AHY birds is $F_{\mathrm{AHY}}=S_{\mathrm{AHY}}\cdot m_{\mathrm{AHY}}$, where S_{AHY} is survival of AHY birds, and m_{AHY} is maternity of adult birds (i.e., birds in their second year or older; Akçakaya et al. 1999). The method for estimating maternity described in the above section is based on all AHY birds, whether subadult or older. Across multiple species, reproductive success increases with breeding experience and age, subadults tend to fledge fewer offspring, and subadult birds of migratory species tend to arrive on the breeding ground later than adults, securing territories and mates later, if at all, and also experiencing lower reproductive success (Ficken and Ficken 1967, Harvey et al. 1985, Nol and Smith 1987, Lemon et al. 1996, Lozano et al. 1996, Cooper et al. 2009). Given minimal knowledge of the relative proportions of subadults versus adults in the population and their reproductive success, one can either assume that maternity is equal for AHY and HY birds, or that maternity is greater for one age class than the other, resulting in the same average maternity values calculated above. I assumed that contribution of AHY birds versus HY birds to maternity was 2:1. For some species, this ratio may under or overestimate maternity for each age class, and subsequently lambda, depending on the proportions of subadults versus adults in the population and their overall reproductive success. I therefore also calculated lambda assuming a ratio of 1:1 and 3:1, to compare the resulting differences in lambda. To estimate lambda, I placed fecundity and survival values into the 2 × 2 matrix,

$$\begin{matrix} F_{\mathrm{HY}} & F_{\mathrm{AHY}} \\ S_{\mathrm{HY}} & S_{\mathrm{AHY}} \end{matrix}$$

and estimated lambda as the dominant eigenvalue of the matrix. This estimate of lambda assumes that populations are at their stable age distribution, meaning the proportion of adults and juveniles in the population is not changing over time, even if the overall population size is changing (Akçakaya et al. 1999).

Statistical Analyses

1) Effect of environmental variables on demographic parameters

I regressed survival, maternity, and lambda (assuming a 2:1 AHY:HY maternity ratio) on hypothesis-based combinations of environmental variables, including human disturbance, for all species for which there were sufficient data across sites to estimate population parameters (Table 2.4). For survival models, I only used AHY survival because HY birds are more likely to have lower survival and lower site fidelity than AHY birds, influencing apparent survival rates. For most species there were also fewer sites for which exact HY survival values could be estimated; therefore, it was necessary to estimate HY survival as a proportion of AHY survival, as described above. I used beta regression to regress survival on environmental variables, because survival values ranged between 0 and 1, and beta regression is appropriate for dealing with rate and proportion data (R package 'betareg', Cribari-Neto and Zeileis 2010). I regressed maternity and lambda on combinations of environmental variables using linear models in the R base 'stats' package. For maternity regressions, I log-transformed maternity and checked residuals for normality. Lambda values were approximately normally distributed, and I checked the residuals of these models for normality.

I regressed each demographic parameter (survival, maternity or lambda) for each species on 23 different model combinations of variables at each site including human disturbance (HD), natural land cover (LC), minimum annual temperature (TMIN) and annual precipitation (PPT; correlation, *r*, between predictor variables was <0.5 across all sites). There were 5 null models that did not include HD, i.e., these models included the intercept, LC, TMIN, and PPT alone. Models with HD included HD alone, and I added LC, an interaction between HD and LC, TMIN, PPT, and an interaction between HD and TMIN to subsequent models (Table 2.4). Due to constraints of the data (small sample size for some of the 22 species), I did not include higher order interaction terms without biological justification. I reported the log-likelihood, AIC_c, and *r*-squared of each model for each species. Within the set of models for each species for each demographic parameter, I also calculated the ΔAIC_c (difference in AIC_c value between each model and the lowest AIC_c value reported for any model), and Akaike models weights as

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{i=1}^{N}\exp(-\frac{1}{2}\Delta_i)}$$

where Δ_i is the ΔAIC_c of the i^{th} model from the model with the lowest AIC_c (Burnham and Anderson 2002). I generally considered models with the lowest AIC_c and models with Δ $AIC_c < 2$ from the model with the lowest AIC_c as the best among the candidate models. However, this may be a false assumption if the +2 penalty for additional parameters does not remove a model from the candidate set that has only one additional parameter from a model that is that same but without this additional parameter (i.e., it does not add any additional information to the model; Arnold 2010). Therefore, I note when a model with one additional parameter is within $\Delta AIC_c < 2$ of the model with the lowest AIC_c without the additional parameter, and thus may not be a better model. I also calculated a model-averaged parameter estimate for HD for each species using the formula, $\hat{\bar{\theta}} = \sum_{i=1}^{N} w_i\hat{\theta}_i$, where $\hat{\theta}$ is the parameter estimate for each individual model from 1 to N, and w_i is the weight of the model (Anderson 2008). The model-averaged estimate for HD provides an overall estimate of the effect of HD on survival, maternity, or lambda across species. Because I used different regression models and parameter transformations across survival, maternity and lambda models, I did not directly compare the effect size across parameters (e.g., compare the effect size of HD on survival versus on maternity versus on lambda). However, I could compare the effect of HD within survival, within maternity, or within lambda estimates across species. The main effect of HD can differ when an interaction between HD and another variable is included in the model, so I computed the model-averaged HD estimate for each species both across all models and only for models without an interaction term. I used a paired t-test to compare these two model-averaged HD estimates (with and without including an interaction term) across species. Lastly, I calculated evidence ratios for each model using the formula $w_{\min}/w_i$ (Anderson 2008). This evidence ratio provides a relative likelihood of the model with the lowest AIC_c with respect to other models, i.e., the model with the lowest AIC_c is x times more likely than the model in question, where x is the evidence ratio. I evaluated support for the effect of HD and HD in combination with natural LC or climate variables on survival, maternity or lambda via combinations of predictor variables in the 'best' candidate models for each species based on Akaike weights and evidence ratios. I used one sample t-tests to determine if HD had an overall positive or negative effect on survival, maternity, or lambda across all species, by comparing all species' model-averaged HD estimates within survival, maternity or lambda models to a mean of 0. I used a binomial test to determine if the overall number of species exhibiting a relationship with HD was significantly different than expected by chance, and to compare the number of species in which HD predicted survival versus maternity or lambda.

2) Comparison of lambda across sites

I used paired t-tests to compare the number of sites for each species in which lambda was greater than one versus less than one, i.e., for which the population was increasing versus decreasing. I also compared the means of the disturbance metric, HD, at sites in which lambda was greater than one versus less than one.

3) Sensitivity analyses

To determine the sensitivity of lambda to values in the Leslie matrix, I increased and decreased the values of AHY survival, AHY maternity or HY survival, and HY maternity at each site for each species by ten percent (Akçakaya et al. 1999). Increasing AHY maternity by ten percent has the same effect on lambda as increasing HY survival because of their positions in the 2×2 matrix. I used the difference between the values of lambda after increasing and decreasing each value in the matrix as the measure of sensitivity (i.e., a smaller difference between the high and low values means lower sensitivity to a particular parameter). For each species, I report the number of sites where lambda was most sensitive to each parameter. I also compared estimates of lambda assuming maternity ratios of AHY:HY birds of 1:1 and 3:1, to the estimates I used which assumed a maternity ratio of 2:1. Finally, to determine the effect of underestimates of survival on lambda, I increased AHY and HY survival across sites and species by 0.1 and 0.2, and compared the resulting lambda averages for each species.

Results

Survival, maternity and lambda estimates varied across species, with averages for survival ranging from ~0.2-~0.5, averages for maternity ranging from ~0.2-~1.4, and averages for lambda ranging from ~0.4-~1.3 (Figure 2.5).

Effect of human disturbance on demographic parameters

Across models predicting survival, maternity and lambda, human disturbance was included in at least one of the best candidate models for 16 of the 22 species (*p*=0.052; Table 2.5). Human disturbance was nearly significant in more often predicting survival than maternity or lambda (*p*=0.069). For some species, models included HD as the only additional parameter in comparison to models with the lowest AIC_c, but ΔAIC_c was still within 2 of the model with the lowest AIC_c, which could mean that HD is an uninformative parameter in these models and does not necessarily represent an actual relationship. After removing models containing HD that were potentially due to an uninformative parameter, human disturbance was included among the best candidate models (i.e., models with the lowest AIC_c or with an AIC_c within 2 of the model with the lowest AIC_c) predicting survival, maternity and/or lambda for 11 of the 22 species: American Redstart, American Robin, Black-and-white Warbler, Downy Woodpecker, Eastern Towhee, Gray Catbird, Northern Cardinal, Red-eyed Vireo, Traill's Flycatcher, Veery, and Yellow Warbler. The model-averaged effect of HD was equally often negative as positive across species for survival and maternity (11-/11+), and was more often negative than positive across species for lambda (13-/9+). Across species, the model-averaged effect of HD did not differ significantly from zero (survival: *t*=-0.34, *df*=21, *p*=0.7373; maternity: *t*=-0.4861, *df*=21, *p*=0.6319; lambda: *t*=0.1615, *df*=21, *p*=0.8733). The model-averaged effect was also not significantly different when models with interaction terms were included (survival: *t*=-1.424, *df*=21, *p*=0.1691; maternity: *t*=0.398, *df*=21, *p*=0.6946; lambda: *t*=0.6394, *df*=21, *p*=0.5295). The largest differences between the model-averaged HD estimates resulting from models with interaction terms versus only models without interaction terms were for survival models of American Redstart and Red-eyed Vireo (a difference of 0.46 and 0.57, respectively, with a smaller survival estimate when interaction terms were included). Including null models, only 12 of the 23 tested models had the lowest AIC_c for predicting demographic parameters across all species; generally these were the models with the fewest parameters (Table 2.6).

Human disturbance alone was among the best candidate models predicting survival in 10 species (Tables 2.6 and 2.7). In 7 of these species the model with the lowest AIC_c was the null model with survival regressed on the intercept alone, and thus HD as one additional parameter may be uninformative (Figure 2.6). The remaining 3 species in which HD alone predicted survival were Gray Catbird, Red-eyed Vireo, and Yellow Warbler (Figure 2.7). This relationship was positive for Gray Catbird and Red-eyed Vireo, and negative for Yellow Warbler. The model with HD alone was the model with the lowest AIC_c and greatest weight for Gray Catbird and Red-eyed Vireo. Models combining human disturbance with land cover (HD+LC) predicted survival in 3 species: Downy Woodpecker, Ovenbird, and Traill's Flycatcher, but was potentially due to an uninformative parameter in Ovenbird. An interaction between HD and LC was included in models predicting survival for American Robin, Gray Catbird, Traill's Flycatcher, and Veery; this was the model with the greatest weight for American Robin. Human disturbance in combination with temperature or precipitation predicted survival in Gray Catbird, Song Sparrow, and Yellow Warbler, but the combination may have been due to uninformative parameters (see Table 2.7). Both American Redstart and Red-eyed Vireo included models with an interaction between HD and temperature among the best candidate models, and both of which explained ~38% of the variance.

Human disturbance alone was among the best candidate models predicting maternity in 4 species (Tables 2.6 and 2.7; Figures 2.8 and 2.9), and was the model with the greatest weight for 1 species: Traill's Flycatcher. This relationship was negative for Traill's Flycatcher, and slightly negative for Black-and-white Warbler. However the negative *r*-squared value for the model for Black-and-white Warbler suggests it does not exhibit a real relationship, or the models I tested do not capture the relationship. HD alone was the single best candidate model predicting maternity for Traill's Flycatcher, and HD had the largest negative effect on maternity in Traill's Flycatcher compared to any other species. The effect of HD ranged from -1.56 to +1.50 for all species except Traill's Flycatcher, whereas in Traill's Flycatcher the effect of HD on maternity was -3.456. Human disturbance in combination with land cover (HD+LC) predicted maternity in only one species, Black-and-white Warbler, though this relationship only included one extra parameter from the model with the lowest AIC_c and thus HD may not be informative in this case. Human disturbance in combination with precipitation or temperature and precipitation predicted maternity in 4 species, but the addition of HD in these models may not be informative.

Human disturbance alone was among the best candidate models predicting lambda in 7 species, but was potentially an uninformative parameter in 3 species. The remaining 4 species for which HD alone clearly predicted lambda were: Black-and-white Warbler, Gray Catbird, Red-eyed Vireo, and Traill's Flycatcher (Tables 2.6 and 2.7; Figures 2.10 and 2.11). The relationship between HD alone and lambda was negative for Black-and-white Warbler and Traills' Flycatcher, and positive for Gray Catbird and Red-eyed Vireo. HD alone predicting lambda was the model with the greatest weight for Gray Catbird and Red-eyed Vireo. Human disturbance in combination with land cover (HD + LC) predicted lambda in only one species, Black-and-white Warbler, and was also the model with the greatest weight. Models with an interaction term between LC and HD were the models with the lowest AIC_c for American Redstart and Northern Cardinal, and this was the model with the greatest weight for American Redstart. Human disturbance in combination with temperature or precipitation predicted lambda in 5 species, but was potentially due to an uninformative parameter in 2 species; the remaining 3 species for which there was a clear relationship were: Eastern Towhee, Traill's flycatcher and Veery. This model had the lowest AIC_c and greatest weight in Traill's Flycatcher.

Comparison of lambda across sites

Across all species except Downy Woodpecker, Song Sparrow, and Tufted Titmouse, lambda indicated that populations were decreasing at more sites than they were increasing (Table 2.8; t=-3.76, df=40, p<0.001). There was not a significant difference in HD between sites at which each species was increasing versus decreasing. Downy Woodpecker, Song Sparrow and Tufted Titmouse each had a single outlier for maternity, and Downy Woodpecker and Tufted Titmouse both had a single outlier for lambda. However, these were only at single sites, so did not significantly change the above results. Removing these outliers also did not significantly change the results of models evaluating the effect of HD; the only difference with regard to the relationship with HD was the addition of a single model for survival of Song Sparrow, which included an interaction between HD and minimum temperature.

Sensitivity analyses

Across species, lambda was generally more sensitive to AHY survival in more sites than to AHY maternity or HY survival (Table 2.8; t=3.62, df = 21, p<0.002). However, there was no significant difference between the number of sites across species at which lambda was more sensitive to AHY maternity or HY survival versus HY maternity, or AHY survival versus HY maternity. The difference in lambda with an increase and decrease of 10% of any parameter was never >0.1, except for HY maternity for Downy Woodpecker, Song Sparrow, and Tufted

Titmouse. Lambda in the latter three species differed by <0.15 between a 10% increase and decrease of HY maternity (Table 2.9).

Lambda was always greatest when a 1:1 AHY:HY maternity ratio was assumed and always smallest when a 3:1 ratio was assumed (Figure 2.12). The difference was greater between a 1:1 and a 2:1 ratio than between a 2:1 and a 3:1 ratio. The difference between assuming a 2:1 AHY:HY maternity ratio versus a 1:1 or 3:1 ratio was only >0.1 for Black-capped Chickadee, Downy Woodpecker, Song Sparrow and Tufted Titmouse (Table 2.10).

With an increase in AHY survival and HY survival of 0.1, or an increase in AHY survival of 0.2, lambda reached 1.0 or greater for only 5 species (one additional species from the original lambda estimate). Increasing both AHY survival and HY survival by 0.2 brought 15 of the 22 species to a lambda estimate of 1.0 or greater.

Discussion

Human disturbance (HD) influenced one or more demographic parameters for many of the bird species examined, and both positive and negative effects were observed. While abundance and richness of species often declines with human disturbances, the demographic responses measured here do not show a similar consistently negative trend. Natural land cover (LC) and/or climate variables predicted demographic parameters for most species, which makes sense as land cover is directly associated with nest site and foraging substrate availability, and climate constrains availability of soft-bodied invertebrates that are critical for provisioning passerine young. Human disturbance alone or in combination with LC more often predicted survival than maternity. In contrast, precipitation alone or temperature and precipitation more often predicted maternity than survival. The importance of natural LC in the context of HD is supported by previous studies that have emphasized maintenance of preferred habitat types for species of interest, especially in urbanizing areas (Jokimäki 1999, Borgmann and Rodewald 2004, Donnelly and Marzluff 2006, Pidgeon et al. 2007). Nonetheless, the considerable variation in the overall effect of HD, and the combination of variables that predicted demographic parameters, suggests that it may be difficult to generalize effects of human disturbance across species.

The variation of demographic responses to HD within and among species was contrary to my initial expectation of an overall negative effect. Species that had an overall positive relationship with HD may be benefiting from factors such as augmented food sources or reduced competition with species less abundant in disturbed sites (e.g., Robb et al. 2008, Suarez-Rubio et al. 2011). These species are unlikely to be of immediate conservation concern, especially if small reserves are maintained. In contrast, species with a negative relationship between demographic variables and HD may be less able to acquire resources, more vulnerable to predation in disturbed areas, or more sensitive to other impacts of human disturbance (e.g., noise, edge effects; Herrera-Montes and Aide 2011, Marzluff 2001). Though some sites may be larger than 20-hectares, for those that are not, it may be necessary to set aside larger natural areas to shield these species from effects of human disturbance (Donnelly and Marzluff 2004, Stratford and Robinson 2005). For species that showed little response to HD, either disturbance is not a major factor affecting demographic parameters, or positive and negative effects associated with human disturbance balance each other out. Unmeasured variables could also influence the overall variation in species' demographic responses to HD. Variables such as noise (Fontana et al. 2011), predation (Balogh et al. 2011), or conspecific attraction (Ahlering and Faaborg 2006) may interact with or have a more direct impact on species than HD alone as measured here.

Alternatively, individuals and populations could be locally adapting to disturbance behaviorally within sites, so that a population-level effect across sites is not apparent (Rodewald and Shustack 2008). Future studies at a finer scale that measures factors such as noise levels, and compare local- versus population-level responses to disturbance could yield insights into the degree to which local adaptation contributes to variation in demographic responses.

The few overall trends in demographic responses suggest that individual species respond differently to human disturbance. Some of these species-specific responses are supported by other studies. For instance, previous studies for Wood Thrush found no effect of urbanization on abundance or productivity (Friesen et al. 2005, but see Friesen et al. 1995), consistent with results of this study in which HD was not included in any models predicting maternity. In Traill's Flycather, HD alone produced the single best candidate model predicting maternity and had the largest negative effect compared to any other species. Previous studies of a related species, the Acadian Flycatcher, revealed a negative relationship between reproduction and urbanization (Rodewald and Shustack 2008), consistent with the results found here for Traill's Flycather. Rodewald and Shustack (2008) did not find a strong effect of urbanization on survival, however they did find that urbanization influenced site fidelity and habitat selection. If the same behavioral processes occur in Traill's Flycatcher, this could explain the negative effect of HD alone on survival (e.g., if HD is influencing site fidelity), and a combination of HD and LC on survival in Traill's Flycatcher in the present study (e.g., if HD is influencing habitat selection).

Human disturbance predicted survival in more species than maternity. While reproductive success varies in response to human disturbances depending on the species being observed and how reproductive success is measured (reviewed by Chamberlain et al. 2009), the lack of importance of HD alone or in combination with LC in predicting maternity for more species in this study is somewhat surprising. The effects of urbanization on nest predation and reproductive success include both positive and negative species-specific responses, and these have been related to differences in urbanization and land cover characteristics (Thorington and Bowman 2003, Chamberlain et al. 2009, Ryder et al. 2010). In a recent study, Balogh et al. (2011) found different rates of nest predation and fledgling survival in Gray Catbirds across landscapes of differing levels of urbanization. In the present study, no candidate models predicting maternity in Gray Catbird included HD, though fledglings could have been predated later in the season after being captured. The results found here suggest differential nest predation associated with variation in HD may not be a strong driver affecting maternity. Precipitation or both temperature and precipitation were among the most important variables predicting maternity in many species, suggesting that after a breeding site has been selected (during which time land cover characteristics may be important), reproductive success may depend more heavily on the ability to procure enough resources to feed offspring. Resource abundance for many of the species in this study, most of which are insectivorous, may be more influenced by precipitation (e.g., Studds and Marra 2007) than specific vegetation types. In addition, if HD is not directly affecting maternity, then it may not be a factor causing sites to become sinks, unless young are more likely to die at sites after they have been censused each year. Once individuals establish territories in an area, maternity may not be affected, and so may also not be cause for decreased site fidelity (e.g., Blums et al. 2002). The greater issue may be ensuring settlement, given that apparent survival, which includes both deaths and failure to return to sites, does appear to be somewhat influenced by HD and natural LC.

For most species and sites, I found that population growth was more likely to be decreasing than increasing. Further, most species were more sensitive to small changes in after hatch year bird survival than to hatch year bird survival or maternity. These results support previous analyses of MAPS data for warblers across a larger region, which found that survival was more important than productivity in driving abundance trends as found in Breeding Bird Survey data (Saracco et al. 2008). The present study across multiple species, one third of which were warblers, suggests that population growth in other groups of species may also be less sensitive to reproduction than survival. However, it should be noted that some of the lambda values were very close to 1, so these populations may actually be stable if lambda values are biased low due to observer error in collection of demographic data. In addition, given that my estimates of survival were slightly lower than those of Institute of Bird Populations and that there is some recapture outside of MAPS netting stations, survival and consequently lambda values across sites are likely underestimated. The underestimate is likely stronger for species such as Wood Thrush or Hermit Thrush that seem, relative to other species, to have a large proportion of recaptures occurring at sites outside of the original sites at which they were captured, i.e., they have greater dispersal distances. Lambda estimates may also be biased if populations are not at their stable age distribution, for instance if disturbance disrupts the stable age distribution. Because I estimated hatch year survival as a proportion of after hatch year survival based on the sites at which enough hatch year birds were captured to obtain a reasonable estimate for hatch year survival, these estimates are not exact and may further introduce error into lambda estimates. Therefore caution should be taken in the interpretation of lambda. However, the approach I took in this study allowed estimation of hatch year survival across multiple species for which there were otherwise too few data points to run the same analyses as for survival and maternity. Unlike in other studies, hatch year survival was estimated from real data within the study, rather than from a single value of juvenile survival taken from the other studies in literature. The hatch year estimates used here take into account variation in survival across sites; this potential variation is not accounted for by using only a single value from the literature. Further, hatch year and after hatch year survival estimates both had to be increased by 0.2 across species to bring lambda for more than half of the species to ≥1.0. Therefore, unless survival estimates across species are severely underestimated, populations of many of these species may still be declining, whether due to human disturbance as measured here, other measures of disturbance not captured in this study, or factors occurring on migratory routes or on the wintering ground for migratory species.

I did not aim here to advocate any best model or to find one combination of variables that most influenced all species, only to demonstrate the relationship or lack thereof between demographic parameters and human disturbance. For some species, the lack of relationship may be due to the temporal or spatial scale at which species are responding to disturbance (e.g., Friesen et al. 2005, Hostetler and Holling 2000, Reidy et al. 2008). For instance, individuals responding to the landscape at a small grain may not be influenced by disturbance outside the 20-hectare areas of this study. Alternatively, the effect of disturbance may be time-lagged and thus not yet detectable (Friesen et al. 2005). In addition, if density dependence is a strong factor regulating populations of some species, this may mute the effect of HD on demographic parameters, specifically lambda. For instance, two species may have very different maximum rates of increase (i.e., average population growth rate under low population density) and population sizes, making one more vulnerable to disturbance than the other. However, their lambda values may be about the same if the populations are regulated by year-to-year density dependent factors that operate in the same way on both species. Thus, average values of demographic rates (including, but not limited to, lambda) may not be a best indicator for discriminating between species threatened with decline and those less threatened. A more definitive approach may be to estimate the density dependence relationship for each demographic parameter, and compare the parameters of those relationships (e.g., R_{max}, the maximum growth rate, or the predicted value of survival under low population densities). This, however, requires more data than was available for this study.

Where there is a relationship between HD and demographic parameters, caution should also be taken in interpreting the meaning of predictor variables, especially if the models that include these predictor variables are within $\Delta AIC_c < 2$ of the model with the lowest AIC_c and only include one additional parameter, because in these cases the additional parameter might not contribute additional information to the model. Errors in prediction may also be associated with extrapolation of climate variables from the PRISM dataset, or potential classification errors in NLCD data. However, the high correlation between the measure of HD used in this study and an independent measure of housing density suggest that HD was relatively reliable estimate of human disturbance.

This study is unique in its attempt to estimate both survival and reproduction parameters across multiple species and sites at a regional scale. Generally studies that estimate demographic parameters focus on only one to a few species and only one demographic parameter (e.g., Reidy et al. 2008, Balogh et al. 2011). Focusing on multiple species at once, and on both components of fitness, can yield a broader and more integrated perspective of how species within taxa as a whole are responding to changes in the environment. This approach can also help to determine if effects of human disturbance can be generalized. Overall, the effects of disturbance and the combinations of variables that predicted survival, maternity and lambda varied both within and between species. The variation in the effect of human disturbance on the three demographic parameters within and across species suggests that the effects of human disturbance at the level tested here may be species-specific, and that using just one demographic measure may miss information important for determining how species are affected by human disturbance. Further, human disturbance alone may not be the most important variable driving species persistence, but its effects may be apparent when considered in combination with other environmental variables. While I did not experimentally test the mechanisms driving survival, maternity, and lambda across landscapes, the patterns observed here are useful for quantifying the variation in species responses and highlighting areas for future research. Because birds provide multiple ecosystem services (Sekercioglu et al. 2004, Sekercioglu 2006, Whelan et al. 2008), understanding how they utilize and persist across different landscapes is useful for minimizing potential negative effects of anthropogenic disturbance. This study highlights the need for research at the individual, population and community level to understand the differences in species responses and to build strategies for effective species conservation. This study especially highlights the importance of building and maintaining programs such as the MAPS program to collect large-scale demographic data. It is only through such continent-wide efforts with the help of hundreds of dedicated volunteers and lovers of nature that we can begin to glimpse and reverse any negative effects of human disturbance on animal communities.

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Table 2.1. Relationship between land cover and NMDS axes

Land cover type	NMDS axis 1	NMDS axis 2
Forest	Negative (–)	Positive (+)
Grassland/herbaceous and pasture/hay	Negative (–)	Negative (–)
Cultivated crop	Negative (–)	No clear relationship
Developed, open space to low	Positive (+)	No clear relationship
Developed, medium to high	Positive (+)	No clear relationship
Emergent herbaceous wetland	Positive (+)	Negative (–)
Woody wetland	No clear relationship	Negative (–)
Shrub/scrub	No clear relationship	No clear relationship

Table 2.2. Institute for Bird Populations' estimates of survival for the northeastern U.S. versus estimates from Cormack-Jolly-Seber models used in this study.

Species	Institute for Bird Populations estimate	Regional estimates for this study	Difference (absolute value)
American Redstart	0.511	0.408	0.103
American Robin	0.460	0.411	0.049
Black-and-White Warbler	0.517	0.478	0.039
Black-capped Chickadee	0.513	0.494	0.019
Blue-winged Warbler	0.403	0.462	0.059
Common Yellowthroat	0.493	0.424	0.069
Chestnut-sided Warbler	0.495	0.467	0.028
Downy Woodpecker	0.443	0.425	0.018
Eastern Towhee	0.483	0.432	0.051
Gray Catbird	0.516	0.473	0.043
Hermit Thrush	0.477	0.439	0.038
House Wren	0.276	0.306	0.030
Magnolia Warbler	0.413	0.391	0.022
Northern Cardinal	0.610	0.573	0.037
Ovenbird	0.570	0.534	0.036
Red-eyed Vireo	0.555	0.551	0.004
Song Sparrow	0.369	0.335	0.034
Traill's Flycatcher	0.457	0.420	0.037
Tufted Titmouse	0.378	0.413	0.035
Veery	0.581	0.515	0.066
Wood Thrush	0.426	0.414	0.012
Yellow Warbler	0.500	0.450	0.050

Table 2.3. Total number of captures and recaptures, total capture sites, and number of additional sites at which recaptures for any individual occurred.

Species	Total outside recaptures[+]	Mean proportion of recaptures occurring in an adjacent site, relative to number of recaptures occurring within adjacent sites	Total sites at which any individual was captured*	Total number of individuals captured (and marked) across sites	Total number of recaptures
American Redstart	0	0	73	2037	662
American Robin	1 (1/4)	0.034	86	3501	658
Black-and-White Warbler	1 (1/2)	0.022	71	1134	277
Black-capped Chickadee	3 (3/7)	0.017	92	3962	1205
Blue-winged Warbler	4 (2/3)	0.107	45	956	248
Common Yellowthroat	5 (3/4)	0.021	85	6466	2748
Chestnut-sided Warbler	0	0	47	1028	395
Downy Woodpecker	0	0	86	1663	390
Eastern Towhee	0	0	57	728	271
Gray Catbird	12 (5/7)	0.014	79	14520	6993
Hermit Thrush	8 (2/2)	0.174	53	1030	581
House Wren	2 (2/2)	0.016	44	1035	353
Magnolia Warbler	2 (2/2)	0.044	48	866	351
Northern Cardinal	4 (2/4)	0.063	67	1617	806
Ovenbird	2 (1/5)	0.014	87	3627	1171
Red-eyed Vireo	0	0	83	2045	690
Song Sparrow	0	0	68	4752	1794
Traill's Flycatcher	0	0	46	1219	308
Tufted Titmouse	2 (2/3)	0.077	59	1650	677
Veery	6 (3/5)	0.020	74	2842	2199
Wood Thrush	122 (6/7)	0.142	73	3835	2840
Yellow Warbler	0	0	53	3122	932
		Total Mean: 0.0348			

[+] In parentheses is the number of pairs of sites outside of which recaptures occurred / total number of pairs of sites considered

*Uncombined sites; species are not recaptured at all sites

Table 2.4. Models used to predict demographic parameters (HD=human disturbance, LC=natural land cover, TMIN=minimum annual temperature, PPT=average annual precipitation, *=interaction between two terms).

	Survival/maternity/lambda ~ Independent variables
1	~1 (null)
2	~LC
3	~TMIN
4	~PPT
5	~TMIN+PPT
6	~HD
7	~HD+LC
8	~HD+LC+HD*LC
9	~HD+PPT
10	~HD+TMIN
11	~HD+TMIN+HD*TMIN
12	~HD+PPT+TMIN
13	~HD+TMIN+PPT+HD*TMIN
14	~HD+LC+PPT
15	~HD+LC+TMIN
16	~HD+LC+TMIN+HD*TMIN
17	~HD+LC+PPT+TMIN
18	~HD+LC+PPT+TMIN+HD*TMIN
19	~HD+LC+HD*LC+PPT
20	~HD+LC+HD*LC+TMIN
21	~HD+LC+HD*LC+TMIN+HD*TMIN
22	~HD+LC+HD*LC+PPT+TMIN
23	~HD+LC+HD*LC+PPT+TMIN+HD*TMIN

Table 2.5. Demographic parameters predicted by human disturbance (HD) or a combination of HD and other variables for each species. An asterisk represents relationships for which HD may be an uninformative parameter. A * indicates that HD may have been an uninformative parameter. A ✓ indicates that HD was not an uninformative parameter. Both a * and ✓ indicate both types of models were present.

Species	**Survival**	**Maternity**	**Lambda**
American Redstart (AMRE) *Setaphoga ruticill*	*✓		✓
American Robin (AMRO) *Turdus migratorius*	✓		
Black-and-white Warbler (BAWW) *Mniotilta varia*	*	*✓	✓
Black-capped Chickadee (BCCH) *Poecile atricapillus*	*		
Blue-winged Warbler (BWWA) *Vermivora cyanoptera*			
Common Yellowthoat (COYE) *Geophlypis trichas*		*	
Chestnut-sided Warbler (CSWA) *Dendroica pensylvanica*			
Downy Woodpecker (DOWO) *Picoides pubescens*$^+$	*✓		
Eastern Towhee (EATO) *Pipilo erythrophthalmus*	*	*	*✓
Gray Catbird (GRCA) *Dumetella carolinensis*	✓		✓
Hermit Thrush (HETH) *Catharus guttatus*			
House Wren (HOWR) *Troglodytes aedon*			
Magnolia Warbler (MAWA) *Dendroica magnolia*	*		
Northern Cardinal (NOCA) *Cardinalis cardinalis*	*	*	*✓
Ovenbird (OVEN) *Seiurus aurocapilla*	*	*	
Red-eyed Vireo (REVI) *Vireo olivaceus*	✓	*	✓
Song Sparrow (SOSP) *Melospiza melodia*	*		
Traill's Flycatcher (TRFL) *Empidonax alnorum/traillii*	✓	✓	✓
Tufted Titmouse (TUTI) *Baeolophus bicolor*			
Veery (VEER) *Catharus fuscescens*	✓	*✓	*✓
Wood Thrush (WOTH) *Hylocichla mustelina*			
Yellow Warbler (YWAR) *Dendroica petechia*	*✓		

Table 2.6. Number of species for which each model combination predicted demographic parameters. The values in parentheses with an asterisk are species for which the model may have been included due to an uninformative parameter. (HD=human disturbance, LC=natural land cover, TMIN=minimum annual temperature, PPT=average annual precipitation, *=interaction between two terms.)

Predictor variables	**Survival**	**Maternity**	**Lambda**
~1 (null)	20	14	14
~LC	6 (4*)	8 (4*)	5 (2*)
~TMIN	9 (5*)	7 (2*)	4 (2*)
~PPT	9 (4*)	**12 (6*)**	8 (4*)
~TMIN+PPT	2 (2*)	**6 (1*)**	5 (3*)
~HD	**10 (7*)**	4 (2*)	7 (3*)
~HD+LC	**3 (1*)**	1 (1*)	1
~HD+LC+HD*LC	**4**	0	2
~HD+PPT	1 (1*)	3 (2*)	4 (1*)
~HD+TMIN	2 (2*)	0	1 (1*)
~HD+TMIN+HD*TMIN	2	0	0
~HD+PPT+TMIN	0	2 (2*)	0
~HD+TMIN+PPT+HD*TMIN	0	0	0
~HD+LC+PPT	0	0	0
~HD+LC+TMIN	0	0	0
~HD+LC+TMIN+HD*TMIN	0	0	0
~HD+LC+PPT+TMIN	0	0	0
~HD+LC+PPT+TMIN+HD*TMIN	0	0	0
~HD+LC+HD*LC+PPT	0	0	0
~HD+LC+HD*LC+TMIN	0	0	0
~HD+LC+HD*LC+TMIN+HD*TMIN	0	0	0
~HD+LC+HD*LC+PPT+TMIN	0	0	0
~HD+LC+HD*LC+PPT+TMIN+HD*TMIN	0	0	0

Table 2.7. Model combinations within ΔAIC$_c$< 2 of the model with the lowest AIC$_c$ for each species See Table 2.5 for species abbreviations. Response variable abbrevations are: HD=human disturbance, LC=natural land cover, TMIN=minimum annual temperature, PPT=average annual precipitation, *=interaction between two terms. Models are listed from greatest weight to lowest weight. An asterisk (*) indicates species for which *all* models with HD only included one additional parameter from the model with the lowest AIC$_c$.

Species	N	Response Variable	Models within <2 of model with the lowest AIC$_c$	R-squared	Log likelihood of model	AIC$_c$	ΔAIC$_c$	Model Weight	Evidence Ratio	Model-averaged HD estimate
AMRE	18	survival	~1	0.00000	9.08036	-13.36072	0.00000	0.25354	0.00038	-0.32904
			~ppt	0.09727	10.11821	-12.52213	0.83859	0.16670	0.00058	
			~**HD**	0.06903	9.67914	-11.64399	1.71673	0.10746	0.00089	
			~**HD**+tmin+**HD***tmin	0.38094	13.29031	-11.58062	1.78010	0.10411	0.00092	
			~tmin	0.04281	9.53775	-11.36122	1.99950	0.09330	0.00103	
AMRO	34	survival	~**HD**+LC+**HD***LC	0.20046	30.13976	-48.13666	0.00000	0.18897	0.00414	-0.11762
			~1	0.00000	26.24873	-48.11036	0.02631	0.18650	0.00420	
			~tmin	0.03745	26.94132	-47.08263	1.05403	0.11156	0.00702	
			~ppt	0.01834	26.58131	-46.36261	1.77405	0.07783	0.01006	
			~LC	0.01440	26.51336	-46.22671	1.90995	0.07272	0.01077	
BAWW*	20	survival	~1	0.00000	8.47090	-12.23591	0.00000	0.23263	0.00011	-0.38554
			~**HD**	0.12002	9.68418	-11.86836	0.36755	0.19358	0.00013	
			~tmin	0.08394	9.32394	-11.14787	1.08804	0.13502	0.00019	
BCCH*	54	survival	~1	0.00000	28.91546	-53.59562	0.00000	0.25682	0.00167	0.06056
			~tmin	0.01864	29.43821	-52.39643	1.19919	0.14100	0.00304	
			~LC	0.01467	29.32124	-52.16247	1.43315	0.12544	0.00341	
			~**HD**	0.01004	29.19226	-51.90451	1.69111	0.11026	0.00388	
BWWA	12	survival	~1	0.00000	4.05395	-2.77456	0.00000	0.54955	0.00000	-0.02592
COYE	45	survival	~1	0.00000	31.47569	-58.66566	0.00000	0.32735	0.00350	-0.02407
CSWA	11	survival	~1	0.00000	3.51959	-1.53918	0.00000	0.57580	0.00000	-0.19563
DOWO	22	survival	~1	0.00000	8.06699	-11.50241	0.00000	0.17387	0.00367	-0.58716
			~**HD**+LC	0.22044	10.87265	-11.39236	0.11005	0.16456	0.00388	
			~**HD**	0.09226	9.17547	-11.01761	0.48480	0.13645	0.00468	
			~LC	0.09487	9.13491	-10.93648	0.56592	0.13102	0.00487	
			~tmin	0.04881	8.58937	-9.84540	1.65701	0.07593	0.00841	

EATO*	20	survival	~1	0.00000	7.54169	-10.37750	0.00000	0.30482	0.00008	0.22452
			~ppt	0.07677	8.29644	-9.09288	1.28461	0.16036	0.00015	
			~**HD**	0.04935	8.06400	-8.62799	1.74950	0.12710	0.00019	
			~LC	0.04570	8.00664	-8.51328	1.86421	0.12002	0.00021	
GRCA	48	survival	~**HD**	0.13992	16.83240	-27.11935	0.00000	0.21758	0.01264	0.91112
			~**HD**+LC+**HD***LC	0.21395	19.05412	-26.67967	0.43968	0.17464	0.01575	
			~**HD**+ppt	0.15908	17.37513	-25.82003	1.29932	0.11363	0.02421	
HETH	22	survival	~1	0.00000	10.04331	-15.45504	0.00000	0.37243	0.00008	0.20255
HOWR	9	survival	~1	0.00000	8.89820	-11.79640	0.00000	0.55419	0.00000	0.08115
			~LC	0.28965	10.50012	-10.20024	1.59617	0.24949	0.00000	
MAWA*	15	survival	~1	0.00000	6.71929	-8.43857	0.00000	0.34025	0.00000	0.27939
			~tmin	0.10982	7.66220	-7.14257	1.29600	0.17798	0.00000	
			~**HD**	0.08684	7.45287	-6.72393	1.71465	0.14437	0.00000	
NOCA*	36	survival	~1	0.00000	16.96004	-29.55644	0.00000	0.28908	0.00255	-0.11627
			~ppt	0.02386	17.40685	-28.06370	1.49274	0.13705	0.00538	
			~**HD**	0.01392	17.21422	-27.67845	1.87799	0.11304	0.00652	
OVEN*	43	survival	~LC	0.05361	19.81603	-33.01667	0.00000	0.19841	0.00989	0.02935
			~1	0.00000	18.65643	-33.01286	0.00381	0.19803	0.00991	
			~ppt	0.02662	19.23559	-31.85579	1.16088	0.11104	0.01768	
			~**HD**+LC	0.06360	20.04252	-31.03241	1.98426	0.07357	0.02668	
REVI	18	survival	~**HD**	0.17886	8.92385	-10.13341	0.00000	0.25764	0.00052	0.46333
			~1	0.00000	7.22620	-9.65241	0.48100	0.20257	0.00067	
			~**HD**+tmin+**HD***tmin	0.38717	11.66517	-8.33034	1.80307	0.10459	0.00129	
SOSP*	31	survival	~tmin	0.08817	26.07312	-45.25735	0.00000	0.21364	0.00161	0.20012
			~**HD**+tmin	0.15571	27.21922	-44.89999	0.35736	0.17869	0.00192	
			~1	0.00000	24.57071	-44.71285	0.54449	0.16272	0.00211	
TRFL	15	survival	~ppt	0.25493	7.90127	-7.62073	0.00000	0.25786	0.00001	-0.69796
			~1	0.00000	5.97993	-6.95987	0.66086	0.18530	0.00001	
			~**HD**+LC	0.28844	9.00807	-6.01615	1.60458	0.11560	0.00002	
			~**HD**+LC+**HD***LC	0.49480	11.17888	-5.69110	1.92963	0.09826	0.00002	
TUTI	20	survival	~ppt	0.13895	19.17988	-30.85977	0.00000	0.27000	0.00010	0.03741
			~1	0.00000	17.61580	-30.52571	0.33406	0.22847	0.00012	
			~tmin+ppt	0.20711	20.01358	-29.36049	1.49928	0.12759	0.00022	
			~tmin	0.06238	18.26581	-29.03161	1.82816	0.10824	0.00026	
VEER	36	survival	~**HD**+LC+**HD***LC	0.21411	15.33818	-18.67636	0.00000	0.26701	0.00270	-0.21738

			~1	0.00000	11.19713	-18.03062	0.64574	0.19333	0.00373	
WOTH	33	survival	~1	0.00000	11.90995	-19.41990	0.00000	0.33521	0.00060	0.06893
			~ppt	0.02985	12.35262	-17.87764	1.54226	0.15503	0.00129	
YWAR	23	survival	~tmin	0.23418	15.78607	-24.30897	0.00000	0.18362	0.00065	-0.42749
			~**HD**+tmin	0.33880	17.24552	-24.26881	0.04016	0.17997	0.00066	
			~tmin+ppt	0.32148	17.05311	-23.88400	0.42497	0.14847	0.00080	
			~**HD**	0.19623	15.10189	-22.94062	1.36835	0.09264	0.00128	
			~ppt	0.17427	14.97759	-22.69203	1.61695	0.08181	0.00145	
AMRE	18	maternity	~1	0.00000	-21.99782	48.79563	0.00000	0.32832	0.00014	0.06995
			~LC	0.03140	-21.16509	50.04446	1.24883	0.17584	0.00026	
AMRO	34	maternity	~ppt	0.10284	-42.09646	90.99291	0.00000	0.35310	0.00091	0.06360
BAWW	20	maternity	~LC	0.08283	-16.51836	40.53671	0.00000	0.16633	0.00320	-0.21207
			~1	0.00000	-17.92363	40.55314	0.01643	0.16496	0.00323	
			~tmin+ppt	0.15597	-15.11566	40.89799	0.36128	0.13884	0.00384	
			~tmin	0.04855	-16.88524	41.27049	0.73378	0.11525	0.00462	
			~**HD**+LC	0.12215	-15.50860	41.68387	1.14716	0.09373	0.00568	
			~**HD**	-0.00494	-17.43224	42.36449	1.82778	0.06669	0.00798	
BCCH	54	maternity	~tmin+ppt	0.06376	-58.75239	126.32111	0.00000	0.16905	0.01599	0.02929
			~ppt	0.03547	-60.08043	126.64085	0.31974	0.14408	0.01877	
			~tmin	0.02961	-60.24402	126.96803	0.64692	0.12233	0.02210	
			~1	0.00000	-61.56977	127.37484	1.05373	0.09982	0.02709	
			~LC	0.00941	-60.80027	128.08053	1.75942	0.07014	0.03855	
BWWA	12	maternity	~1	0.00000	-17.68148	40.69630	0.00000	0.40771	0.00000	-0.14122
			~ppt	0.11302	-16.39000	41.78001	1.08371	0.23715	0.00000	
COYE*	45	maternity	~tmin+ppt	0.15260	-54.42314	117.84628	0.00000	0.29927	0.00650	0.16780
			~ppt	0.10161	-56.26730	119.11996	1.27368	0.15830	0.01229	
			~**HD**+ppt+tmin	0.14342	-54.12323	119.78493	1.93865	0.11353	0.01714	
CSWA	11	maternity	~1	0.00000	-15.29683	36.09366	0.00000	0.37793	0.00000	0.13311
			~ppt	0.14600	-13.84930	37.12717	1.03351	0.22542	0.00000	
			~LC	0.13435	-13.92384	37.27626	1.18260	0.20922	0.00000	
DOWO	22	maternity	~tmin	0.08919	-28.67467	64.68267	0.00000	0.23973	0.00073	0.00836
			~1	0.00000	-30.23902	65.10962	0.42695	0.19364	0.00090	
			~tmin+ppt	0.13958	-27.48442	65.32178	0.63910	0.17416	0.00100	
EATO*	20	maternity	~ppt	0.26515	-20.99943	49.49885	0.00000	0.33677	0.00004	0.65089
			~**HD**+ppt	0.32558	-19.56966	49.80599	0.30714	0.28882	0.00005	

GRCA	48	maternity	~1	0.00000	-51.00468	106.27602	0.00000	0.28573	0.00185	-0.00841
			~ppt	-0.00003	-50.48915	107.52375	1.24773	0.15311	0.00345	
			~tmin	-0.01405	-50.82345	108.19236	1.91634	0.10960	0.00482	
			~LC	-0.01554	-50.85853	108.26252	1.98650	0.10582	0.00499	
HETH	22	maternity	~tmin	0.20085	-26.43275	60.19884	0.00000	0.48516	0.00008	0.09566
HOWR	9	maternity	~LC	0.34641	-11.97375	34.74749	0.00000	0.43495	0.00000	-0.11104
			~1	0.00000	-14.48837	34.97674	0.22925	0.38784	0.00000	
MAWA	15	maternity	~1	0.00000	-19.08102	43.16205	0.00000	0.38185	0.00000	-0.05853
			~tmin	0.03737	-18.23955	44.66092	1.49888	0.18048	0.00000	
NOCA*	36	maternity	~1	0.00000	-42.16824	88.70012	0.00000	0.26970	0.00287	-0.14124
			~ppt	-0.00485	-41.73350	90.21699	1.51687	0.12633	0.00612	
			~LC	-0.00541	-41.74367	90.23734	1.53723	0.12505	0.00619	
			~**HD**	-0.01408	-41.89811	90.54621	1.84609	0.10716	0.00722	
OVEN*	43	maternity	~1	0.00000	-58.27949	120.85897	0.00000	0.23770	0.00170	-0.09912
			~ppt	0.02670	-57.17960	120.97459	0.11561	0.22435	0.00180	
			~**HD**	-0.01624	-58.10783	122.83104	1.97206	0.08867	0.00456	
REVI*	18	maternity	~ppt	0.37200	-22.18919	52.09267	0.00000	0.44522	0.00008	0.95858
			~**HD**+ppt	0.40486	-21.12461	53.32614	1.23346	0.24029	0.00015	
SOSP	31	maternity	~tmin+ppt	0.33034	-23.54709	56.63263	0.00000	0.46329	0.00203	-0.17055
TRFL	15	maternity	~**HD**	0.47916	-13.13919	34.46019	0.00000	0.61918	0.00000	-3.45635
TUTI	20	maternity	~1	0.00000	-19.75925	44.22439	0.00000	0.42569	0.00001	0.02538
VEER*	36	maternity	~tmin+ppt	0.20011	-42.83329	94.95691	0.00000	0.31805	0.00133	0.50710
			~**HD**+ppt+tmin	0.20264	-42.22255	96.44510	1.48819	0.15113	0.00280	
			~**HD**+ppt	0.16625	-43.57953	96.44939	1.49248	0.15080	0.00281	
WOTH	33	maternity	~1	0.00000	-41.51844	87.43688	0.00000	0.28547	0.00095	-0.03662
			~ppt	0.01848	-40.68688	88.20136	0.76447	0.19479	0.00139	
YWAR	23	maternity	~ppt	0.08760	-30.11743	67.49801	0.00000	0.24880	0.00023	-0.11013
			~1	0.00000	-31.70670	68.01341	0.51539	0.19228	0.00030	
			~tmin	0.01742	-30.96961	69.20239	1.70437	0.10611	0.00054	
			~LC	0.01354	-31.01498	69.29312	1.79511	0.10140	0.00057	
AMRE	18	lambda	~**HD**+LC+**HD***LC	0.52100	0.92947	13.14107	0.00000	0.67637	0.00005	0.22597
AMRO	34	lambda	~ppt	0.07186	-14.19080	35.18159	0.00000	0.31526	0.00116	-0.00400
			~1	0.00000	-15.98158	36.35026	1.16867	0.17575	0.00208	
BAWW	20	lambda	~**HD**+LC	0.18372	-5.23843	21.14353	0.00000	0.15429	0.00073	-0.33072
			~**HD**	0.09169	-6.87838	21.25677	0.11323	0.14580	0.00077	

			~1	0.00000	-8.38072	21.46732	0.32378	0.13123	0.00086	
			~tmin	0.05555	-7.26851	22.03702	0.89349	0.09870	0.00114	
			~tmin+ppt	0.13421	-5.82731	22.32128	1.17775	0.08562	0.00132	
			~LC	0.03177	-7.51714	22.53428	1.39074	0.07697	0.00147	
BCCH	54	lambda	~ppt	0.05900	-19.54042	45.56084	0.00000	0.23714	0.01126	-0.02353
			~tmin+ppt	0.05991	-18.98997	46.79627	1.23544	0.12786	0.02089	
			~LC	0.02667	-20.45254	47.38509	1.82425	0.09525	0.02804	
BWWA	12	lambda	~1	0.00000	-6.30158	17.93649	0.00000	0.52076	0.00000	-0.08146
COYE	45	lambda	~ppt	0.12732	-18.47576	43.53689	0.00000	0.31639	0.00542	0.05234
			~tmin+ppt	0.13659	-17.70622	44.41245	0.87555	0.20422	0.00840	
CSWA	11	lambda	~1	0.00000	-6.82302	19.14605	0.00000	0.38492	0.00000	0.03259
			~ppt	0.20739	-4.96523	19.35903	0.21298	0.34604	0.00000	
DOWO	22	lambda	~1	0.00000	-18.70040	42.03238	0.00000	0.29939	0.00013	-0.05091
			~tmin	0.03235	-17.80199	42.93732	0.90493	0.19043	0.00021	
EATO	20	lambda	~1	0.00000	-11.93910	28.58408	0.00000	0.23991	0.00023	0.39289
			~**HD**	0.04106	-10.97921	29.45842	0.87434	0.15495	0.00035	
			~ppt	0.02384	-11.15709	29.81418	1.23010	0.12970	0.00042	
			~**HD**+ppt	0.10967	-9.66518	29.99702	1.41294	0.11836	0.00046	
GRCA	48	lambda	~**HD**	0.04670	-22.98934	52.52414	0.00000	0.23915	0.00259	0.28609
			~1	0.00000	-24.65325	53.57317	1.04902	0.14154	0.00438	
			~**HD**+tmin	0.04228	-22.57274	54.07570	1.55156	0.11009	0.00562	
HETH	22	lambda	~tmin	0.15209	-12.51762	32.36857	0.00000	0.42373	0.00007	0.03645
HOWR	9	lambda	~LC	0.37666	-5.69549	22.19098	0.00000	0.50153	0.00000	0.03984
			~1	0.00000	-8.42339	22.84678	0.65580	0.36132	0.00000	
MAWA	15	lambda	~1	0.00000	-7.43862	19.87724	0.00000	0.46980	0.00000	-0.02453
NOCA	36	lambda	~1	0.00000	-13.87212	32.10787	0.00000	0.26901	0.00254	-0.11820
			~**HD**	-0.01414	-13.60304	33.95607	1.84820	0.10677	0.00641	
			~**HD**+LC+**HD***LC	0.06725	-11.00595	34.01191	1.90404	0.10383	0.00659	
			~LC	-0.01734	-13.65987	34.06973	1.96186	0.10087	0.00678	
OVEN	43	lambda	~1	0.00000	-23.75519	51.81038	0.00000	0.27540	0.00128	-0.02331
			~ppt	0.00723	-23.08101	52.77740	0.96703	0.16982	0.00208	
			~LC	-0.01053	-23.46234	53.54007	1.72970	0.11598	0.00304	
REVI	18	lambda	~**HD**	0.24802	-8.14153	23.99735	0.00000	0.35463	0.00005	1.59618
			~**HD**+ppt	0.27188	-7.27047	25.61786	1.62051	0.15772	0.00011	
SOSP	31	lambda	~tmin+ppt	0.36142	-12.62358	34.78562	0.00000	0.46257	0.00080	-0.09274

TRFL	15	lambda	~**HD**+ppt	0.47697	-5.53364	23.06729	0.00000	0.38373	0.00001	-1.56226
			~**HD**	0.30127	-8.30617	24.79415	1.72686	0.16182	0.00002	
TUTI	20	lambda	~1	0.00000	-11.65961	28.02511	0.00000	0.41784	0.00001	-0.00383
VEER	36	lambda	~1	0.00000	-18.05659	40.47682	0.00000	0.16734	0.00907	0.23116
			~**HD**	0.02316	-17.11306	40.97612	0.49930	0.13037	0.01164	
			~ppt	0.00690	-17.41027	41.57055	1.09373	0.09685	0.01567	
			~**HD**+ppt	0.03366	-16.38121	42.05275	1.57593	0.07610	0.01994	
WOTH	33	lambda	~1	0.00000	-24.22104	52.84209	0.00000	0.35150	0.00023	-0.01442
			~tmin	-0.01664	-23.96953	54.76664	1.92456	0.13428	0.00060	
YWAR	23	lambda	~ppt	0.17858	-18.64071	44.54459	0.00000	0.32981	0.00039	-0.17591
			~tmin+ppt	0.18283	-18.01994	46.26210	1.71752	0.13974	0.00091	

Table 2.8. Number of sites for each species for which lambda (λ) was greater than one versus less than one and statistics for λ within species across sites.

Species	λ > 1	λ < 1	Mean λ	St. Dev. λ	Min. λ	Max. λ
American Redstart	5	**13**	0.84662	0.28906	0.32003	1.35600
American Robin	8	**26**	0.79387	0.30717	0.34591	1.44804
Black-and-White Warbler	4	**16**	0.75477	0.26628	0.30220	1.29755
Black-capped Chickadee	26	**28**	1.05577	0.39263	0.47383	2.07243
Blue-winged Warbler	2	**10**	0.63670	0.29401	0.30305	1.27544
Common Yellowthroat	12	**33**	0.81282	0.31384	0.34278	1.71571
Chestnut-sided Warbler	5	**6**	0.86939	0.28244	0.22366	1.19317
Downy Woodpecker	**18**	4	1.70635	1.15384	0.48398	5.90340
Eastern Towhee	5	**15**	0.82593	0.36921	0.27760	1.84309
Gray Catbird	14	**34**	0.84530	0.30913	0.24605	1.65243
Hermit Thrush	6	**16**	0.82328	0.45844	0.30206	2.31027
House Wren	2	**7**	0.66658	0.43832	0.18135	1.55218
Magnolia Warbler	1	**14**	0.54220	0.23651	0.28445	1.11649
Northern Cardinal	11	**25**	0.86421	0.31284	0.34871	1.79506
Ovenbird	18	**25**	0.98279	0.43294	0.37467	2.51916
Red-eyed Vireo	2	**16**	0.65441	0.32018	0.21396	1.58868
Song Sparrow	**19**	12	1.20143	0.54512	0.34059	2.80212
Traill's Flycatcher	1	**14**	0.50773	0.25222	0.14642	1.20145
Tufted Titmouse	**15**	5	1.49895	0.73436	0.69870	3.66704
Veery	6	**30**	0.72206	0.26763	0.22900	1.42075
Wood Thrush	4	**29**	0.65328	0.27674	0.13293	1.26839
Yellow Warbler	7	**16**	0.84832	0.51270	0.18412	2.36778
OUTLIERS Removed						
Downy Woodpecker			1.506488	0.6893540	0.4839849	2.939512
Song Sparrow			1.148074	0.4648703	0.3405866	2.157734
Tufted Titmouse			1.384839	0.5425373	0.6986971	2.387043

Table 2.9. Mean difference in lambda (λ) with a 10% increase or decrease in matrix parameters. (After hatch year birds=AHY and hatch year birds=HY.)

Species	Mean difference in λ with a ±10% change in AHY survival	Mean difference in λ with a ±10% change in AHY maternity/ HY survival	Mean difference in λ with a ±10% change in HY maternity
American Redstart	0.04275	**0.04988**	0.02691
American Robin	**0.04209**	0.04033	0.03608
Black-and-White Warbler	**0.05510**	0.03587	0.02417
Black-capped Chickadee	0.04808	0.05065	**0.06184**
Blue-winged Warbler	**0.04202**	0.02624	0.03287
Common Yellowthroat	**0.04483**	0.03882	0.04016
Chestnut-sided Warbler	**0.05137**	0.04457	0.03344
Downy Woodpecker	0.03632	0.07603	**0.15295**
Eastern Towhee	**0.04680**	0.04121	0.03602
Gray Catbird	**0.04940**	0.03877	0.04217
Hermit Thursh	**0.05498**	0.03565	0.03842
House Wren	0.02095	0.02763	**0.05714**
Magnolia Warbler	0.04264	0.01049	**0.04477**
Northern Cardinal	**0.05964**	0.04278	0.02771
Ovenbird	**0.06048**	0.04612	0.04388
Red-eyed Vireo	**0.06627**	0.02430	0.01602
Song Sparrow	0.02233	0.04973	**0.11852**
Traill’s Flycather	**0.03604**	0.02069	0.02416
Tufted Titmouse	0.02919	0.06158	**0.14747**
Veery	**0.06222**	0.02759	0.02702
Wood Thrush	**0.04375**	0.02874	0.02944
Yellow Warbler	0.03153	**0.04922**	0.03981

Table 2.10. Absolute value of mean difference in lambda (λ) between a 2:1 hatch year (AHY) to hatch year (HY) maternity ratio and a 1:1 AHY: HY maternity ratio, and between a 2:1 AHY:HY maternity ratio and a 3:1 AHY:HY maternity ratio.

Species	Mean difference in λ assuming a 1:1 AHY:HY maternity ratio versus a 2:1 ratio	Mean difference in λ assuming a 3:1 AHY:HY maternity ratio versus a 2:1 ratio
American Redstart	0.036	0.015
American Robin	0.060	0.025
Black-and-White Warbler	0.026	0.010
Black-capped Chickadee	**0.112**	0.046
Blue-winged Warbler	0.067	0.029
Common Yellowthroat	0.068	0.027
Chestnut-sided Warbler	0.050	0.021
Downy Woodpecker	**0.328**	**0.139**
Eastern Towhee	0.061	0.025
Gray Catbird	0.073	0.030
Hermit Thursh	0.071	0.031
House Wren	**0.125**	0.050
Magnolia Warbler	**0.110**	0.048
Northern Cardinal	0.039	0.016
Ovenbird	0.083	0.035
Red-eyed Vireo	0.033	0.014
Song Sparrow	**0.259**	**0.110**
Traill’s Flycather	0.042	0.018
Tufted Titmouse	**0.324**	**0.137**
Veery	0.052	0.022
Wood Thrush	0.057	0.024
Yellow Warbler	0.062	0.026

Table 2.11. Average lambda values when after hatch year (AHY) and hatch year (HY) survival are increased by 0.1 and 0.2 across sites and species.

Species	Original Lambda	Increase AHY survival by 0.1	Increase AHY and HY survival by 0.1	Increase AHY survival by 0.2	Increase AHY and HY survival by 0.2
American Redstart	0.508	0.568	0.637	0.637	0.756
American Robin	0.847	0.905	0.949	0.968	1.052
Black-and-White Warbler	0.794	0.853	0.912	0.916	1.026
Black-capped Chickadee	0.755	0.819	0.881	0.888	1.001
Blue-winged Warbler	1.056	1.109	1.186	1.166	1.311
Common Yellowthroat	0.637	0.697	0.761	0.763	0.879
Chestnut-sided Warbler	0.813	0.871	0.938	0.935	1.058
Downy Woodpecker	0.869	0.929	0.980	0.994	1.090
Eastern Towhee	1.706	1.748	1.839	1.793	1.967
Gray Catbird	0.826	0.885	0.943	0.950	1.057
Hermit Thursh	0.845	0.902	0.975	0.963	1.098
House Wren	0.823	0.888	0.944	0.958	1.060
Magnolia Warbler	0.667	0.715	0.814	0.772	0.948
Northern Cardinal	0.542	0.600	0.706	0.664	0.845
Ovenbird	0.864	0.928	0.981	0.997	1.094
Red-eyed Vireo	0.983	1.045	1.101	1.111	1.216
Song Sparrow	0.654	0.730	0.764	0.811	0.872
Traill’s Flycather	1.201	1.238	1.348	1.278	1.486
Tufted Titmouse	1.499	1.536	1.647	1.576	1.788
Veery	0.722	0.789	0.847	0.862	0.966
Wood Thrush	0.653	0.714	0.776	0.781	0.892
Yellow Warbler	0.848	0.903	0.955	0.964	1.060

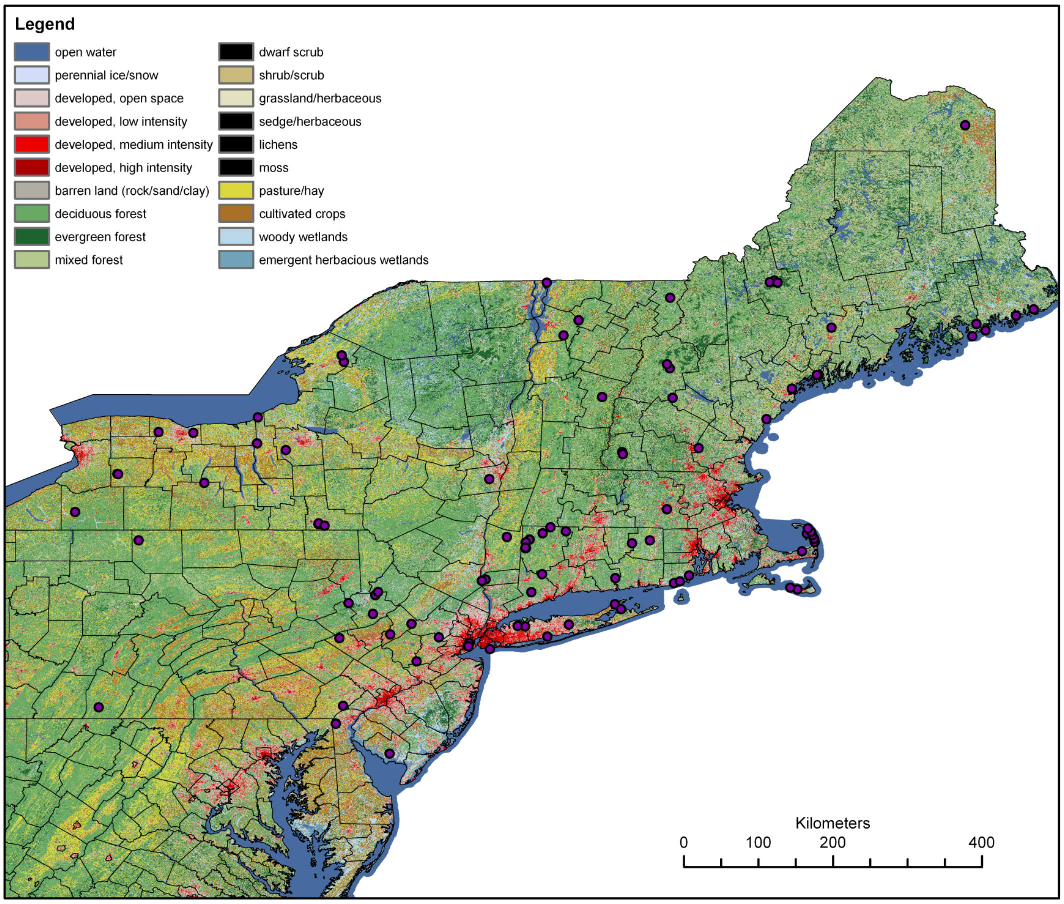

Figure 2.1. Map of banding locations and land cover types.

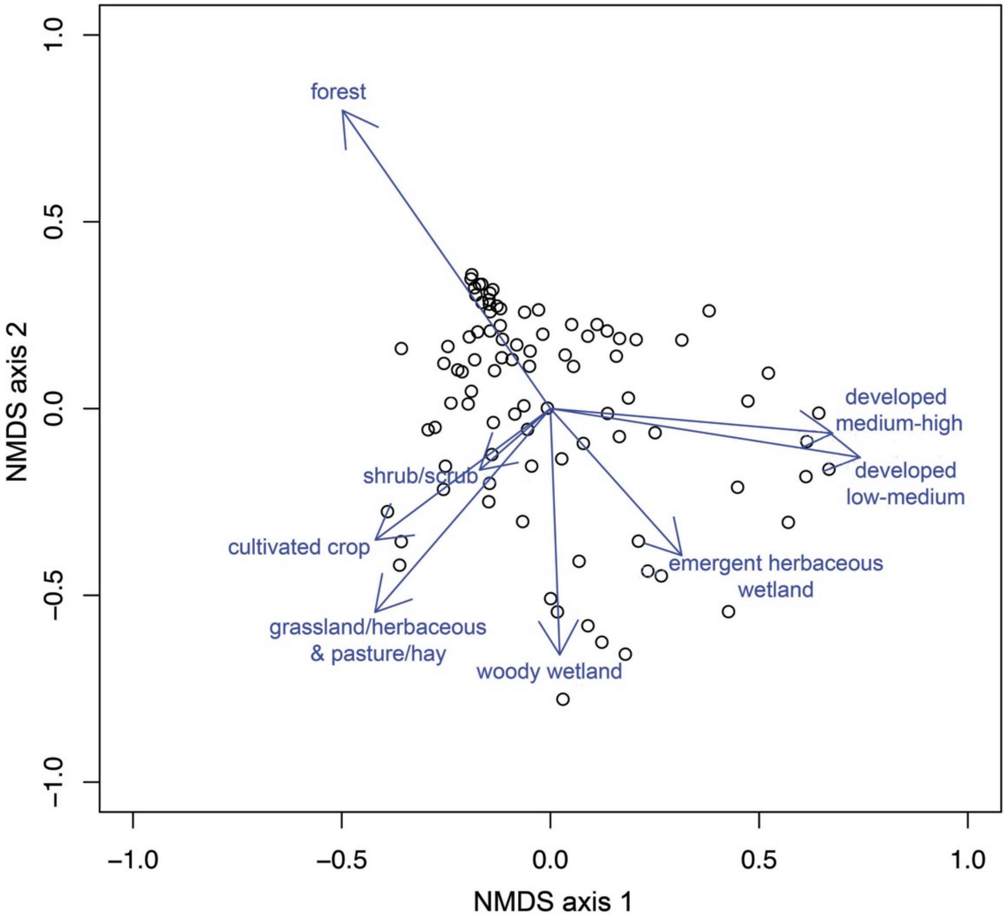

Figure 2.2. NMDS plot of vectors of land cover types.

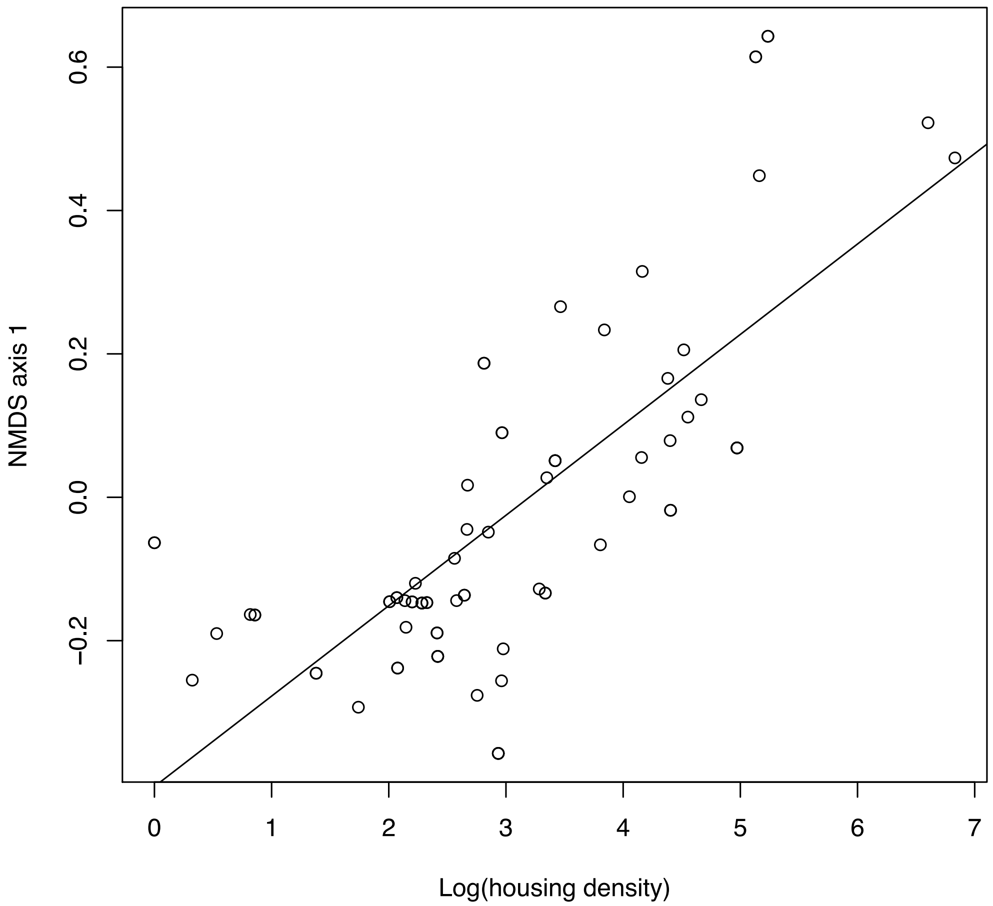

Figure 2.3. Relationship between housing density and NMDS axis of human disturbance (axis 1; *t*=9.52, *df*=76, *r*=0.737, *p*<0.0001).

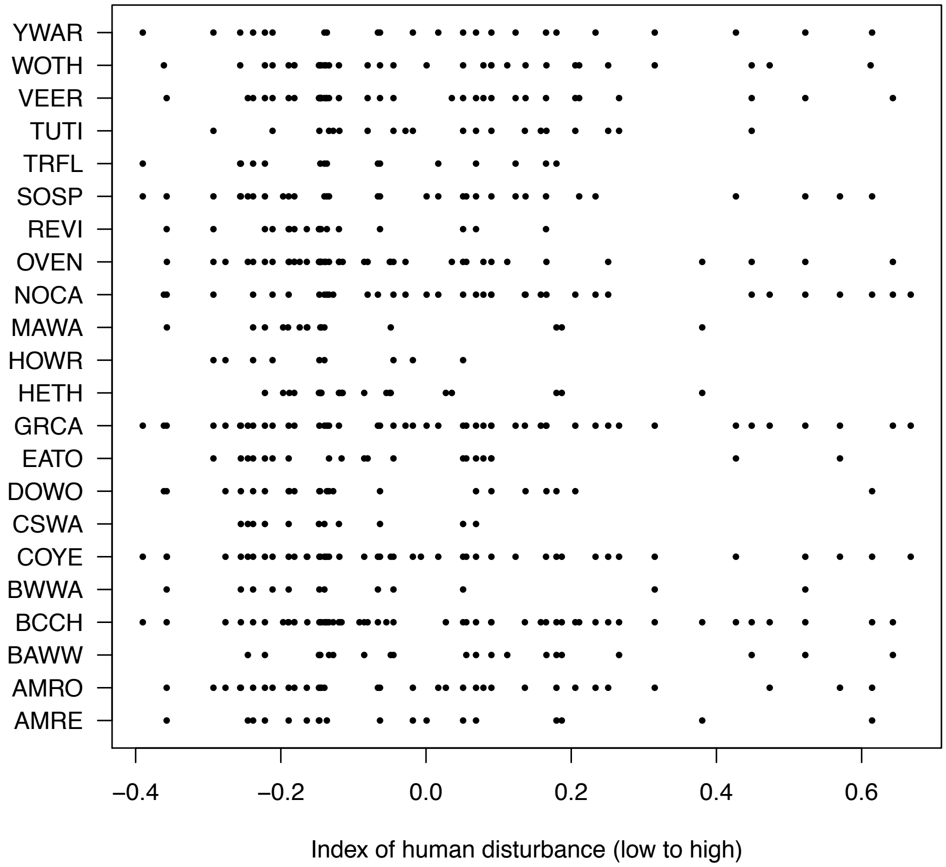

Figure 2.4. Variation in disturbance across locations at which each species was captured (index of disturbance is NMDS axis); species abbreviations are American Redstart=AMRE, American Robin=AMRO, Black-and-white Warbler=BAWW, Black-capped Chickadee=BCCH, Blue-winged Warbler=BWWA, Common Yellowthroat=COYE, Chestnut-sided Warbler=CSWA, Downy Woodpecker=DOWO, Eastern Towhee=EATO, Gray Catbird=GRCA, Hermit Thrush=HETH, House Wren=HOWR, Magnolia Warbler=MAWA, Northern Cardinal=NOCA, Ovenbird=OVEN, Red-eyed Vireo=REVI, Song Sparrow=SOSP, Traill's Flycatcher=TRFL, Tufted Titmouse=TUTI, Veery=VEER, Wood Thrush=WOTH, Yellow Warbler=YWAR.

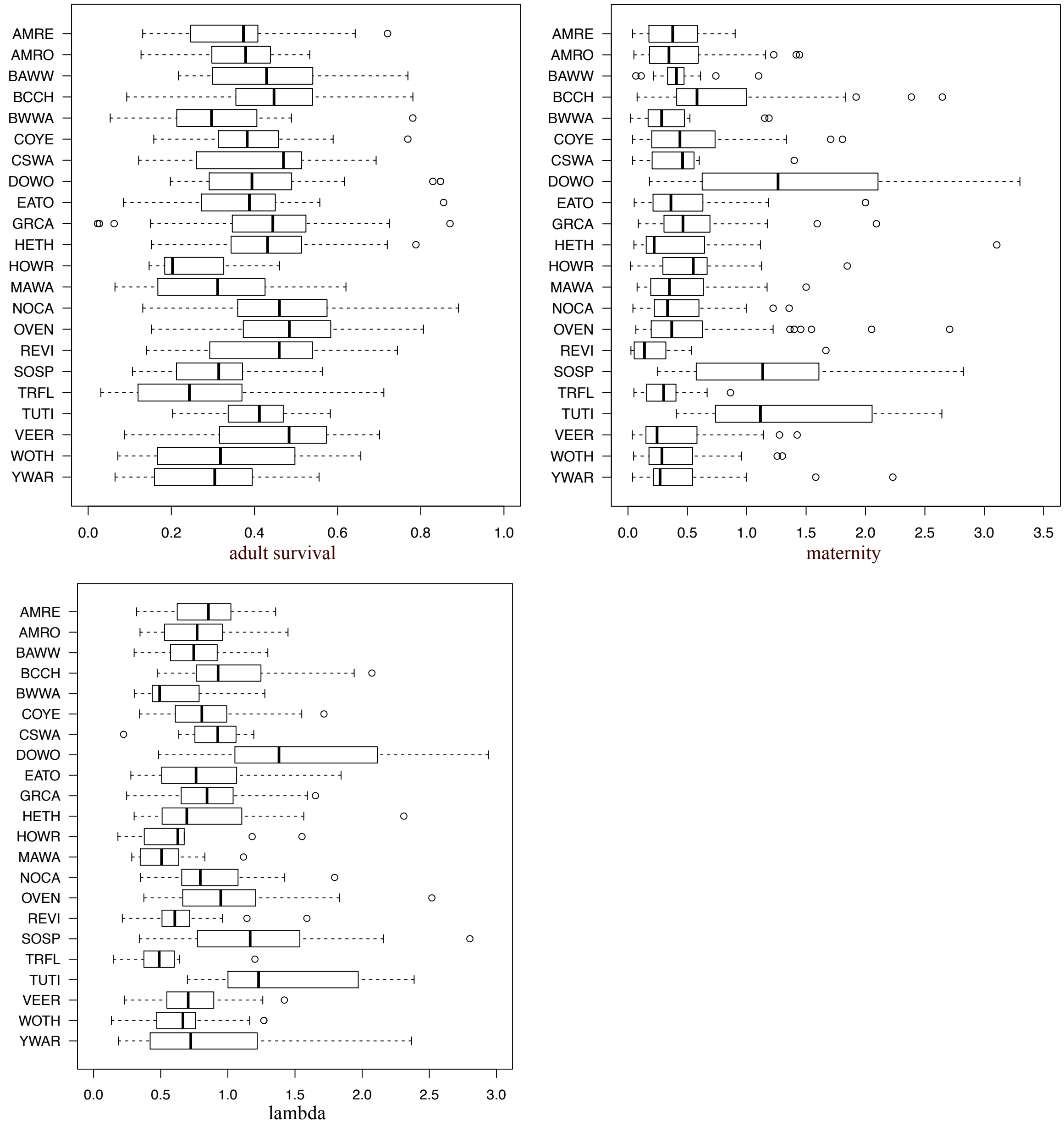

Figure 2.5. Demographic parameter values for each species across locations. See Figure 2.4 for species abbreviations. Single outliers are not shown on the maternity plot for Downy Woodpecker (7.55), Song Sparrow (3.77) and Tufted Titmouse (4.83); and on the lambda plot for Downy Woodpecker (5.90) and Tufted Titmouse (3.67). The outliers for Downy Woodpecker and Tufted Titmouse were both at the same location.

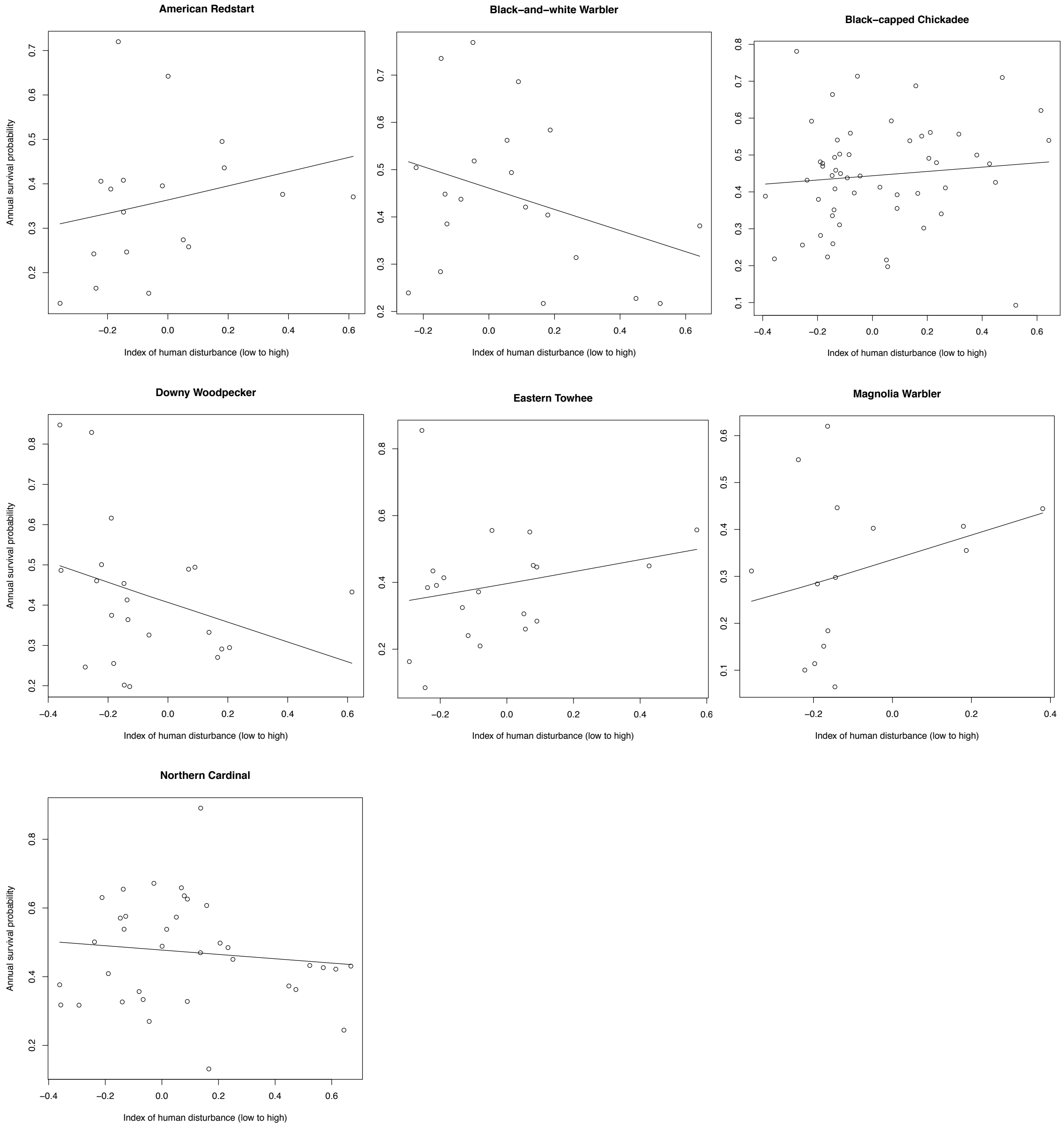

Figure 2.6. Species for human disturbance (HD) alone predicted survival, and in which human disturbance may have been an uninformative parameter.

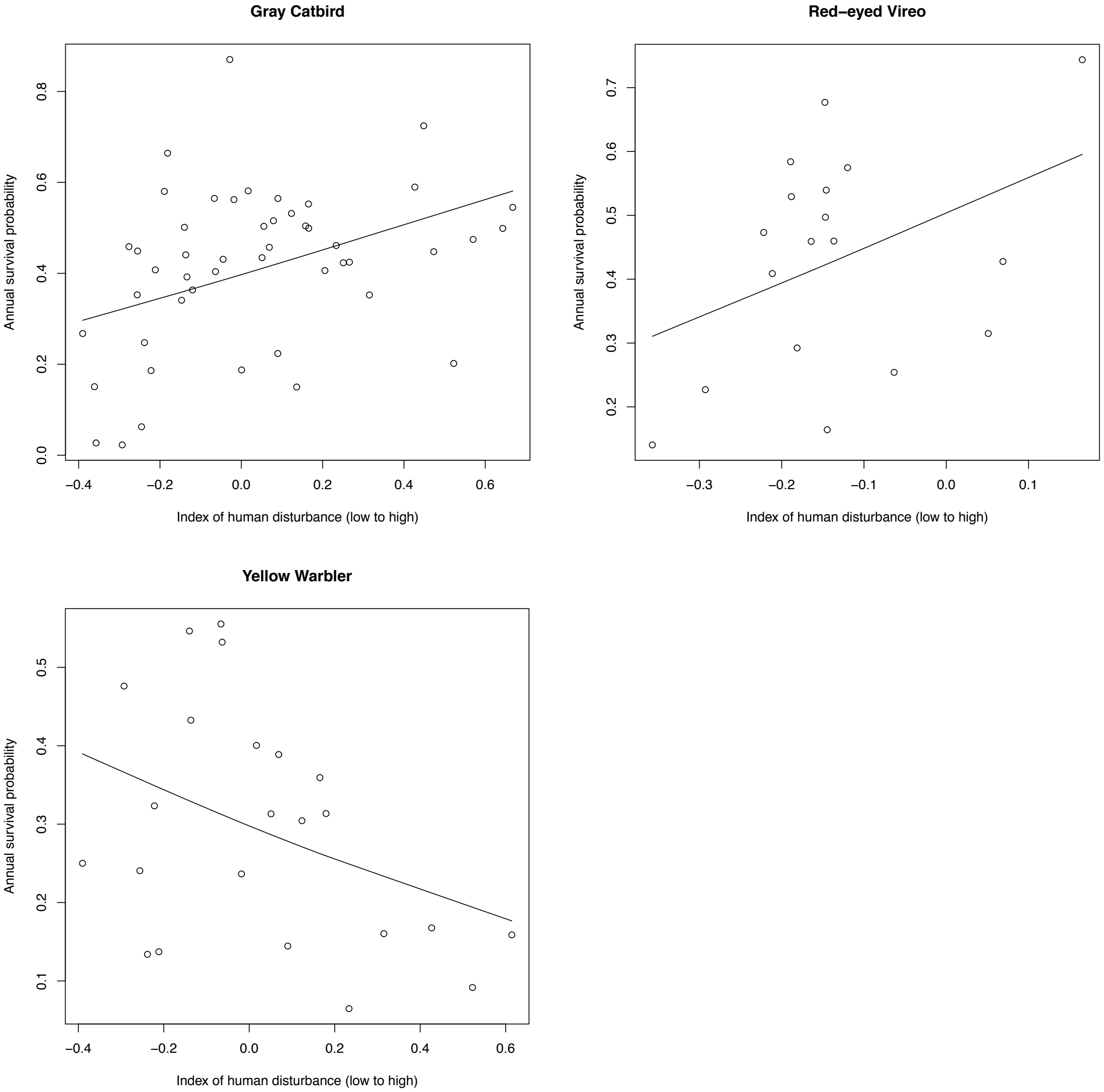

Figure 2.7. Species for human disturbance (HD) alone predicted survival, and in which human disturbance was not an uninformative parameter. In Gray Catbird and Red-eyed Vireo, the model with HD alone was the model with the lowest AIC$_c$.

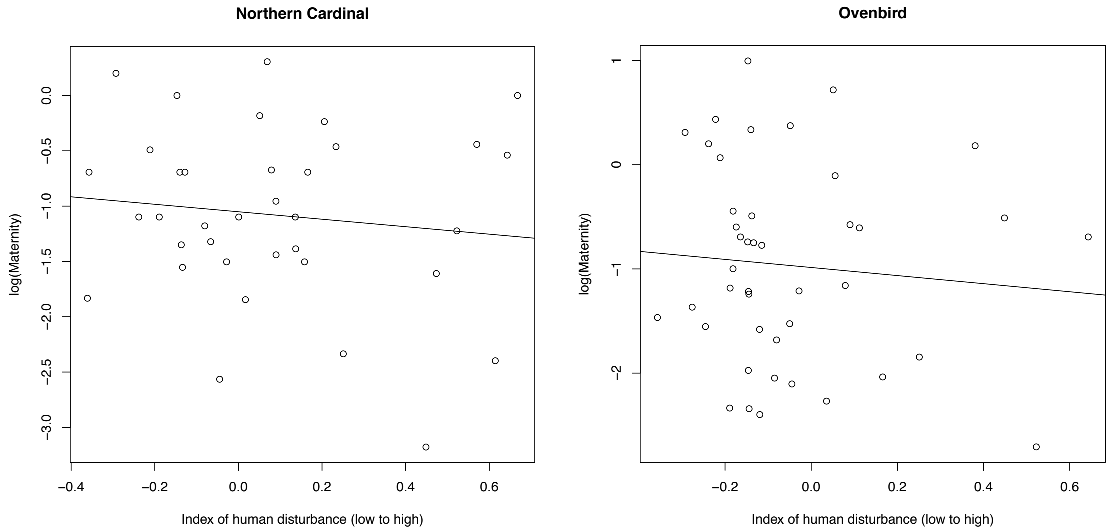

Figure 2.8. Species for human disturbance (HD) alone predicted maternity, and in which human disturbance may have been an uninformative parameter.

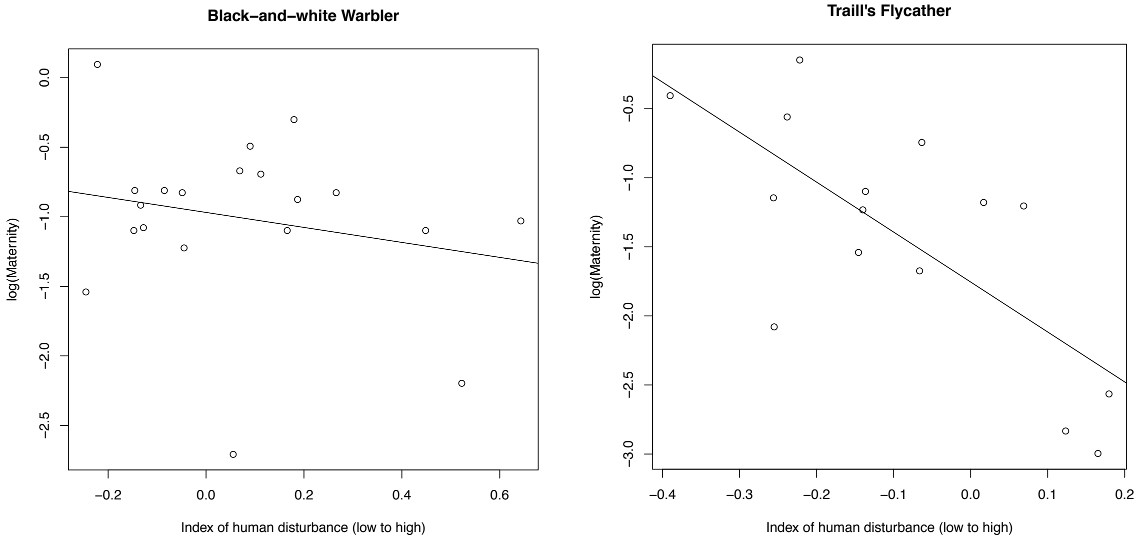

Figure 2.9. Species for human disturbance (HD) alone predicted maternity, and in which human disturbance was not an uninformative parameter. In Traill’s Flycatcher, the model with HD alone was the model with the lowest AIC_c.

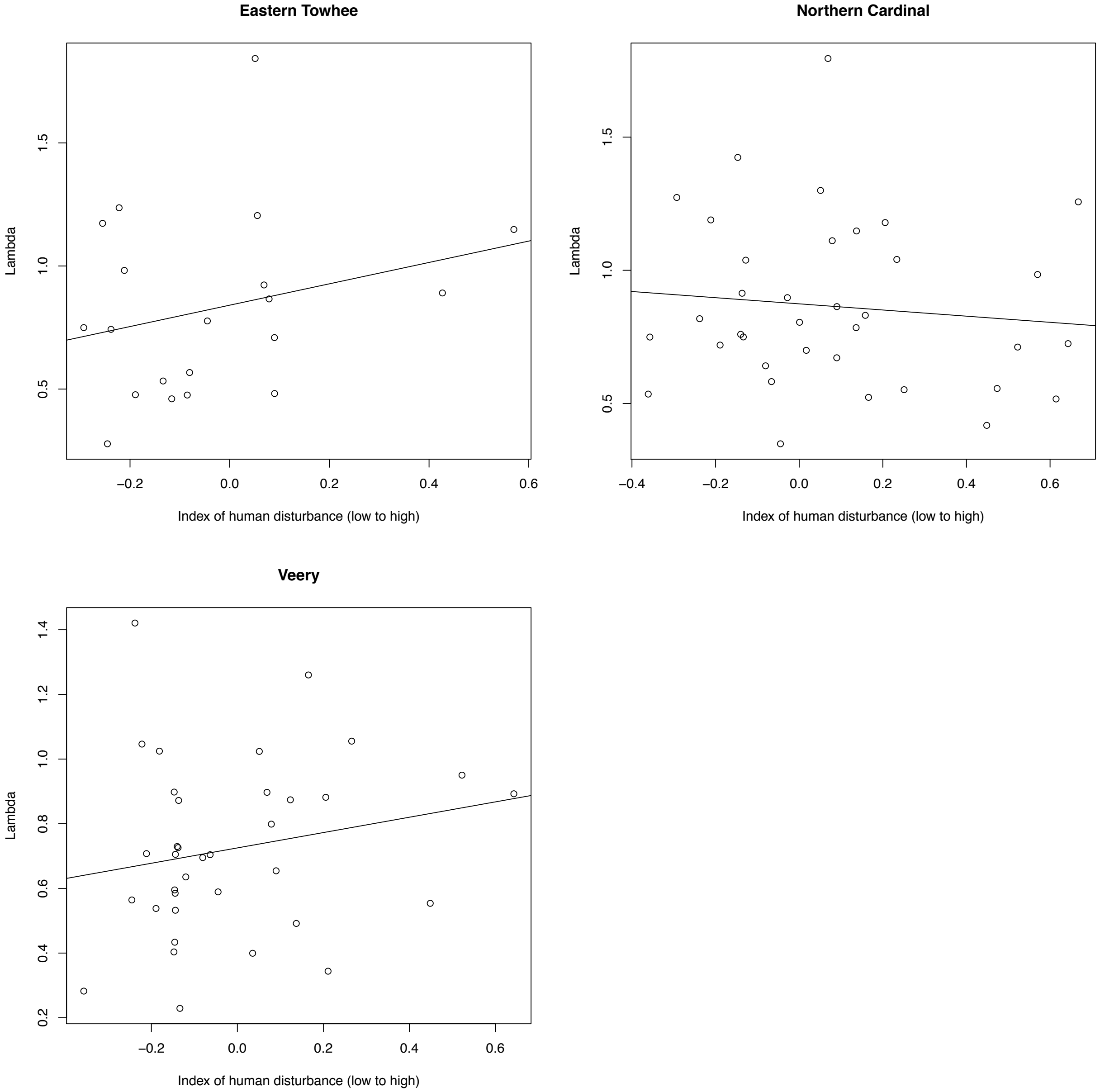

Figure 2.10. Species for human disturbance (HD) alone predicted lambda, and in which human disturbance may have been an uninformative parameter.

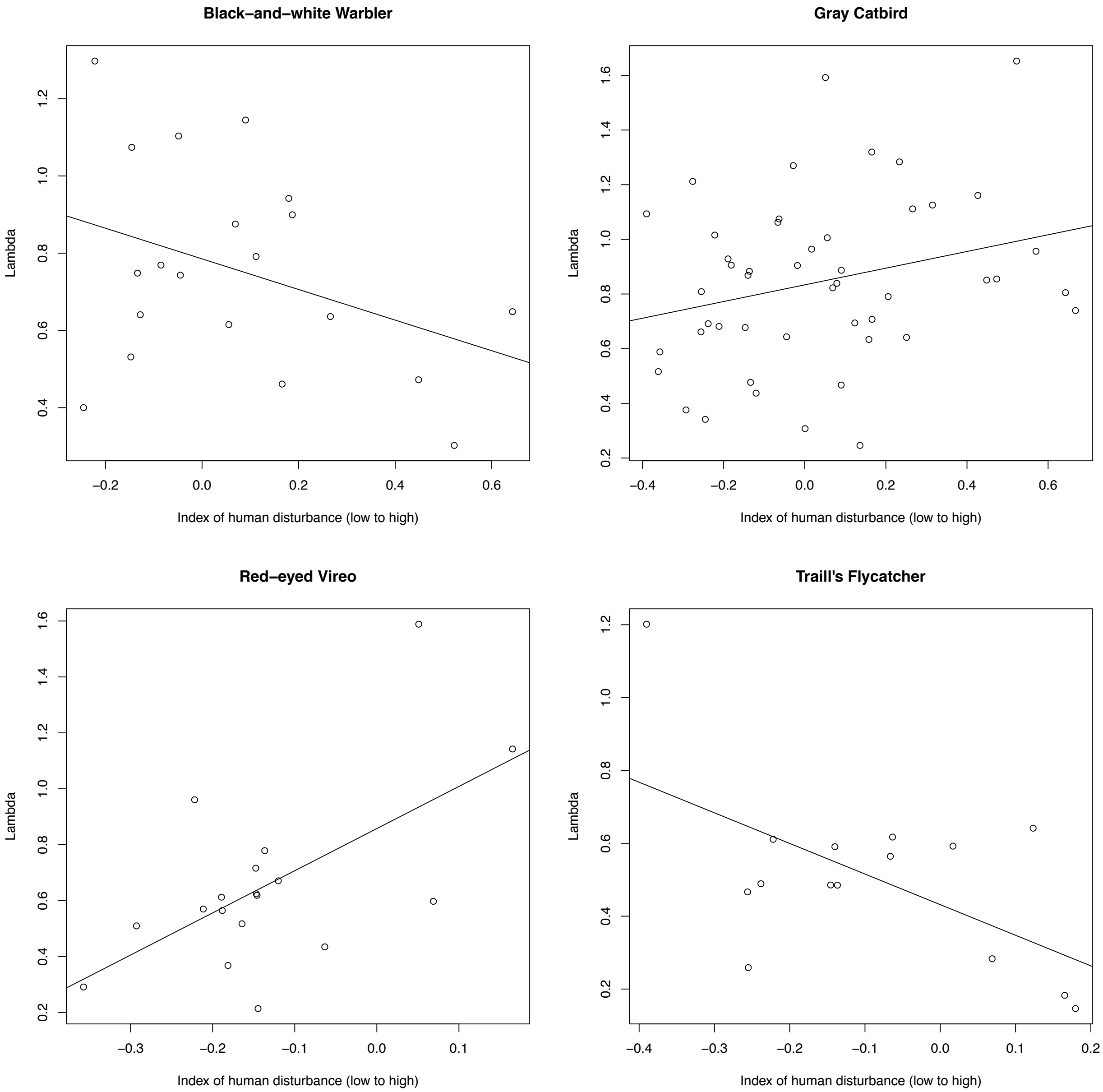

Figure 2.11. Species for human disturbance (HD) alone predicted lambda, and in which human disturbance was not an uninformative parameter. In Gray Catbird and Red-eyed Vireo, the model with HD alone was the model with the lowest AIC_c.

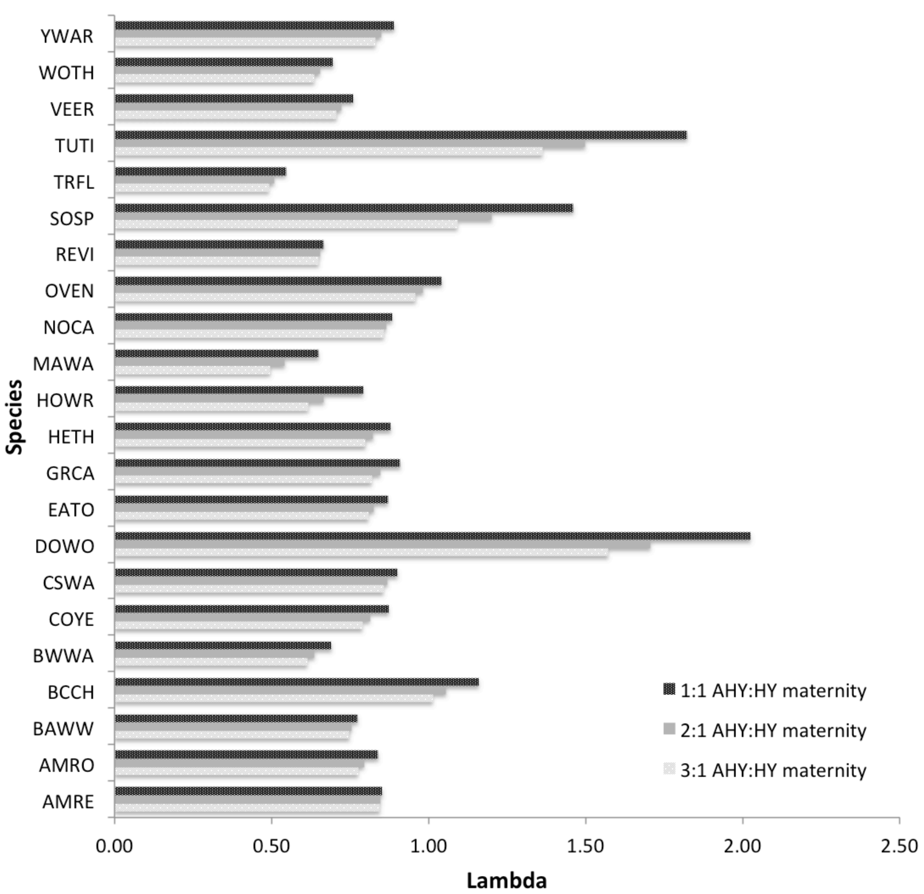

Figure 2.12. Average lambda values assuming 1:1, 2:1, and 3:1 after-hatch year (AHY) to hatch year (HY) maternity ratios.

Chapter 3:
The relationship between demographic parameters and species' characteristics: Can we make generalizations about the effects of human disturbance?

Abstract

Generalizations about the types of species most likely to be affected by human disturbance have been made based on changes in species' abundance or richness across regions of varying levels of human disturbance. Survival and reproduction are the underlying mechanisms driving population growth and species' abundances, but how life history characteristics influence demographic parameters across varying levels of disturbance is largely unknown. Across 24 species breeding in the northeastern United States, I investigated the influence of seven groups of species' life history characteristics on mean demographic parameter values, and the effect of an interaction with human disturbance. Across species' characteristics, nest location and mass predicted reproduction and population growth, and mass interacted with human disturbance to predict reproduction. Within species' characteristics, forest species and birds with the smallest masses declined in population growth and maternity, respectively, in response to human disturbance. Further, maternity in partial insectivores and short-distance migrants increased with human disturbance relative to a decrease in insectivores and long-distance migrants. Several differences within species' characteristics were also found, but were not influenced by human disturbance. Reproduction was most often predicted by species' characteristics, and predictions of the species' characteristics based on previous studies of abundance or richness were only partially supported. Finally, when assessing the effect of species' life history characteristics on demographic responses to human disturbance, pre-existing differences between characteristics in the absence of human disturbance should be considered.

Introduction

There is little argument that human alteration of landscapes negatively impacts species and drives local extinctions. Losses of biodiversity and ecosystem services marked by biotic homogenization have been extensively studied over the past decade, showing clear patterns across multiple taxa (Lockwood and McKinney 2001, McKinney 2006). At the same time, a few species successfully exploit and thrive in human disturbed areas (Marzluff 2001, Devictor 2008a, McKinney 2008). Minimizing negative effects of habitat fragmentation and urbanization requires knowing which species are affected by these changes and how, and enacting policies that will protect or create habitat suitable for more vulnerable species. This presents a conundrum for conservation practitioners. Studying every species-specific set of responses to disturbance is clearly not possible. Alternatively, inferences can be made about which species will be negatively affected by human disturbances, based on the degree to which they share life history characteristics of species with a known response to human-induced changes. However, there are limitations to basing generalizations about how multiple species are affected, and which species are most affected, on a limited set of single- or few-species studies (Blumstein et al. 2005).

The concept of *environmental filtering* (Keddy 1992, Mayfield et al. 2009), whereby human-disturbed areas can be thought of as filters that allow only species with certain characteristics to survive and even thrive (Lizée et al. 2011), has recently been used to evaluate which species will persist in disturbed landscapes. Environmental filtering has been evaluated based on abundance or richness of species with various life history traits in urbanizing regions, to determine if there are shared traits among multiple species found in urban to rural environments (e.g., Clergeau et al. 2006, Kark et al. 2007, Croci et al. 2008, Evans et. al 2011, Lizée et al. 2011, Hanspach et al. 2012). While this approach can undoubtedly be useful for predicting which species will be affected by land cover change and human disturbance (Hanspach et al. 2012), as applied it does not get at the underlying mechanisms driving patterns of presence and abundance (e.g., where species are abundant, are these source or sink habitats?). Ultimately, species presence and abundance in a region are driven by survival and site fidelity, reproduction, and their combined effect on species' ability to persist (Saracco et al. 2008). As a result, while one can look for traits that explain the presence or abundance of species, understanding the relationship between demographic parameters and these traits across regions of varying levels of human disturbance may yield insight into species responses to anthropogenic influences that can useful for management practices. Here, I test some common generalizations about the types of species that will be affected by human disturbances, based on expected relationships between traits and human disturbance from multiple studies and reviews in the literature. To test these generalizations, I use a subset of mark-recapture data from the Monitoring Avian Productivity and Survivorship (MAPS) dataset of the Institute for Bird Populations (IBP; DeSante et al. 1995). Rather than relating presence and abundance of species in urban and rural regions to their traits, I determine if demographic parameters can be predicted by species' characteristics across sites of varying disturbance levels.

Generalizations about species' responses to urbanization have been made based on single- or few-species studies (Blumstein 2006), reviews or compilations of multiple studies (e.g., Marzluff 2001, Chace and Walsh 2006, Chamberlain et al. 2009), or studies of the distribution of traits between disturbed and undisturbed regions (e.g., Devictor 2008b, Hanspach et al. 2012). Predictions about the sensitivity of species to human disturbance may be based on life history characteristics, or on differences in environmental variables, such as predator abundance or availability of supplemental food sources, predicted to affect specific traits. The numerous studies of avian responses to human disturbance and fragmentation make birds a model group on which to test hypotheses examining if generalizations can be made about life history characteristics influence demographic parameters, and how or if these responses differ in the context of disturbance. In general, the more specialized a species, the less prevalent it is expected to be in fragmented and disturbed areas (Devictor 2007, Devictor et al. 2008b, Evans et al. 2011). Predation is expected to be greater in urbanizing areas due to an increase in cats and avian predators (Lepczyk et al. 2004a, van Heezik et al. 2010, Balogh et al. 2011, Stracey 2011), and species that nest on or near the ground may be especially vulnerable (Gilbert 1989, Jokimäki and Huhta 2000, Evans et al. 2011). Cavity-nesting species, on the other hand, may benefit from human disturbance, especially those species that use existing cavities, for which nest boxes are often an accepted substitute (Lepczyk et al. 2004b, LeClerc et al. 2005); evidence for competition with exotic cavity-nesting species common in urbanizing areas, such as European Starlings, is equivocal (Koenig 2003). Species that require forest interior are expected to disappear from urbanizing regions, while edge species should thrive (Chace and Walsh 2006). Granivorous and omnivorous species are expected to be more prevalent in urbanizing areas (Chace and Walsh 2006, Kark et al. 2007), and may benefit from human subsidies (e.g., from birdfeeders) or food sources associated with human settlement, especially if these increase survival during harsh winters, or improve breeding success in the following season (Robb et al. 2008). "Fast-living species," e.g., those with larger clutches, smaller body size, and shorter life spans, may be more resilient to human disturbances than "slow-living species" because they invest in reproduction at the cost of their own survival, and so are less likely to flee nearby disturbances at the expense of their offspring (Bisson et al. 2009). In addition to species with larger clutches, species that are able to produce more than one brood per season are more likely to have higher fecundity (Martin 1995), and be able to successfully reproduce in human-disturbed areas (Reale and Blair 2005). Whether in the absence or presence of disturbance, resident species may have higher population growth and persistence because they can respond to local scale environmental variables, exploit resources, and establish territories before migrants arrive (Both et al. 2010). Finally, body size has been found to be associated with species' responses to habitat fragmentation and human disturbances (e.g., Blumstein 2005, Blumstein et al. 2006, Vargas et al. 2012). For instance, larger-bodied species have a greater flight-initiation distance, which may make them more wary of local disturbance (Blumstein 2006).

While previous studies provide indications of some expected patterns in species' responses to human disturbance, variation across studies warrants greater investigation into how species with different characteristics respond to human disturbance. For this study, I hypothesized that certain life history characteristics (nest location, food preference, habitat preference, migratory strategy, number of brood attempts, clutch size, and mass) may influence demographic parameters (apparent survival, reproduction, and population growth), potentially making some species more vulnerable to disturbance than others. I first compared survival, reproduction and population growth across all of the above life history characteristics, to determine if these characteristics differed in their overall effect on demographic parameters (e.g., if nest location has a greater effect on survival than food preference), and to see if there was any interaction with disturbance. I then compared survival, reproduction and population growth within each life history characteristic (e.g., the effect of nesting in cavities versus on or near the ground), and compared the response to disturbance. I expected that species' characteristics that conferred lower survival, reproduction, or population growth might be associated with a more negative impact of human disturbance. Alternatively, a relationship within life history characteristics that disappears in the context of disturbance may mean that these species, in spite of having lower values of demographic parameters, may be more resilient to disturbance.

Including an interaction with disturbance in models, I expected that 1) reproduction in ground-nesting species would be more negatively affected by disturbance than in cavity nesting or shrub- and tree-nesting species, though secondary cavity-nesting species could have decreased reproduction if they are negatively influenced by competition for nesting sites in more urban areas (European starlings are not included in the species examined in this study so this cannot be tested here); 2) survival, and possibly reproduction, in insectivorous species would be more negatively affected by disturbance than in omnivorous species (i.e., because specialists are expected to be more affected by disturbance than generalists, and diversity and abundance of invertebrate prey tend to decrease with urbanization; Paul and Meyer 2001, McKinney 2008), and species with a diet including mainly insects but also fruit or seeds (but not both) on the breeding ground would fall between insectivorous species and omnivorous species; 3) survival in species that prefer forest would be more negatively affected than in edge species or species preferring more open habitats; 4) having more than one brood would confer higher reproduction overall and with disturbance than having only one brood; 5) having a larger clutch size would confer higher reproduction overall and with disturbance than having a smaller clutch size; 6) survival and reproduction (and consequently population growth) in residents would be higher than in short-distance or long-distance migrants, and short-distance migrants would be at an advantage relative to long distance migrants; and 7) apparent survival in larger-bodied species may be lower than in smaller bodied species, due to a greater flight-initiation distance making them less likely to return to disturbed sites. While I expected that some species' characteristics such as nest location, number of broods, and clutch size might have a greater effect on reproduction than on apparent survival, these characteristics may indirectly influence apparent survival, which includes both true survival and return to a site, because site fidelity is likely to be influenced by previous years' reproductive success (Haas 1998). I evaluated the influence of these characteristics on demographic parameters in 24 bird species across sites of differing levels of human disturbance in the northeastern United States, to determine if the trait-based patterns found in studies of abundance and richness are confirmed in this analysis of mark-recapture data. Where generalizations can be made, the hope is that this analysis of demographic data can yield insight into the processes driving patterns of abundance and richness, the traits that make species vulnerable, and provide support for generalizations that can help to guide management practices for conservation.

Methods

Bird banding data and sites

I obtained MAPS banding data from the Institute for Bird Populations for 98 banding sites in the northeastern United States (ME, VT, NH, MA, CT, NY, PA, NJ, DE, RI), ranging from 4-19 years of data spanning 1989-2007. Each banding site spans an approximately 20-hectare area in which mist nets are placed and birds are banded according to a standard-effort protocol (DeSante et al. 1995, DeSante et al. 2012). These sites are typically located in wooded or semi-wooded areas that are expected to remain relatively unchanged so as to facilitate long-term monitoring.

I checked the recorded latitude and longitude for each banding site using Google Earth (Version 5.2, build date Sep 1, 2010). I verified locations of the 98 sites based on the overall vegetation structure of the banding sites as recorded by the operators, and site location names compared with similarly named locations (e.g., parks or landmarks) on Google Earth. I also compared the land cover in which each banding site appeared to fall in the Google Earth image with the vegetation recorded by operators. I moved locations of twelve of the 98 stations, all by less than one kilometer, for the following reasons. I have personally worked at two of these sites and so was aware of their exact location. The latitude/longitude coordinates of three sites were recorded as in water, and two were located on city streets. These latter five sites and three additional sites were all named based on their occurrence in national or state parks. I moved these sites within the boundaries of the parks to the closest area with vegetation consistent with that recorded by station operators (e.g., deciduous forest, as opposed to water or city streets). The coordinates of two additional sites were in fields adjacent to wooded areas, but the site operators had recorded these sites as being in wooded areas. I moved these two sites to occur just within the wooded area. I created a 1-km analysis buffer around each site to further account for error or variation in GPS records, and to encompass variation in human developed land cover surrounding the sites. For stations located less than 1-km apart in which buffers overlapped by more than 10%, I combined the buffers and station data. Only two pairs of stations that overlapped were not combined, and the buffers for these stations overlapped by 2% and <6%, respectively. Fifteen of the 98 stations were combined, 12 into pairs and 3 into one group.

Housing density data

I obtained United States housing density data for the year 2000 from the SILVIS laboratory of the University of Wisconsin (http://silvis.forest.wisc.edu/). The spatial resolution of these data ranges from 1.80 to 3.93 km^2 (Hammer et al. 2004). The 1-km buffer encompassing a single MAPS banding site may encompass more than one partial block group, the unit within which housing density is estimated from census data. Therefore, I calculated a weighted average of housing density based on the proportion of each location's buffer that fell within each partial block group. To calculate the weighted average, I converted the buffer polygon for each station to a point-shapefile, and extracted the values of the housing density layer to the buffer points. I assumed a high correlation between housing density and human population (Lepczyk et al. 2008), and so did not use population census data as an additional predictor variable. These housing density data were highly correlated ($p<0.0001$) with an index of disturbance independently obtained from a nonmetric multidimensional scaling analysis (NMDS) of land cover data from the National Land Cover Database (NLCD 2001, version 2, http://www.mrlc.gov/; Brown, Chapter 1).

Parameter estimates

I estimated apparent survival of adult birds (after-hatch year, AHY) and juvenile birds (hatch-year, HY) using the Cormack-Jolly-Seber (CJS) model in Program MARK (White and Burnham 1999). Survival estimates are 'apparent survival' because they include lack of return to a site, due to either death or dispersal from the site. The CJS model in Program MARK yields parameter estimates for both apparent survival and recapture by breaking each capture history into an overall probability of survival and recapture, and evaluating the probabilities and their frequency across all capture histories using maximum likelihood. The survival and recapture parameters can each be estimated by time, by group (i.e., by site for this analysis), or as a constant, single value. Program MARK provides an Akaike Information Criterion (AIC) value for each CJS model, varying depending on how each parameter is estimated. The Akaike Information Criterion varies as a function of the model likelihood and the number of parameters in the model, whereby each additional parameter is penalized by +2. For each species, I estimated apparent survival by site, and recapture by both site and as a constant (a single overall value for all sites, expected if banding is based on a sampling-wide constant-effort protocol). For each site, I retained the survival estimates from the CJS model with the lowest AIC, whether recapture was allowed to vary by site or was estimated as a single value. This allowed me to account for some variation in recapture rates between sites, e.g., if recapture differs greatly between sites due to differences in sampling effort then these are less likely to affect survival estimates. Prior to estimating survival, I deleted unbanded, dead, and injured individuals from the capture history database, because these individuals were not likely to be recaptured at later time periods. I only estimated apparent survival for species that had at least 300 individual capture histories, and I did not include data from sites that did not have at least one recapture record during the years in was in operation. Across the 24 species examined here, I was able to calculate 666 survival estimates from populations of birds within 12 families at 85 sites (Table 3.1).

I used maternity as a measure of reproduction for each species at each site. The maternity values I calculated represent a "post-breeding" census because the juveniles are counted in the same year that they were born (Akçakaya et. al 1999). For each species at each site, I calculated maternity using the formula

$$\text{a)}\ \frac{f_1 + f_2 + f_3 + \ldots f_n}{N_1 + N_2 + N_3 + \ldots N_n}$$

where f is the number of juveniles captured in years 1 to n, and N is the number of adults captured in years 1 to n. An alternative way to estimate maternity is

$$\text{b)}\ \frac{\frac{f_1}{N_1} + \frac{f_2}{N_2} + \frac{f_3}{N_3} + \cdots + \frac{f_n}{N_n}}{n}$$

The values obtained from equation a) are weighted averages (maternity, f/N, weighted by sample size, N, for each year), and thus take into account variation in effort (as measured by sample size) across time steps, such that estimates of maternity from years with small N contribute less to the time-averaged maternity estimates (H. R. Akçakaya, *pers. comm*). Given that sampling effort varies across years in the MAPS program as new sites are initiated and monitoring at other sites is discontinued or other factors may interfere with monitoring effort (e.g., weather), I used the values from equation a) to calculate maternity. Across 24 species, I calculated 1001 maternity estimates for populations of birds within 12 families at 87 locations (Table 3.1).

I calculated population growth, hereafter lambda, for each species at all sites where each species was found and for which estimates of hatch year bird (HY) survival, in addition to after hatch year (AHY) survival, could be obtained. Program MARK will not output a reasonable survival estimate or confidence interval if there are not enough data from which to obtain a maximum likelihood estimate. To obtain lambda values for each species at each site, I first estimated fecundity of HY and AHY birds. Because HY birds are counted in the same year as they are born, and not captured again until the following year when they are potentially breeding, fecundity of HY birds is $F_{\mathrm{HY}}=S_{\mathrm{HY}}\cdot m_{\mathrm{HY}}$, where S_{HY} is survival of HY birds, and m_{HY} is maternity of subadult birds, i.e., birds in their first year following a post-breeding census (Akçakaya et al. 1999). Similarly, fecundity of AHY birds is $F_{\mathrm{AHY}}=S_{\mathrm{AHY}}\cdot m_{\mathrm{AHY}}$, where S_{AHY} is survival of AHY birds, and m_{AHY} is maternity of adult birds (i.e., birds in their second year or older; Akçakaya et al. 1999). The method for estimating maternity described in the above section is based on all AHY birds, whether subadult or older. Across multiple species, reproductive success increases with breeding experience and age. Subadults tend to fledge fewer offspring, and subadult birds of migratory species tend to arrive on the breeding ground later than adults, securing territories and mates later, if at all (Ficken and Ficken 1967, Harvey et al. 1985, Nol and Smith 1987, Lemon et al. 1996, Lozano et al. 1996, Cooper et al. 2009). Given that it is often difficult to distinguish subadults from adults in the hand, we have minimal knowledge of the relative proportions of subadults to adults in a given population. In calculating population growth estimates, one can either assume that maternity is equal for AHY and HY birds, or that maternity is greater for the AHY age class than HY age class. I assumed that contribution of AHY birds versus HY birds to maternity was 2:1. For some species, this ratio may under or overestimate maternity for each age class, and subsequently lambda, depending on the proportions of subadults versus adults in the population and their overall reproductive success. However, the above evidence suggests that assuming a 1:1 ratio is likely unrealistic. Further, across all species, lambda from a previous analysis assuming a 3:1 ratio differed from a 2:1 ratio by ≤ 0.05 ratio in 86% (19/22) of species, and differed by <0.14 in the remaining species (Brown, Chapter 1). To estimate lambda, I created a 2 × 2 matrix of fecundity and survival values,

$$\begin{matrix} F_{\text{HY}} & F_{\text{AHY}} \\ S_{\text{HY}} & S_{\text{AHY}} \end{matrix}$$

and estimated lambda as the dominant eigenvalue of the matrix. This method assumes that populations are in a stable age distribution, meaning the proportion of adults to juveniles in the population is not changing over time, even if the overall population size is changing (Akçakaya et al. 1999). Across 22 species, I calculated 205 lambda values for bird populations within 10 families at 63 locations (I excluded American Goldfinch and Red-winged Blackbird because these species did not have enough HY recaptures to estimate HY survival; Table 3.1).

Species characteristics

I obtained life history information for each bird species from the Birds of North America Online database (Poole 2005) and Valiela and Martinetto (2007). I grouped species by similarity of life history characteristics, including nest location, food preference, expected habitat type during the breeding season, number of broods generally attempted (1 or ≥1), average clutch size (≤4 or ≥4), and migratory behavior (Table 3.2). I also obtained maximum body mass from the CRC Handbook of Avian Masses (Dunning 1993) as a measure of body size for each species, consistent with Blumstein (2005) and Blumstein at al. (2006; Table 3.2). I used maximum mass estimates from the literature rather than from the MAPS data itself to have an independent measure of mass, not dependent on location or observer error within the MAPS data. All of these data except for mass were categorical predictor variables. I used both the continuous measures of mass as well as a categorical value of mass for models. The log-transformed mass values ranged from 2.40-4.63. For the purposes of breaking into roughly even groups, I divided the log-transformed values into three mass categories: low mass (a log-transformed mass of <3.00, or <20 grams; 10 species), medium mass (a log-transformed mass of 3.00–<4.00, or 20-54.9 grams to <55 grams; 9 species), and high mass (a log-transformed mass of >4.00, or >55 grams; 5 species).

Statistical Analyses

I used linear mixed-effects models to examine the effect of nest location, food preference, habitat preference, number of broods, clutch size, migratory strategy, mass, and housing density on each of three response variables: survival, reproduction (maternity) and population growth (lambda). Mixed-effects models are useful for analyses with repeated measures that may contribute to non-independence of data points, because they treat certain factors as fixed effects (the factors being tested) and other factors as random effects (factors that may contribute to variation in the response variables, but are not themselves being modeled). For all models, I treated species, family, and location as random factors that may contribute to the variation in survival, maternity or lambda, but are not being directly modeled. Holding these as random factors allowed pooling of the data so that multiple data points could be used, even if they were collected at the same location, belonged to the same species, or belonged to the same family, with the latter category included to capture the influence of phylogenetic similarity in responses.

I ran two sets of mixed-effects models using the R package 'lme4' (Bates et al. 2011, R Development Core Team 2012). First, I regressed survival, maternity, and lambda each on the full set of species characteristics (with mass as a continuous variable) and housing density, including an interaction with housing density. I summarized these results in anova tables and calculated *p*-values from the anova table statistics to determine if there was a strong overall effect of any particular species' characteristic. I also estimated the effect sizes of species' characteristics, measured as the range of values of each response variable (using the R package 'languageR', Baayen 2011). Finally, I estimated the maximum *p*-value for species' characteristics to be considered significant via the Bonferroni correction as $\propto/N$, where $\propto$ is a significance level of 0.05 and *N* is number of the comparisons. These models with the full complement of predictor variables analyzed in anova tables allowed me to evaluate the effect of broad categories of species' characteristics on demographic parameters (e.g., the influences of nest location versus food preference versus migratory strategy).

Second, I individually regressed each of the species' characteristics, including an interaction with housing density, on demographic parameters. Looking at the effect of characteristics individually allowed me to determine how variation within these characteristics affected demographic parameters and interacted with housing density (e.g., not just the importance of nest location versus food preference on survival, but the effect of being a cavity-nesting versus a ground-nesting species, or of being an insectivorous versus an omnivorous species). For all species characteristics, I plotted the mean value (i.e., regression coefficient estimate) of demographic parameters at 0, 50, and 100 housing units/km^2 using the R package 'ggplot2' (Wickham 2009). For predictions at 50 and 100 housing units/km^2, I estimated standard errors using the delta method and the R package 'emdbook' (Bolker 2008, Bolker 2012). Where there was an effect of HD, I also plotted the strength and direction of the effect of HD on coefficient estimates, and the standard errors of the effect of HD using the R package 'arm' (Gelman et al. 2012). I considered coefficient estimates greater than two standard errors from the mean to be significant, corresponding to a *t*-value greater than 2 (Gelman and Hill 2006; there is considerable controversy over applying *p*-values to mixed models, and they are not even available in the package 'lme4'). I also report *t*-values greater than 1.5 as these may be nearly significant. I excluded the predictor categories of 'variable nest location' and 'granivorous' (in Red-winged blackbirds and American Goldfinch, respectively) because they each included only one species. I used categories of body masses to simplify and aid visualization of the relationship between mass and demographic parameters. This also meant that body mass was consistent with other predictor variables, all of which were categorical.

I checked predictor variables for colinearity using data for the 24 species rather than for the entire dataset, using Fisher's tests to account for small sample size. I took into account any colinear relationships between variables when interpreting the results.

Results

Demographic parameters predicted across species' characteristics

In models with the full complement of predictor variables, survival was not predicted by any of the species characteristics (Table 3.3). Nest location predicted maternity (*p*=0.0002; Table 3.4) and lambda (*p*=0.0067; Table 3.5). There was a negative effect of housing density (*p*=0.0369) and a positive effect of mass on lambda (*p*=0.0092; Table 3.5). An interaction between housing density and mass also predicted maternity (*p*=0.0014; Table 3.4). Applying a Bonferroni correction set the significance level for models at 0.0031. Assuming a Bonferroni level of significance, nest location and an interaction between mass and housing density remained predictors of maternity. Given that the Bonferroni correction may be overly conservative (Nakagawa 2004), the relationships between nest location and lambda, and between mass and lambda, should not be disregarded.

Mass had the largest effect size (the range of values for the response variable) on survival and lambda, and was a positive effect in both cases (Table 3.5). Nest location, followed by food preference and housing density had the largest effect sizes on maternity (Table 3.4). The effect of housing density on maternity and lambda was negative.

Demographic parameters predicted within species' characteristics

1) Differences between demographic parameters within species' characteristics, holding human disturbance constant

Cavity-nesting species had higher maternity than shrub- and tree-nesting species (*t*=2.34; Figure 3.1). Insectivorous species had higher maternity than omnivorous species (*t*=2.36; Figure 3.2). Residents had higher maternity than short-distance migrants (*t*=2.30; Figure 3.3), and higher lambda than long-distance migrants (*t*=2.22; Figure 3.4).

There was a trend towards ground-nesting species having higher maternity than shrub- and tree-nesting species (t=1.76; Figure 3.1), insectivorous species having higher maternity than birds with a diet of insects and fruit or seeds (*t*=1.90; Figure 3.2), and edge species having higher maternity than open-area species (*t*=1.98; Figure 3.5).

In addition, food preference and migratory status revealed the expected trends in survival. Omnivorous species showed a trend of higher survival than birds with a diet of insects and fruit or seeds, and the latter showed a trend of higher survival than insectivorous species (Figure 3.6). Residents trended toward higher survival than short-distance migrants, and short-distance migrants trended toward higher survival than long-distance migrants (Figure 3.6). Lastly, birds with larger clutches tended to have higher survival, maternity and lambda than birds with a single clutch, and this effect as expected was most pronounced in lambda (Figure 3.7).

2) Effect of housing density (HD) on mean demographic parameter values within species' characteristics

In birds with the lowest masses, there was a negative effect of HD on maternity (*t*=2.17; Figure 3.8) and lambda (*t=2.*14; Figure 3.9). There was also a negative effect of HD on lambda in edge species (*t*=2.03; Figure 3.5). Contrary to expectation, there was not a negative effect of HD on forest species.

There was a difference between the positive effect of HD on birds with a diet of insects and fruit or seeds, and the expected negative effect of human disturbance on fully insectivorous species (*t*=2.78; Figure 3.2). The negative effect of HD on maternity in long distance migrants differed from the positive effect on short distance migrants (*t*=2.25; Figure 3.3). The negative effect of HD on maternity in birds with low masses differed from the positive effect in birds with medium (*t*=2.99) or high masses (*t*=2.69; Figure 3.8). Contrary to expectation, maternity in ground-nesting species was not more affected by disturbance than in other types of nesters.

There was a trend towards a negative effect of HD on lambda in open species (*t*=1.81; Figure 3.5), and in birds with a single brood (*t*=1.84; Figure 3.10). There was also a trend towards a negative effect of HD on maternity in residents differing from the positive effect in short-distance migrants (*t*=1.88; Figure 3.3), and an expected negative effect of HD on maternity in single-brooded birds differing from the positive effect of having more than one brood (*t*=1.85; Figure 3.11).

Correlation among variables

Nest location was significantly correlated with clutch size ($p<0.02$). Migratory strategy was significantly correlated with nest location ($p<0.04$), food preference ($p<0.001$), habitat preference ($p<0.04$), and number of broods ($p<0.02$). Mass category (low, medium, high) was significantly correlated with number of broods ($p<0.004$).

Discussion

Predicting how species respond to anthropogenic disturbances is essential for ensuring their conservation and maintaining vital ecosystem services. In this study, using a multi-species mark-recapture dataset covering a broad geographic region, several effects of species' characteristics on demographic parameters were revealed. However, these were not entirely consistent with relationships predicted from previously documented patterns of abundance or richness in the literature. Further, the relationship between life history characteristics and demographic parameters when disturbance was considered constant in models was not necessarily indicative of the relationship when an interaction was included; human disturbance may in fact alter the relationship between demographic parameters and species' characteristics. When comparing the effect of human disturbance on different groups of species, one should consider if the effects are relative to undisturbed areas, versus relative to the relationship between species' characteristics themselves. In other words, if the abundance of a group of species declines in disturbed areas, did these species already have lower abundance relative to other groups in less disturbed areas? The relationships found between species' characteristics, disturbance, and demographic parameters suggest that it may be possible to generalize species' responses to human disturbance. However these relationships may be more complex than can be inferred from studies of patterns of abundance and richness alone.

Among the relationships found between species' characteristics and human disturbance, maternity was the demographic parameter most often affected. This reinforces the importance of considering multiple demographic parameters as response variables, as an effect of human disturbance may not be consistent across all parameters and only measuring one could elicit misleading results. Based on this study, at the trait-level human disturbance appears to have the strongest effect on maternity, consistent with other studies that have found effects of disturbance on nest and fledgling survival in certain guilds (e.g., Chace and Walsh 2006, Chamberlain et al. 2009) However, these results differ from species-level analyses in previous work (Brown, Chapter 1) which found that human disturbance has a greater effect on apparent survival. Species differ in their response to human disturbance (i.e., some are more positively or negatively affected than others) and there is known variation in dispersal across species (Brown, Chapter 1, Greenwood and Harvey 1982, Paradis et al. 1998). Trait differences causing variation in maternity across gradients of disturbance could drive apparent survival at the species level if responses to annual reproduction and to human disturbance affect site fidelity differently across species. Based on the results found in this study, maternity may be the most sensitive of the demographic parameters affected by disturbance, but behavioral decisions in response to disturbance may act at the species-level, as individuals within species decide whether or not to breed in the same location in following years (e.g., Haas 1998). Maternity may also be more affected by species' characteristics than survival if all species simultaneously breeding in a region are similarly affected by the same external factors. However, survival may be more affected at the species level because it influences populations year-round across their entire annual cycles, which vary geographically. If the extent to which demographic parameters are affected by disturbance differs depending on scale (e.g., if local breeding factors have the largest effect on demographic parameters vs. other variables acting throughout the annual cycle), this could have implications for how to manage species. In such a scenario, the best mitigation practices for reducing the effects of environmental changes will depend on which demographic parameters are most influenced by what factors, i.e., some effects of human disturbance may need to be managed at the species level, whereas others may be manageable by enacting policies that benefit groups of species.

The effect of nest location on reproduction found here, in both full and individual models, is supported by previous studies suggesting a relationship between fecundity and nest location (Martin 1995). However, human disturbance did not affect the relationship between nest location and demographic parameters. Some studies have suggested that human disturbance benefits cavity-nesting species over other types of nesters (e.g., Lepczyk et al. 2004b), but the results of this study imply that cavity nesting species already have higher maternity overall, which is also reflected in responses to human disturbance. Studies finding a positive effect of disturbance on cavity-nesting species have often been based on the use of nest boxes, which may not be available to the secondary cavity-nesting species examined at sites in this study. Further, a potential negative effect of invasive cavity-nesting species competing for nest sites (e.g., Strubbe and Matthysen 2009) was not investigated here because these species (e.g., House sparrows and European starlings) were not commonly captured in mist-nets, which may reflect low abundance at the locations in this study. The patterns found here also support the idea that ground or near ground-nesting species and shrub- and tree-nesting species have lower maternity, but not that they are more susceptible to disturbance as expected from previous studies (Marzluff 2001, Jokimäki and Huhta 2002, Jokimäki et al. 2005, Blair and Johnson 2008, Lepczyk et al. 2008). This does not negate findings of previous work, but does suggest that lower prevalence of certain types of species in more urbanized areas does not necessarily mean that those remaining species are suffering more from reduced survival or reproductive success relative to other types of species.

In addition to nest location, body mass was also important in predicting maternity in both full and individual models, providing greater support for the observed relationship. Mass also interacted with disturbance, supporting the importance of mass as a predictor of how species respond to disturbance (e.g., Blumstein et al. 2005, Blumstein 2006). I expected birds with larger masses to have lower apparent survival than birds with smaller masses when disturbance was included in models, due to potential lower site fidelity caused by a greater propensity to flee disturbances (Blumstein et al. 2005). However, the direction of the effect of mass in both full and individual models was positive, and the interaction with disturbance affected maternity and lambda, but not survival. If birds with larger masses have greater flight-initiation distances, this could reflect greater vigilance in disturbed areas, and this awareness may make them less likely to put their young in danger by foraging in the presence of predators (Frid and Dill 2002). Larger birds may also be more aggressive towards nest predators (Larsen et al. 1996). Although mass and food preference were not correlated, all excepting one (4/5) of the species in this study with the highest masses were also omnivorous or included fruits or seeds in their diet. At the same time, all excepting one (10/11) of the species with the smallest masses were insectivorous species. These larger species that use other food sources in addition to insects may benefit from supplemental food for provisioning young, either from bird feeders or increases in fruiting exotic shrubs or invasive plants associated with human settlement (e.g., Daniels and Kirkpatrick 2006).

This is further supported in this study by an increase in maternity with disturbance in birds preferring insects and fruit or seeds, that contrasted the decrease in maternity of insectivorous birds, the latter of which may be susceptible to declines of invertebrate prey in urbanizing areas (Paul and Meyer 2001, McKinney 2008). Surprisingly, omnivores had the lowest maternity, even in disturbed areas, though survival trends reflected the expected relationship whereby omnivorous species had the highest survival and insectivorous species had the lowest survival.

Some correlations between species characteristics may confound interpreting their relationships with demographic variables. For instance, migratory strategy was important in predicting maternity in individual models, and interacted with disturbance. Residents had higher maternity than long-distance or short-distance migrants, lambda decreased from residents to short-distance migrants to long-distance migrants, and survival followed same trend. However, migratory strategy was highly correlated with nearly all other variables that showed a relationship with demographic parameters (nest location, food preference, habitat preference). The majority of resident species in this study were also cavity-nesting, and either omnivorous or with a diet of insects and fruit or seeds, both of which also influenced demographic parameters. In addition, although not significant, maternity increased with disturbance in birds with more than one brood and decreased in birds with less than one brood. While consistent with previously documented negative effects of disturbance on single-brooded birds (e.g., Reale and Blair 2005), all short-distance migrants had more than one brood and were also positively affected by disturbance, neither of which was true for residents or long-distance migrants. Further, mass was also correlated with brood number, so the nearly significant effect of an interaction between disturbance and brood on maternity could have been driven by the interaction between disturbance and mass that affected maternity. Although correlations exist between some variables examined here, this does not mean these variables do not act independently to influence demographic parameters. Studying carefully selected species for which the correlated traits in this study are controlled, if possible, would help to tease apart these effects.

While I found differences in demographic parameter values between traits when disturbance was held constant in models, these differences were not necessarily reflected in responses to disturbance. Species with lower survival may still have the lowest survival with human disturbance and thus could be more vulnerable, but this isn’t always the case. For instance, short-distance migrants had the lowest mean maternity, but there was a positive effect of human disturbance on maternity in short-distance migrants relative to residents or long-distance migrants. In addition, insectivores had the highest maternity, but this declined more than in other food preference groups with an interaction with disturbance. Finally, birds with the lowest masses also had the highest maternity, but this value too decreased significantly when an interaction with disturbance was included in models. For several other relationships between species’ characteristics and demographic parameters though, including nest location and habitat preference, an interaction with disturbance did not change which characteristics conferred the highest and lowest values of demographic parameters. In these cases, higher values of demographic parameters with disturbance may reflect higher survival, reproduction or rates of population growth overall. Species’ baseline investment (i.e., without disturbance) in demographic parameters is important in that it may help to buffer some species from the effects of human disturbance. In assessing the effect of human disturbance it is important to determine if there is actually an effect of disturbance, versus an already existing relative difference between species’ characteristics.

There are several possible reasons why some of the relationships between species characteristics and demographic parameters did not interact with disturbance as predicted. First, species with similar characteristics may have similar responses to disturbance, but these differences may not be consistent when different groups of species with similar characteristics are studied, or in different regions. Second, different processes than those reflected in the demographic parameters examined here may drive previously found patterns of species' abundance or richness. For instance, survival may not affect local abundance, or behavioral influences such as competition between individuals for optimal territories may be more important drivers of local abundance than survival or reproduction (e.g., Shochat et al. 2006). Third, individuals found in an area may persist in large numbers, but they may not always return to that site if they have low maternity at that site (e.g., sink habitats). Fourth, the effects of disturbance may not be apparent if they are due to factors not measured here, such as collisions with buildings or vehicles that may negatively affect species and were not considered here (Chace and Walsh 2006). The metric of human disturbance used in this study was housing density. However, other studies using different metrics of human disturbance such as noise levels or the extent of fragmentation may yield different results. If analyses of demographic parameters lead to different conclusions than analyses of patterns of abundance and richness in disturbed areas, continued investigations of potential processes driving these patterns, such as the demographic parameters tested here, should aid in understanding the effects of disturbance on species, and generating new hypotheses.

Some statistical considerations could influence the interpretation of my results. First, the two approaches that I used to investigate the influence of species characteristics on demographic parameters - including all species' characteristics in a single model, and looking at the effects of the species' characteristics individually - did not yield entirely congruent results. Models that included the full complement of species' characteristics may not entirely reflect the relationships found in individual models because they may have had too few degrees of freedom, especially when interactions are included. Each, however, have their advantages, such as the ability to estimate and compare overall effect sizes from the full models, and may be useful depending on the level of detail one hopes to gain. Second, I did not use a standard phylogenetic regression method (e.g., phylogenetic least squares or independent contrasts) to correct for phylogenetic relatedness among species because I had replicates of species and locations, making mixed models an appropriate approach. To use a phylogenetic regression method, I would have had to average values across sites to have only one value for each species, resulting in a loss of statistical power, and not allowing me to investigate differences within species across sites, which may cancel out in averaging. While phylogenetic mixed models have been developed (e.g. Housworth et al. 2004, Ives and Helmus 2011), these are not yet easily implemented or available in packages such as R. Lastly, results from lambda in this analysis should be interpreted with caution, as these models had the fewest data points, and lambda is derived from other parameters, all of which are measured with error. In addition, lambda estimates may be biased if populations are not at their stable age distribution, for instance if disturbance disrupts the stable age distribution. However, it may be a reasonable assumption that averaging parameter values over time captures enough of the variation within years to get at the stable age distribution. Given the number of assumptions used to estimate lambda, the few relationships with lambda may not be indicative of actual processes.

In conclusion, some of the generalizations on which my hypotheses were based, specifically regarding nest location, food preference, and migratory strategy affecting maternity, were at least partially supported in the absence of disturbance. In the presence of disturbance, however, only predictions about a negative effect on insectivorous species and long-distance migrants were supported. The prediction of number of broods predicting maternity was nearly significantly supported, but may have been driven by the strong relationship between mass and disturbance, given the correlation between number of broods and mass. From a conservation perspective, the ability to predict how species' respond to disturbance based on their characteristics is ideal for developing strategies to manage species (e.g., protecting or providing breeding sites, and augmenting food sources), and both single-species studies and collective studies using multiple metrics of disturbance may contribute. However, more studies to challenge and confirm the current state of knowledge are necessary before broad generalizations should be made. This study is the first to my knowledge to investigate how species' characteristics may cause differences in demographic parameters, and how human disturbance influences these relationships. Further insights, such as those gained in this study into the mechanisms driving species' relationships with disturbance, will be useful to guide further research and conservation initiatives.

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Table 3.1. Number of data points for each demographic parameter used in models, and the number of species, families, and locations included in each dataset.

Response Variable	N data points	N species	N families	N locations
Survival	666	24	12	85
Maternity	1001	24	12	87
Lambda	205	22	10	63

Table 3.2. Species' characteristics used as predictor variables in models. Migratory strategy and preferred habitat are based on Birds of North America online (Poole 2005) and classifications of Valiela and Martinetto (2007). Mass values are from the CRC Handbook of Avian Masses (Dunning 1993). All other characteristics are from the Birds of North American online (Poole 2005). Latin names and families are validated from the American Ornithologists' Union's Checklist of North American birds (1998), recent supplements to the checklist (Chesser 2011), and the searchable online database (http://www.aou.org/checklist/north/index.php).

Common name	**Latin name**	**Family**	**Migratory strategy**	**Food preference**	**Nest location**	**Preferred habitat**	**Clutch size**	**Brood number**	**Maximum mass**
American goldfinch	*Spinus tristis*	Fringillidae	Short distance	Granivore	Shrubs, trees	Edge to open	≥ 4	>1	20.7 (medium)
American redstart	*Setaphoga ruticilla*	Parulidae	Long distance	Insectivore	Shrubs, trees	Forest	≤ 4	single	12 (low)
American robin	*Turdus migratorius*	Turdidae	Short distance	Insects/Other	Shrubs, trees	Forest to edge	≤ 4	> 1	103 (high)
Black-and-white warbler	*Mniotilta varia*	Parulidae	Long distance	Insectivore	On/near ground	Forest	≥ 4	single	15.2 (low)
Black-capped chickadee	*Poecile atricaillus*	Paridae	Resident	Omnivore	Cavities	Forest to edge	≥ 4	single	13.6 (low)
Blue-winged warbler	*Vermivora cyanoptera*	Parulidae	Long distance	Insectivore	On/near ground	Forest to edge	≥ 4	single	11 (low)
Common yellowthroat	*Geophlypis trichas*	Parulidae	Long distance	Insectivore	On/near ground	Forest to edge	≤ 4	single	15.5 (low)
Chestnut-sided warbler	*Setaphoga pensylvanica*	Parulidae	Long distance	Insectivore	On/near ground	Forest to edge	≤ 4	single	13.1 (low)
Downy woodpecker[+]	*Picoides pubescens*[+]	Piciformes[+]	Resident	Omnivore	Cavities	Forest to edge	≥ 4	single	32.2 (medium)
Eastern towhee	*Pipilo erythrophthalmus*	Emberizidae	Short distance	Omnivore	On/near ground	Forest to edge	≤ 4	> 1	52.3 (medium)
Gray catbird	*Dumetella carolinensis*	Mimidae	Long distance	Insects/Other	Shrubs, trees	Forest to edge	≤ 4	> 1	56.5 (high)
Hermit thrush	*Catharus guttatus*	Turdidae	Short distance	Insectivore	On/near ground	Forest to edge	≥ 4	> 1	37.4 (medium)
House wren	*Troglodytes aedon*	Troglodytidae	Long distance	Insectivore	Cavities	Forest to edge	≥ 4	> 1	14.2 (low)
Magnolia warbler	*Setaphoga magnolia*	Parulidae	Long distance	Insectivore	On/near ground	Forest	≤ 4	single	12.9 (low)
Northern cardinal	*Cardinalis cardinalis*	Cardinalidae	Resident	Omnivore	Shrubs, trees	Forest to edge	≤ 4	> 1	64.9 (high)
Ovenbird	*Seiurus aurocapilla*	Parulidae	Long distance	Insectivore	On/near ground	Forest	≥ 4	single	28.8 (medium)
Red-eyed vireo	*Vireo olivaceus*	Vireonidae	Long distance	Insectivore	Shrubs, trees	Forest	≤ 4	single	25.1 (medium)
Red-winged blackbird	*Agelaius phoeniceus*	Icteridae	Short distance	Omnivore	Variable	Edge to open	≤ 4	> 1	81.1 (high)
Song sparrow	*Melospiza melodia*	Emberizidae	Long distance	Insectivore	On/near ground	Forest to edge	≤ 4	> 1	29.9 (medium)
Traill's flycatcher	*Empidonax alnorum/traillii*	Tyrannidae	Long distance	Insectivore	Shrubs, trees	Forest	≤ 4	single	16.4 (low)
Tufted titmouse	*Baeolophus bicolor*	Paridae	Resident	Insects/Other	Cavities	Forest to edge	≥ 4	single	26.1 (medium)
Veery	*Catharus fuscescens*	Turdidae	Long distance	Insects/Other	On/near ground	Forest	≤ 4	single	41.7 (medium)
Wood thrush	*Hylocichla mustelina*	Turdidae	Long distance	Insectivore	Shrubs, trees	Forest	≤ 4	> 1	57.7 (high)
Yellow warbler	*Setaphoga petechia*	Parulidae	Long distance	Insectivore	Shrubs, trees	Edge to open	≤ 4	single	16 (low)

Table 3.3. Anova table and effect sizes across species' characteristics predicting survival (full model). Effect sizes are the range of values of the response variable for each predictor variable. (+) or (–) indicates the direction of the relationship between predictor variable and response variable for continuous predictors.

Response variable	Predictor variable	Df	Sum Sq	Mean Sq	*F*-value	*p*-value	Effect size (range)
survival	Housing density	1	0.0539	0.0539	0.0916	0.7622	0.3306 (+)
	Mass (continuous)	1	1.1203	1.1203	1.9044	0.1681	**0.7949** (+)
	Nest location	2	1.9132	0.9566	1.6261	0.1975	0.5113
	Food preference	2	1.7458	0.8729	1.4839	0.2275	0.1934
	Preferred habitat	2	0.8242	0.4121	0.7006	0.4967	0.2625
	Clutch size	1	1.9150	1.9150	3.2554	*0.0717* ·	0.3265
	Number of broods	1	1.8673	1.8673	3.1743	*0.0753* ·	0.4359
	Migratory habit	2	0.1878	0.0939	0.1596	0.8525	0.3157
	Mass (continuous) x housing density	1	0.0005	0.0005	0.0009	0.9763	-
	Nest location x housing density	2	0.3815	0.1907	0.3242	0.7232	-
	Food preference x housing density	2	0.0133	0.0067	0.0113	0.9887	-
	Preferred habitat x housing density	2	0.9884	0.4942	0.8401	0.4321	-
	Clutch size x housing density	1	0.0942	0.0942	0.1602	0.6891	-
	Number of broods x housing density	1	0.7714	0.7714	1.3114	0.2526	-
	Migratory habit x housing density	2	1.8649	0.9325	1.5851	0.2057	-

Significance level indicators are <0.001***, <0.01**, <0.05*, <0.1 ·.

Table 3.4. Anova table and effect sizes across species' characteristics predicting maternity (full model). Effect sizes are the range of values of the response variable for each predictor variable. (+) or (–) indicates the direction of the relationship between predictor variable and response variable for continuous predictors.

Response variable	Predictor variable	Df	Sum Sq	Mean Sq	*F*-value	*p*-value	Effect size (range)	
maternity	Housing density	1	0.1339	0.1339	0.1834	0.6686	**0.6253**	(–)
	Mass (continuous)	1	0.0222	0.0222	0.0305	0.8615	0.1609	(+)
	Nest location	2	12.4069	6.2034	8.4972	0.0002***	**0.9072**	
	Food preference	2	0.9328	0.4664	0.6389	0.5281	**0.6402**	
	Preferred habitat	2	2.0235	1.0118	1.3859	0.2506	0.1740	
	Clutch size	1	0.1084	0.1084	0.1485	0.7000	0.1252	
	Number of broods	1	0.0009	0.0009	0.0012	0.9721	0.2332	
	Migratory habit	2	1.4230	0.7115	0.9746	0.3777	0.7785	
	Mass (continuous) x housing density	1	7.5164	7.5164	10.2957	0.0014**	-	
	Nest location x housing density	2	1.0677	0.5338	0.7312	0.4816	-	
	Food preference x housing density	2	0.4679	0.2340	0.3205	0.7259	-	
	Preferred habitat x housing density	2	1.9445	0.9722	1.3317	0.2645	-	
	Clutch size x housing density	1	1.4623	1.4623	2.0030	0.1573	-	
	Number of broods x housing density	1	0.2736	0.2736	0.3747	0.5406	-	
	Migratory habit x housing density	2	3.8884	1.9442	2.6631	*0.0702·*	-	

Significance level indicators are <0.001***, <0.01**, <0.05*, <0.1·.

Table 3.5. Anova table and effect sizes across species' characteristics predicting lambda (full model). Effect sizes are the range of values of the response variable for each predictor variable. (+) or (–) indicates the direction of the relationship between predictor variable and response variable for continuous predictors.

Response variable	Predictor variable	Df	Sum Sq	Mean Sq	*F*-value	*p*-value	Effect size (range)	
lambda	Housing density	1	0.4967	0.4967	4.4216	0.0369*	0.3154	(–)
	Mass (continuous)	1	0.7628	0.7628	6.7912	0.0092**	**0.8202**	(+)
	Nest location	2	1.1561	0.5781	5.1463	0.0067**	0.2356	
	Food preference	2	0.1145	0.0573	0.5097	0.6015	0.4096	
	Preferred habitat	2	0.0226	0.0113	0.1008	0.9042	0.0786	
	Clutch size	1	0.0759	0.0759	0.6755	0.4122	0.1314	
	Number of broods	1	0.4197	0.4197	3.7360	*0.0548·*	0.3317	
	Migratory habit	2	0.3759	0.1880	1.6732	0.1905	0.7492	
	Mass (continuous) x housing density	1	0.2171	0.2171	1.9326	0.1662	-	
	Nest location x housing density	2	0.1493	0.0746	0.6646	0.5157	-	
	Food preference x housing density	2	0.0952	0.0476	0.4236	0.6554	-	
	Preferred habitat x housing density	2	0.0883	0.0442	0.3932	0.6755	-	
	Clutch size x housing density	1	0.0967	0.0967	0.8609	0.3547	-	
	Number of broods x housing density	1	0.0173	0.0173	0.1542	0.6950	-	
	Migratory habit x housing density	2	0.3916	0.1958	1.7421	0.1779	-	

Significance level indicators are <0.001***, <0.01**, <0.05*, <0.1 ·.

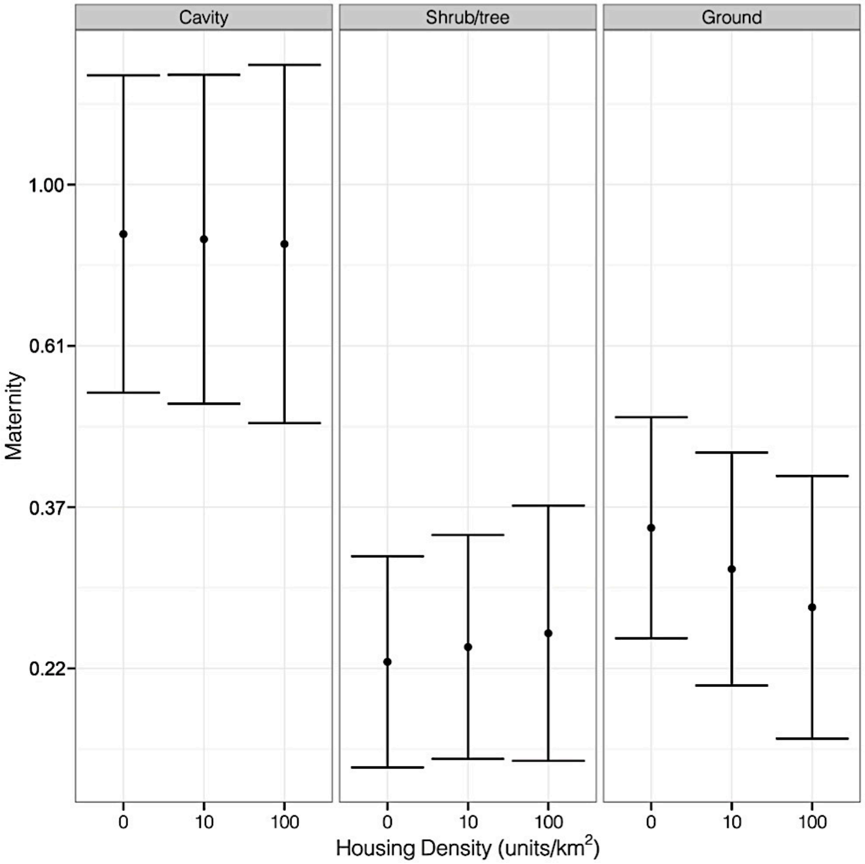


Figure 3.1. Mean and standard error of maternity by nest location. Maternity at 0 housing units/km^2 was higher for cavity nesting species than shrub- and tree-nesting species (*t*=2.34). Ground-nesting species trended toward also having higher maternity than shrub- and tree-nesting species at 0 housing units/km^2 (*t*=1.76).

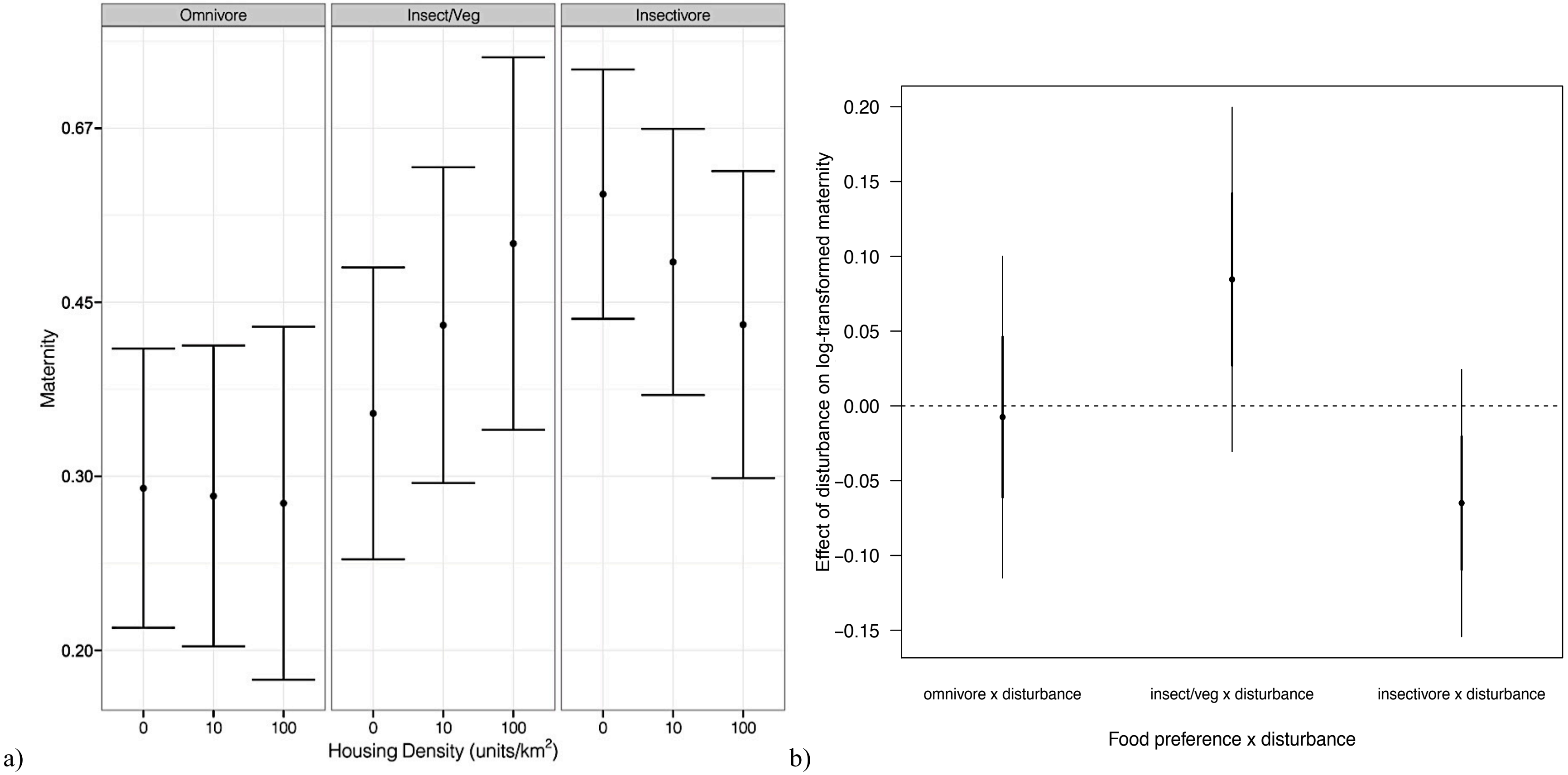


Figure 3.2. Mean and standard error of maternity by food preference. a) Insectivorous species had higher maternity at 0 housing units/km^2 than omnivorous species (t=2.36); there was a trend toward insectivorous species having higher maternity than birds with a diet of insects and fruit or seeds (insect/veg; t=1.90). b) There was a difference between the positive effect of disturbance (housing density) on birds with a diet of insects and fruit or seeds (insect/veg), and the negative effect on insectivores (t=2.78).

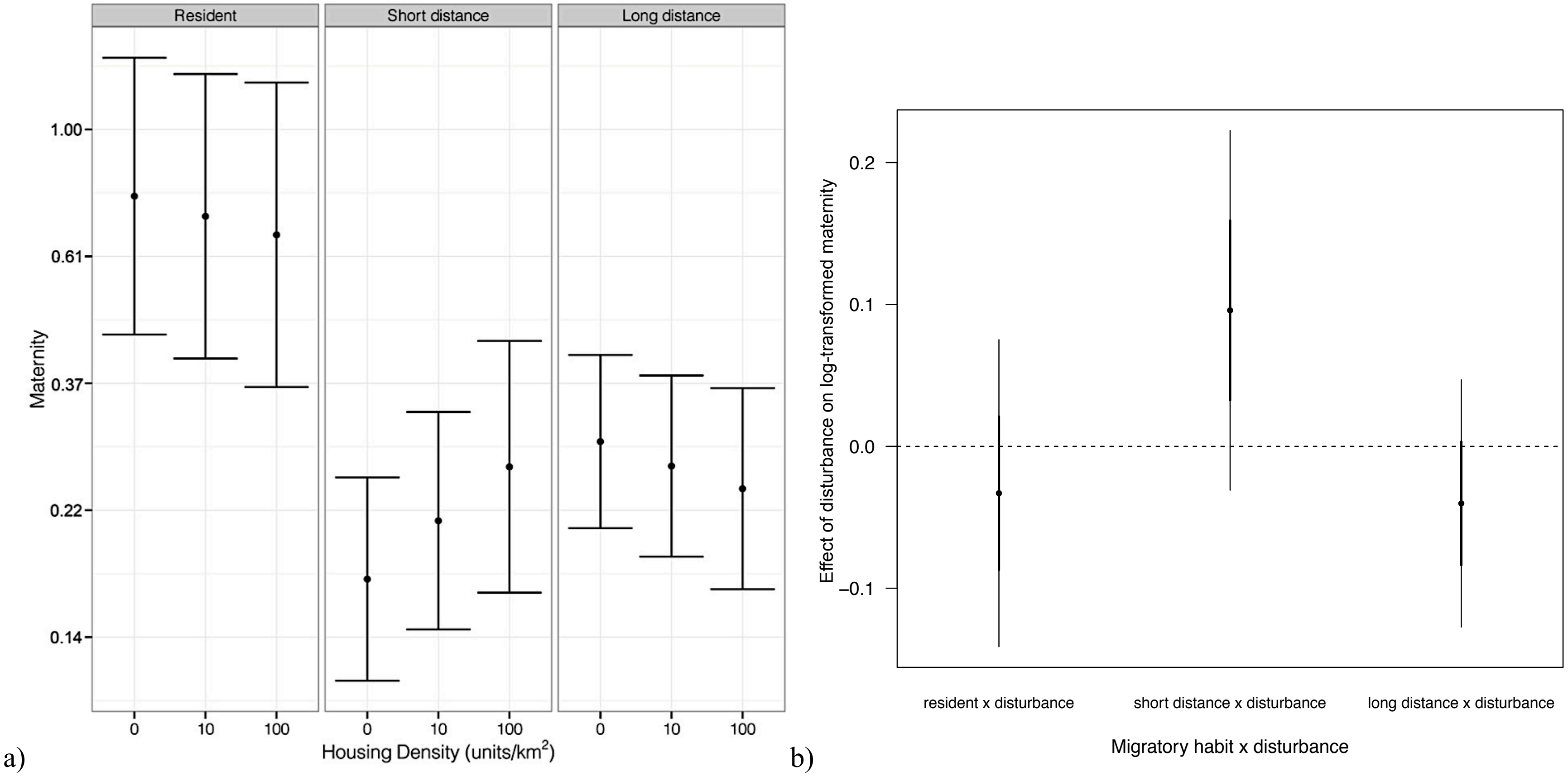


Figure 3.3. Mean and standard error of maternity by migratory strategy. a) At 0 housing units/km^2, residents had higher maternity than short-distance migrants (*t*=2.30). b) There was a difference between the positive effect of disturbance (housing density) on short-distance migrants, and the negative effect on long-distance migrants (*t*=2.25); there was a trend towards a positive effect of disturbance on maternity in short-distance migrants differing from the negative effect in residents (*t*=1.88).

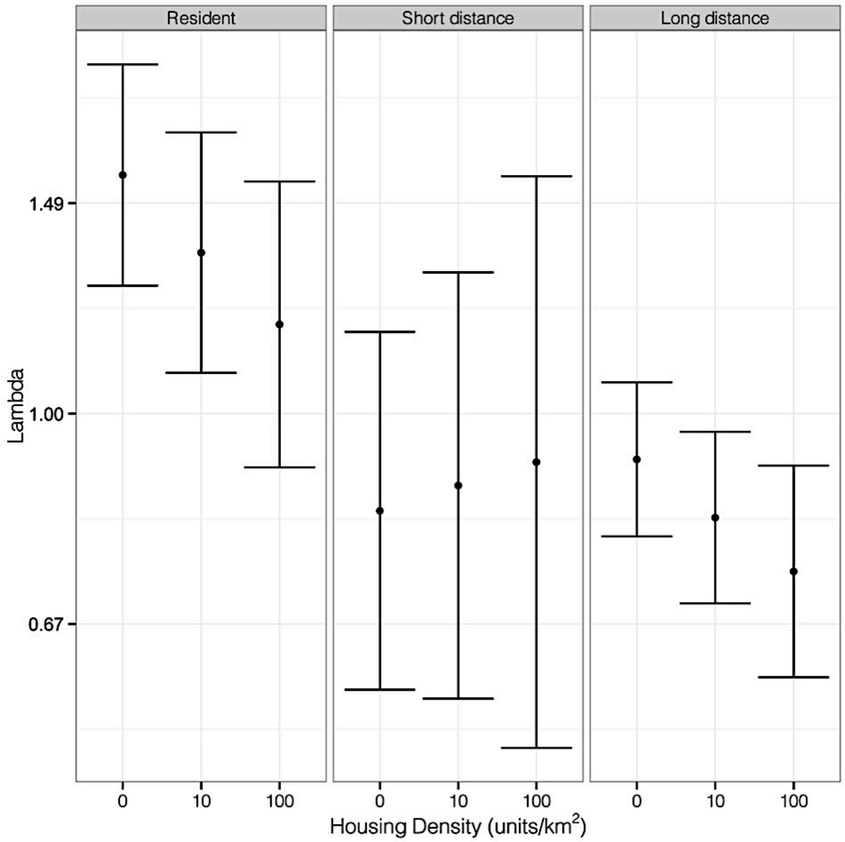
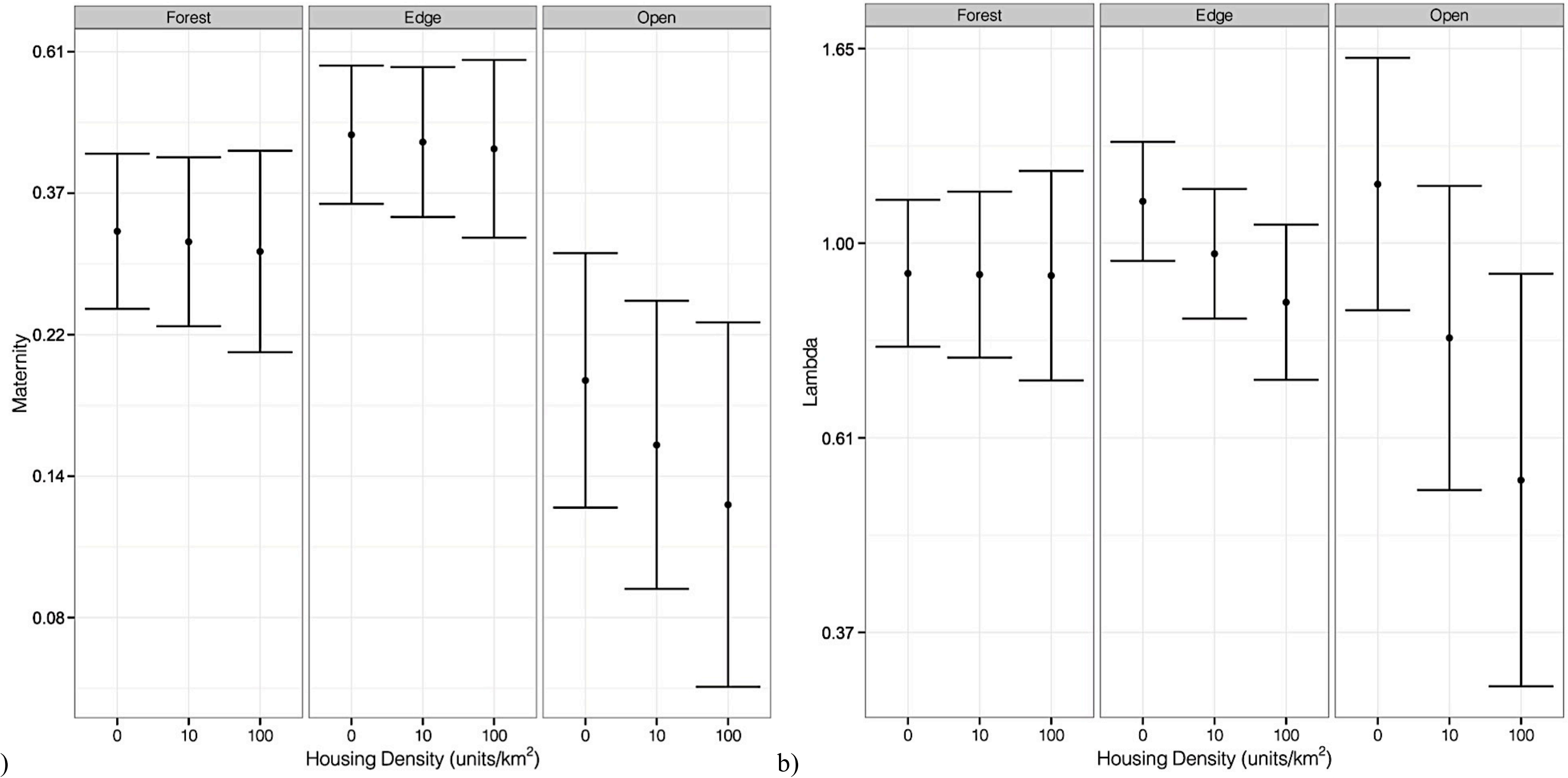


Figure 3.4. Mean and standard error of lambda by migratory strategy. At 0 housing units/km^2, residents had higher lambda than long-distance migrants (t=2.22).



a) b)

Figure 3.5. Mean and standard error of a) maternity and b) lambda by habitat preference. a) At 0 housing units/km^2, edge species trended toward having higher maternity than species preferring open habitat (t=1.98). b) There was a negative effect of housing density on lambda in edge species (t=2.03), and a trend towards a negative effect on lambda in species inhabiting open areas (t=1.81).

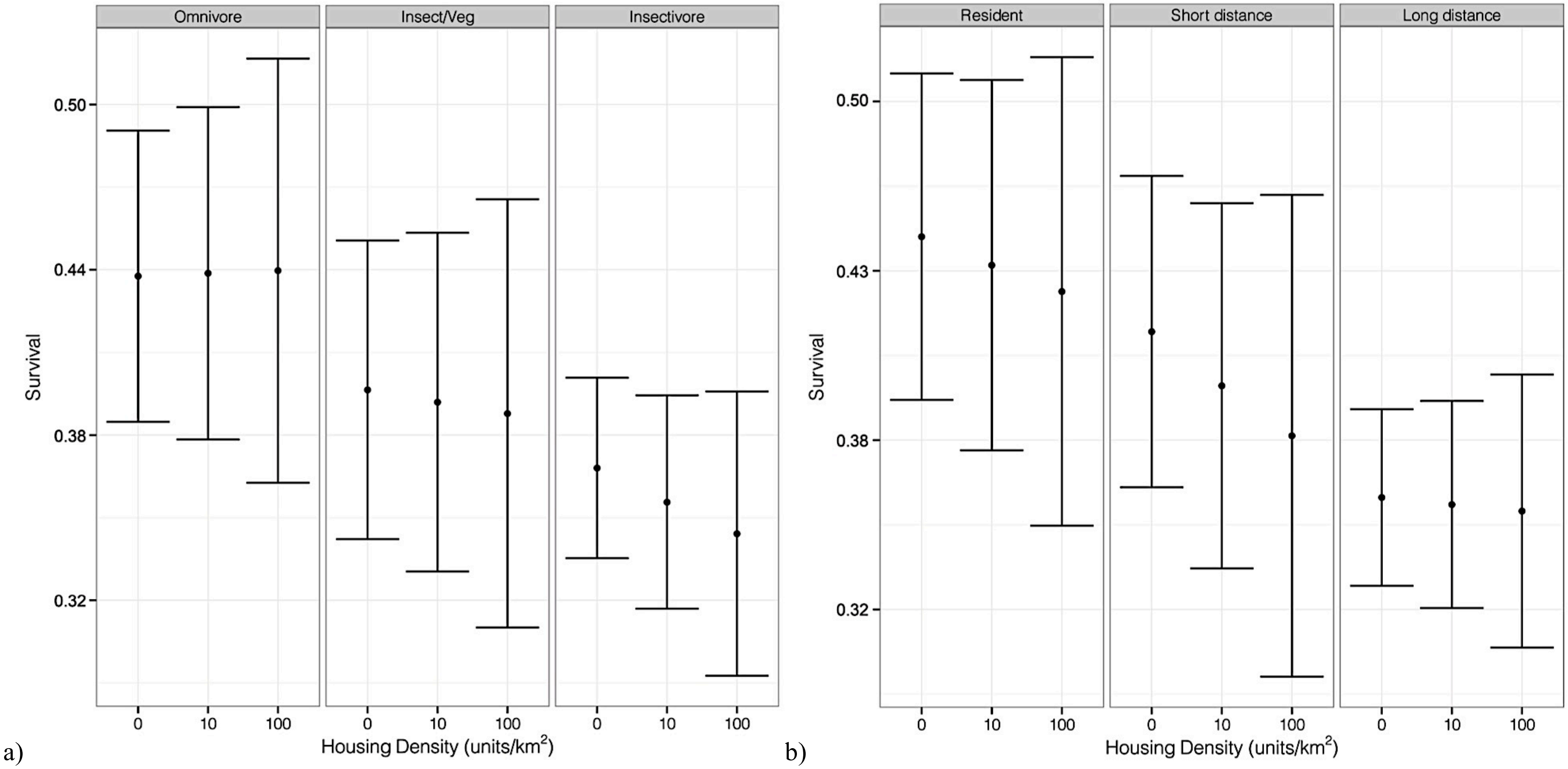


Figure 3.6. Mean and standard error of survival by a) food preference and b) migratory strategy. These relationships were not significant but were in the expected direction at all levels of housing density.

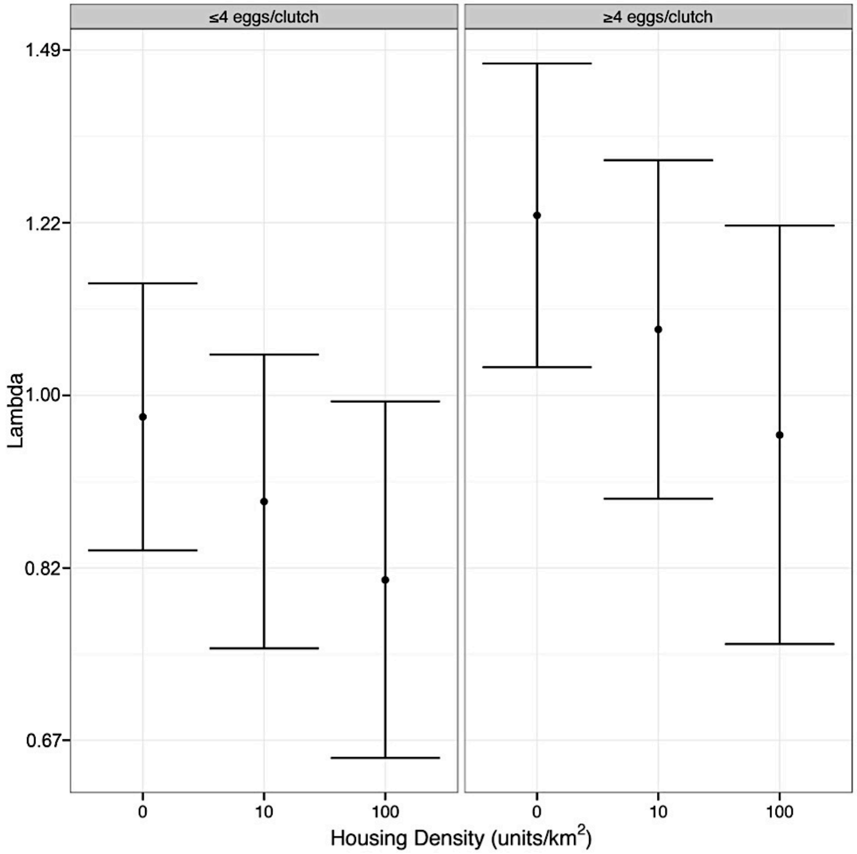


Figure 3.7. Mean and standard error of lambda by clutch size. These relationships were not significant but were in the expected direction where birds with larger clutches have higher lambda than birds with smaller clutches.

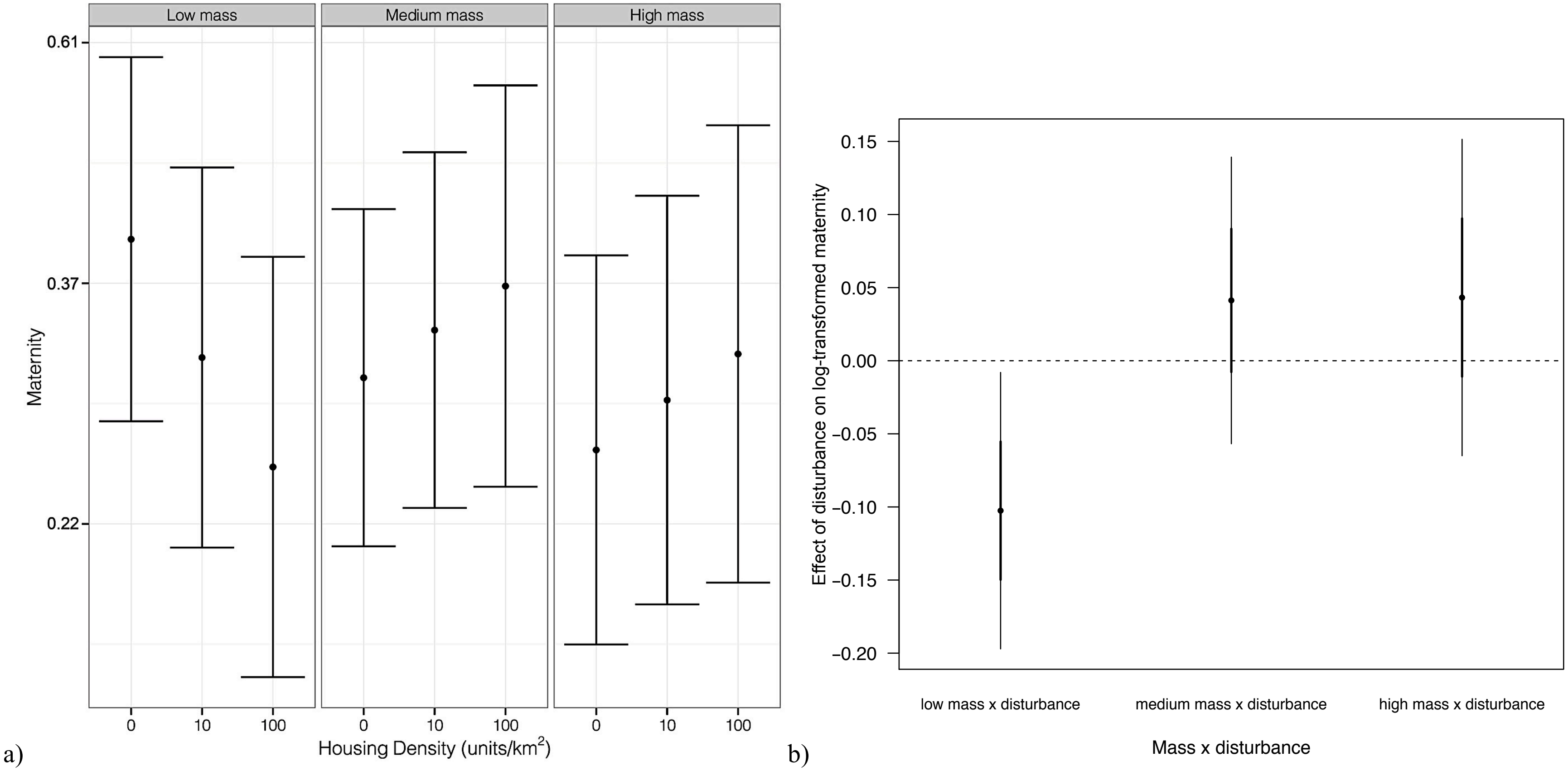


Figure 3.8. Mean and standard error of maternity by mass category. a) There was a negative effect of disturbance (housing density) on maternity in birds with the lowest masses (*t*=2.17). b) There was a difference between the negative effect of disturbance on birds with the lowest masses, and the positive effect on birds with medium (*t*=2.99) or high masses (t=2.69).

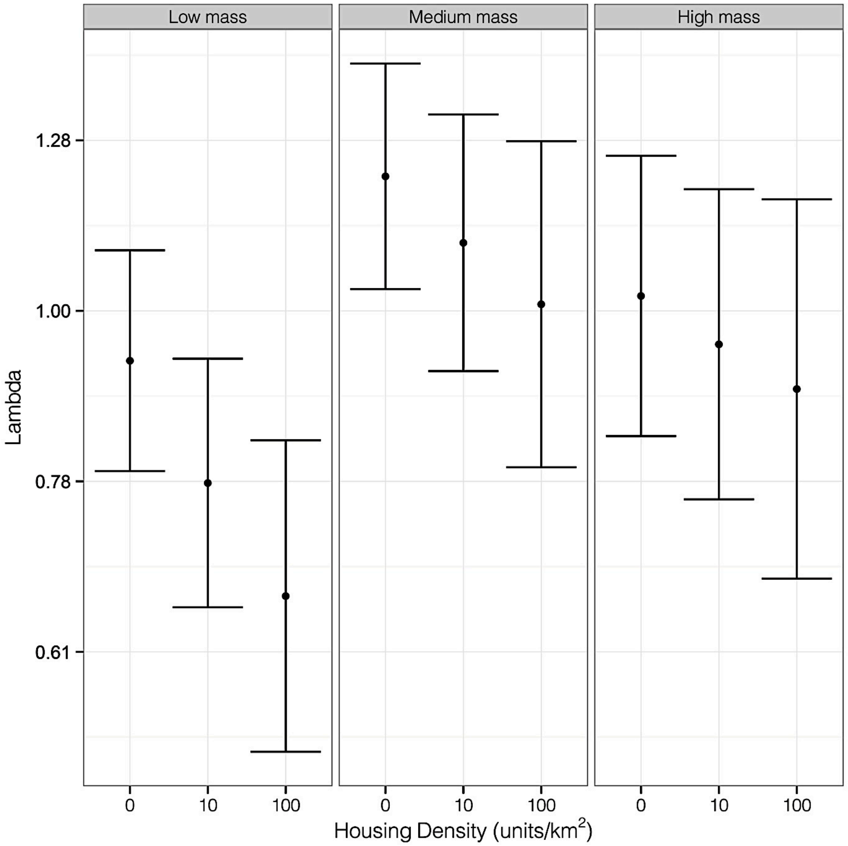


Figure 3.9. Mean and standard error of lambda by mass category. There was a negative effect of disturbance (housing density) on lambda in birds with the smallest masses (*t*=2.14).

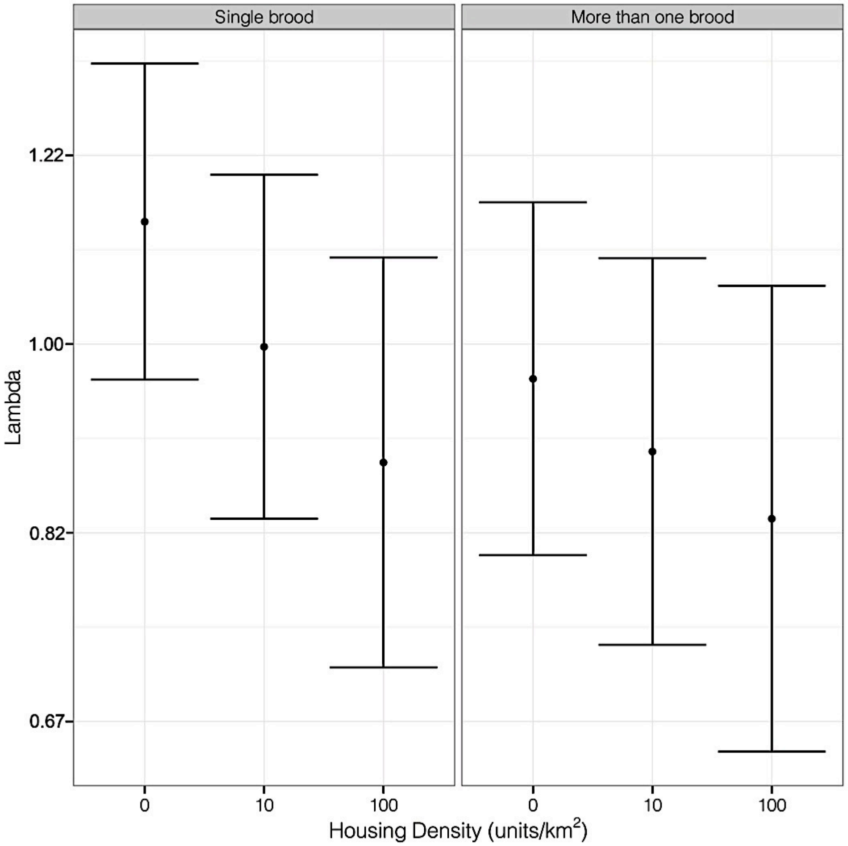


Figure 3.10. Mean and standard error of lambda by brood number. There was a trend towards a negative effect of housing density on lambda in birds with a single brood (*t*=1.84).

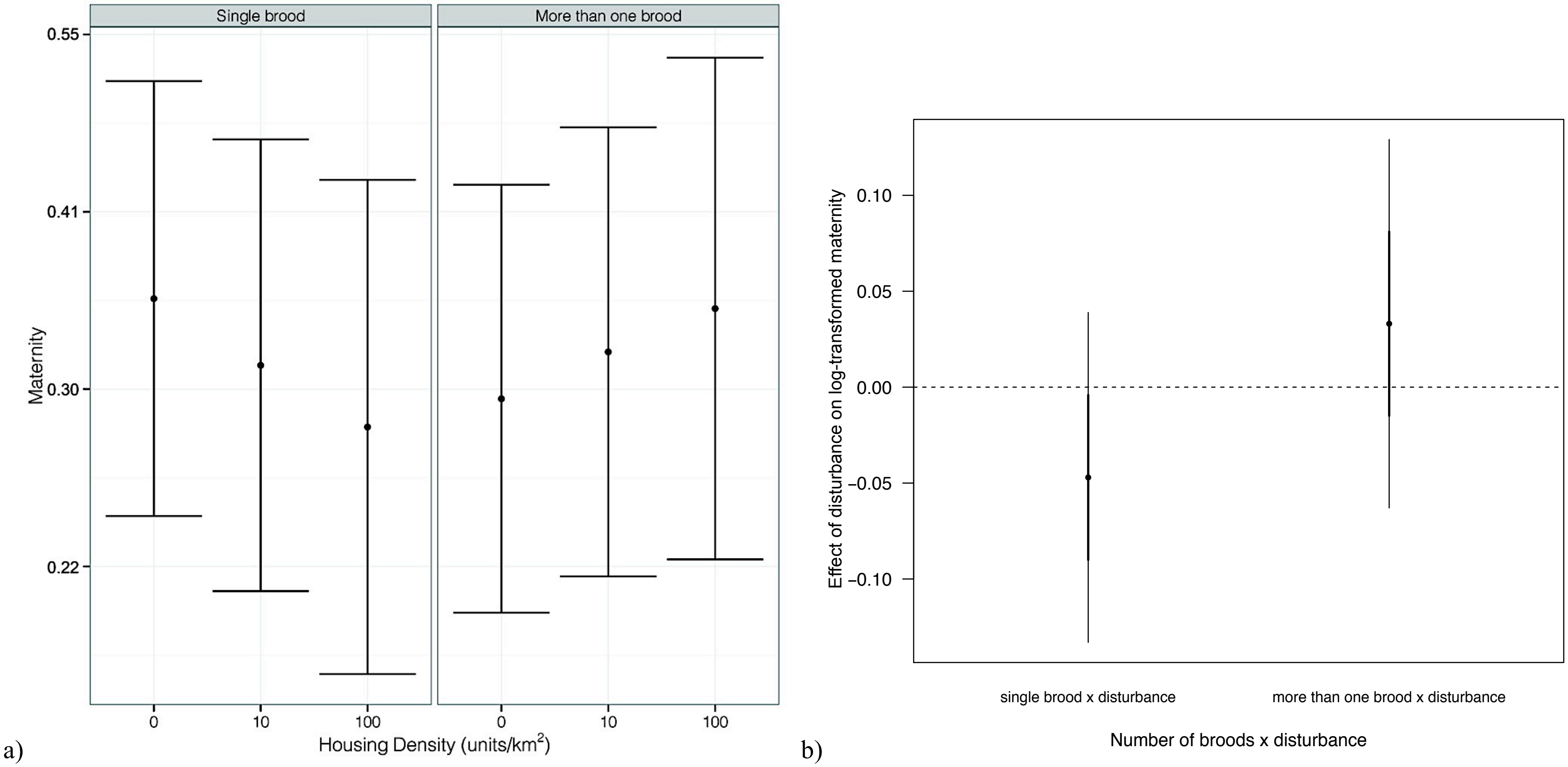


Figure 3.11. Mean and standard error of maternity by brood number. a) There was tendency for maternity in species with a single brood to decline with disturbance (housing density), and maternity in birds with more than one brood to increase. b) The difference in effect of disturbance on birds with a single brood versus more than one brood was nearly significant (*t*=1.85).

Chapter 4:
Invoking life history theory to understand species responses to human disturbance: Does disturbance mediate trade-offs?

Abstract

Human disturbance confers several threats to wildlife populations, such as altered food abundance and actual or perceived predation risk. These threats may increase costs of reproduction on survival or future reproduction, and alter trade-offs that occur in less-disturbed locations. Across 24 species in the northeastern United States, I tested for evidence of a trade-off between survival and reproduction, and determined if the direction of the relationship between survival and reproduction changed between less disturbed and more disturbed locations. Within each of these 24 species, I also tested for a trade-off between survival and reproduction across all locations, in only less disturbed locations, and in only more disturbed locations. Finally, I tested for a year-to-year trade-off within species between current reproduction and future survival, and between current reproduction and future reproduction, in all locations, and in only less disturbed or only more disturbed locations. Within species, I found no trade-offs, and I found a positive relationship between current and future reproduction. Across species, I observed a trade-off between survival and reproduction in all locations and in less disturbed locations, but this trade-off no longer occurred in more disturbed locations. The negative relationship between survival and reproduction across species was more strongly supported when body metrics were included in models, as the relationship between survival and reproduction became more negative, and there was a positive relationship between body size and survival. The lack of a trade-off between survival and reproduction across species likely reflects a highly variable and non-uniform response to human disturbance across species.

Introduction

The presence of trade-offs between energetically costly activities is a well-established aspect of life history theory. Trade-offs between current reproduction and future survival or future reproduction are among the most expected and well-studied examples in life history theory (Stearns 1989). While many studies have documented trade-offs in natural populations, including plants, fishes, amphibians and reptiles, mammals, insects, and birds (reviewed by Reznick 1985, Roff 1992, Stearns 1992), little is known about how human disturbance might influence these trade-offs. Human-disturbed areas present individuals and populations with unnatural or modified environments in which they may thrive, simply persist, or disappear. The challenges posed by human-disturbed regions include altered food abundance, altered predation rates and predator communities, diseases caused by crowding or novel exposure, and additional challenges to survival such as roads and buildings (e.g., Klem 1989, Lepczyk et al. 2004, Hotchkiss et al. 2005, Chace and Walsh 2006). The threats of these environments may put undue stress on already stressed individuals and populations. Disturbed environments could in such cases elicit a greater or more obvious cost of reproduction on survival or future reproduction relative to undisturbed habitats, if they present more stressful breeding conditions (Reznick 1985). Because life history trade-offs may be fundamentally important in directing species' population trajectories (Clark and Martin 2007), understanding how life history trade-offs are affected by disturbance is imperative to predicting how species will respond to future environmental change.

Trade-offs have been especially well studied in birds (e.g., Cody 1966, Martin 1995, Bennett and Owens 2002), making them an ideal group on which to focus questions in life history theory. As in other taxa, trade-offs in birds may be caused by a variety of factors, including food limitation, predation, and even disease. Species that evolve in food-limited environments may invest less in reproduction to secure their own survival, for instance by having fewer offspring or by having larger clutches but with lower quality eggs (Martin 1987). Predation may also play a major role in life history evolution (Lima and Dill 1990), and may be even more influential than food limitation in shaping life history strategies (Martin 1995, Ferretti et al. 2005). Life history differences between species in response to predation include variation in clutch size, number of brood attempts, and time spent in the nest (Cody 1966, Martin 1995), but may also evolve as differences in direct response to external stimuli. For example, species differ in the average distance at which individuals flee upon recognition of a potential threat, termed "flight-initiation distance" (FID; Ydenberg and Dill 1986, Blumstein et al. 2003). FID is correlated with body mass and age at first reproduction (Blumstein 2006), suggesting that variation in FID as a predator avoidance behavior could have evolved in concert with life history. Finally, there is a negative relationship between reproduction and immune function (Gustafsson et al. 1994, Hanssen et al. 2005), so species evolving in areas of high pathogen prevalence or diversity may have lower reproductive rates to maintain immune function and increase chances of survival. Species have evolved different behaviors and physiological traits to respond to challenges posed by environments, and these should be evident in comparisons of the relative trade-off between reproduction and survival across species.

At shorter scales than evolutionary time, environmental variation may also lead to differences in life history trade-offs between individuals or populations, both among and within species. These trade-offs may be manifest as overall differences in investment in survival or reproduction between environments, or as yearly differences within environments. For instance, across species, if predation risk is experimentally increased, parents may visit nests less often, and the extent of this effect varies with the direction of the threat (i.e., directed at parent versus offspring) and the species' overall investment in survival versus reproduction (Ghalambor and Martin 2001). Birds also respond to reduced levels of nest predation across breeding seasons by increasing egg mass and activities that improve female condition for future reproduction (Fontaine and Martin 2006). Costs of reproduction in stressful environments may compromise survival to the following year, whether mortality is caused from predation or from increased physiological stresses of reproduction, or may cause decreases in clutch size in subsequent years (Julliard et al. 1997, Doligez and Clobert 2003). However, there may be a threshold body condition only below which a trade-off is evident, such that birds that are already in lower condition are most vulnerable (Cichon et al. 1998, Descamps et al. 2009). Hence, the strength of the cost of reproduction on future reproduction and survival both within and across species may vary depending on the stresses of environment and individual measures of condition.

While a trade-off is always expected between energetically costly activities (Roff 1992), certain environments may make these more apparent. Given the many stresses imposed by human disturbances, one might predict a cost of reproduction to be more evident in disturbed environments. If the cost of reproduction is physiological, it may be associated with variation in body condition. This could be due to food-limitation, or mass-dependent risk of predation (Lima 1986, Witter and Cuthill 1993). If birds perceive human disturbance as predation risk (reviewed by Frid and Dill 2002), this may generate a cost of reproduction similar to that seen in response to predation. Several studies have shown that FID varies in response to human presence (Blumstein et al. 2005, Møller 2008, Valcarcel and Fernandez-Juricic 2009). However, some species do not seem to respond to human disturbance, possibly owing to having a "fast"-paced life history where reproduction is favored over parental survival (Bennett and Owens 2002, Bisson et al. 2009). If human disturbance mimics predation threat but does not have the same consequences for adult or juvenile mortality, then there may not be a cost of reproduction on survival or future reproduction. Individuals may instead adapt to human disturbance upon recognizing the level of threat, lowering the potential effect of disturbance on trade-offs (Møller 2008).

In this study, I evaluated the trade-off between reproduction and survival, and between current and future reproduction in populations of 24 bird species in the northeastern United States. I compared the overall presence or absence of a trade-off between reproduction and survival across all species and all locations, only more disturbed locations, only less disturbed locations. I included mean body mass, mean wing length, and an index of body condition as cofactors that may also influence rates of survival. I then looked within species for evidence of an overall tradeoff between survival and reproduction across locations, a temporal tradeoff between current reproduction and future survival, and a temporal tradeoff between current and future reproduction. This study is the first to my knowledge to compare life history phenomena across regions of human disturbance. Trade-offs between costly life history activities may influence overall population trends, hence understanding species responses to impacts of human disturbance in the context of life history may be useful in evaluating conservation and management decisions.

Methods

Bird banding data and locations

I obtained bird banding data from the Monitoring Avian Productivity and Survivorship (MAPS) program of the Institute for Bird Populations (Desante et al. 1995). MAPS banding locations are 20-hectare or larger areas typically located in wooded or semi-wooded areas, in which birds are captured in mist nets operated according to a standard-effort protocol (Desante et al. 2012). For every individual bird captured, these data include the date, capture location, a unique band number, body mass, wing length, age, sex, and breeding status. The data I obtained consisted of 98 banding locations in the northeastern United States sampled from 4-19 years between 1989-2007.

I checked the recorded latitude and longitude for each banding location using Google Earth (version 5.2, 2010), and verified locations based on the vegetation structure of the banding locations as recorded by the operators, and location names compared with similarly named landmarks (e.g., parks) on Google Earth. I moved locations of twelve of the 98 stations, all by less than one kilometer, for the following reasons. I have personally worked at two of these sites and so was aware of their exact location. The latitude/longitude coordinates of three sites were recorded as in water, and two were located on city streets. These latter five sites and three additional sites were all named based on their occurrence in national or state parks. I moved these sites within the boundaries of the parks to the closest area with vegetation consistent with that recorded by station operators (e.g., deciduous forest, as opposed to water or city streets). The coordinates of two additional sites were in fields adjacent to wooded areas, but the site operators had recorded these sites as being in wooded areas. I moved these two sites to occur just within the wooded area. I created a 1-km buffer around each location to further account for variation in GPS records, and to encompass variation in human development around locations. I combined locations situated less than 1-km apart in which buffers overlapped by more than 10%. Fifteen of the 98 stations were combined, 12 into pairs and 3 into one group. The focal species of this study occurred in 84 of the final locations.

Housing density data

I obtained United States housing density data for the year 2000 from the SILVIS laboratory of the University of Wisconsin (http://silvis.forest.wisc.edu/). The spatial resolution of these data ranges from 1.80 to 3.93 km^2 (Hammer et al. 2004). The 1-km buffer encompassing a single MAPS banding site may encompass more than one partial block group, the unit within which housing density is estimated from census data. Therefore, I calculated a weighted average of housing density based on the proportion of each location's buffer that fell within each partial block group. To calculate the weighted average, I converted the buffer polygon for each station to a point-shapefile, and extracted the values of the housing density layer to the buffer points. I assumed a high correlation between housing density and human population (Lepczyk et al. 2008), and so did not use population census data. I divided locations into less and more disturbed categories following the classifications of Thorington and Bowman (2003) wherby low density housing has <20 houses/40 hectare, and high density housing has >40 houses/40 hectare. These correspond to locations with <50 housing units/km^2 and locations with >100 housing units/km^2 as less and more disturbed, respectively. For all analyses, I looked for evidence of trade-offs across all locations, using only locations with <50 housing units/km^2, and using only locations >100 housing units/km^2.

Phylogenetic data

I obtained published phylogenies of 24 focal species from Jonsson and Fjeldsa (2006), and Lovette et al. (2010). I combined these phylogenies to build a phylogenetic tree using Mesquite, version 2.74 (Maddison and Maddison 2010; Figure 4.2). I specified ultrametric branch lengths, which assume equal time along branch lengths to a common ancestor, or a molecular clock (e.g., following Lee et al. 2008).

Parameter estimates

Prior to estimating survival, I deleted unbanded individuals and those recorded as dead or injured from the database of individual capture histories, because these individuals were not likely to be recaptured at later time periods. I only considered species that had at least 300 individual capture histories total, and I did not include data from locations that did not have at least one recapture record during the years of monitoring, resulting in the species analyzed here.

I estimated apparent survival for adult birds using the Cormack-Jolly-Seber (CJS) model in Program MARK (White and Burnham 1999). Survival estimates are 'apparent' because survival rates include lack of return to a location due to death or due to dispersal. The CJS model in Program MARK yields parameters estimates for both apparent survival and recapture by breaking each capture history into an overall probability of survival and recapture, and evaluating the probabilities and their frequency across all capture histories using maximum likelihood. The survival and recapture parameters can each be estimated by time, by group (i.e., by year or location for these analyses), or as a constant, single value. Program MARK provides an Akaike Information Criterion (AIC) value for each CJS model, which varies depending on how each parameter is estimated. The Akaike's Information Criterion varies as a function of the model likelihood and the number of parameters in the model, whereby each additional parameter is penalized by +2.

For each species, I estimated survival in three ways: 1) as a constant, single value aggregating all captures across locations, 2) a value for each location, and 3) a yearly value aggregating captures across locations. For the constant single value and the yearly values, I estimated these values across all locations, using capture histories from only less disturbed locations, and using capture histories from only more disturbed locations. In all methods of estimating survival, I allowed recapture to vary by both location and as a constant (a single overall value for all locations, expected if banding is based on a sampling-wide constant-effort protocol), and chose the survival estimates from the CJS model with the lowest AIC. This allowed me to account for some variation in recapture rates between locations, e.g., if recapture differs greatly between locations due to differences in effort or vegetation structure, then these will be accounted for in survival estimates.

I used maternity as a measure of reproduction for each species at each location. Maternity is the proportion of juveniles to adults for a given age class, and here represents a "post-breeding" census because the juveniles are counted in the same year that they were born (Akçakaya et al. 1999). For each species at each location, I defined maternity as

$$\frac{f_1 + f_2 + f_3 + \ldots f_n}{N_1 + N_2 + N_3 + \ldots N_n}$$

where *f* is the number of juveniles captured in years 1 to *n*, and *N* is the number of adults captured in years 1 to *n*. This estimate of maternity is a weighted average (maternity, *f*/*N*, weighted by sample size, N, for each year), and thus takes into account variation in effort (as measured by sample size) across time steps, such that estimates of maternity from years with small N contribute less to the time-averaged maternity estimates (H. R. Akçakaya, *pers. comm*).

For each species, I estimated maternity in three ways: 1) a single value for each species across all locations, across only less disturbed locations, and across only more disturbed locations, 2) a value for each location at which each species was present, and 3) a yearly value for each species across all locations, in less disturbed locations, and in more disturbed locations.

Body metrics

I expected that differences in trade-offs between more and less disturbed locations might be associated with differences in body metrics or body condition. To investigate this effect and control for confounding effects of body metrics on the relationship between life history parameters, I included body metrics in regression models (e.g., following Barton and Capellini 2011). I estimated the mean and variance of mass and wing length for all captured individuals of each species 1) across all locations, 2) across locations with <50 housing units/km^2, 3) across locations with >100 housing units/km^2, and 4) within locations. I checked individual values of mass and wing length and included only those that fell within a reasonable range of values obtained from Pyle's Identification Guide to North American Birds (Pyle 1997), the CRC Handbook of Avian Masses (Dunning 1993), or values found in the Birds of North America (Poole 2005) for each species. Using the individual mass and wing length values for all species across all locations, I also estimated an index of body condition. Condition indices are sometimes preferred to measures of body mass alone because they scale mass to body size, effectively separating the components of mass reflecting overall condition from mass due to structural body size (Green 2001). I followed the suggested method of Peig and Green (2009), where the condition index C_i for any individual is

$$C_i = M_i \left[\frac{L_0}{L_i}\right]^{b_{OLS}/r}$$

and where M_i and L_i are respectively the mass and wing length of the individual, L_0 is the mean wing length across all individuals, b_{OLS} is the slope of the ordinary least squares regression of all log-transformed masses against all log-transformed wing lengths, and r is the correlation coefficient of the relationship between wing length and mass. Within locations, I averaged individual condition indices for each species. This condition index relies on a strong correlation between wing length and mass. Due to individual variation within species, the relationship between wing length and mass was not always strong within species, but across all individuals of all species, the two values were highly correlated (Figure 4.1). Therefore, I did not create a condition index for within species analyses or analyses where each species needed a unique value, only for inclusion in cross species analysis (see mixed-effects models below). Some authors have suggested that condition indices are not always better than mass (Schamber et al. 2009), so omission of the condition index from the other analyses does not diminish the value of mass and wing length as potential indicators of processes occurring across locations.

Statistical analyses

1) Tradeoffs across species

To look for evidence of an overall tradeoff between reproduction and survival, I used phylogenetic regression and mixed-effects models. I used phylogenetic regression to account for species relatedness. This is important because if species are more related than expected by chance, then values used in the regression of maternity on survival for each species are not independent data points, and would violate the assumptions of regression. However, the phylogenetic models employed here necessitate a single value of survival and maternity for each species, limiting sample size and potentially masking variation across locations that might reveal an effect of disturbance on trade-offs. I used mixed-effects models because these allowed me to incorporate a value of maternity and survival for all species at all locations the species was present, and account for variation due to repeated measures within species or within locations by holding species and location as random factors. This resulted in a much larger data set from which to evaluate the across species relationship between survival and maternity. Given that error is expected in measures of both reproduction and survival, I confirmed results with a standardized major axis estimation using the species averages for both values across sites.

For phylogenetic regressions, I estimated a single value of survival and maternity for each species, aggregating individual capture histories 1) across all locations, 2) in only less disturbed locations, and 3) in only more disturbed locations. I ran phylogenetic regressions in R, version 2.15.0, using the package 'caper' (Orme et al. 2012, R Development Core Team 2012). I specified maximum likelihood to estimate phylogenetic signal (Pagel's λ) in models. I compared the estimated value of λ to 0 (no phylogenetic signal) and 1 (a Brownian motion model of trait evolution) using a likelihood ratio test (implemented in Orme et al. 2012, see also Nunn 2011). Sample sizes of <30 species for estimating λ may lead to uncertainty in maximum likelihood estimates (Nunn 2011). Therefore, when the maximum likelihood estimate of λ was 0 in the initial models with only survival and maternity, I compared model results to models setting λ to 1, and vice versa. I regressed survival against maternity alone, and then in models including mean or variance of body mass and wing length in models. I log-transformed body mass and wing length, and checked all model residuals and bivariate plots for normality. I compared models with and without body metrics using likelihood ratio tests in the R package 'lmtest' (Zeileis and Hothorn 2002). Finally, I regressed body metrics against maternity to check for a confounding effect of mass or wing length on maternity that could drive the relationship between maternity and survival.

Using mixed-effects models, I again evaluated the relationship between all values of survival and maternity 1) in all locations, 2) in only less disturbed locations, and 3) in only more disturbed locations. Rather than aggregating capture histories for each species across all locations as for the phylogenetic regressions, I estimated a value of survival and reproduction for each species from capture histories within each location. Mixed-effects models allow potentially non-independent data points to be pooled by accounting for factors contributing to variation due to non-independence (random effects), while separately modeling factors being directly tested in the model (fixed effects). I treated species identity, family, and location as random factors that may contribute to variation in demographic parameters. Including these as random effects allowed pooling of data points, even if they were collected at the same location, belonged to the same species, or belonged to the same family, the latter of which may capture the influence phylogenetic similarity in responses. This larger data set of 600 data points has greater statistical power than the 24 values tested above which are aggregated across locations for each species. I used data that had associated body mass and wing length (N=500) to estimate the influence of mean and variance of body mass and wing length, and a condition index, on the relationship between reproduction and survival. I log-transformed body metrics and maternity, and logit-transformed survival in all models. I assumed a t-value of ≥2.00 in models as significant (Gelman and Hill 2006). I compared models that included mass, wing length, or body condition data using AIC values. I again separately regressed maternity on body metrics to check for a confounding effect of mass, wing length or body condition on maternity that could drive the relationship with survival. In regressing maternity on body metrics, I used values for all individuals across all locations in mixed-effects models, and treated species, location, and sex as random factors. I ran mixed-effects models in the R package 'lme4' (Bates et al. 2011).

Because error occurs in both maternity and survival, I confirmed the direction of the slopes of the above regressions using standardized major axis fit in the R package 'smatr' (Warton et al. 2012).

2) Tradeoffs within species

Within species, I tested for evidence of a trade-off between maternity and survival across locations, between overall maternity in year n and survival in year n+1 across time, and between overall maternity in year n and maternity in year n+1 across time. To test for evidence of a tradeoff between maternity and survival within species across locations, I estimated the correlation between maternity and survival values estimated using: 1) all locations, 2) only less disturbed locations, and 3) only more disturbed locations. I only included species that had maternity and survival estimates for >5 locations.

To evaluate the relationship between maternity in year n and survival to year n+1 for each species, I used yearly values of maternity and survival estimated: 1) in all locations, 2) in only less disturbed locations, and 3) in only more disturbed locations. Prior to estimating the relationship between maternity and survival, I removed the temporal trend from these two parameters. I used two general methods for removing a temporal trend, differencing and detrending. Both methods have advantages and disadvantages depending on the underlying stochastic process of the data (Chan et al. 1977, Yue and Pilon 2003), and can yield different results (Shumway and Stoffer 2006). Differencing is sometimes preferred because it does not require estimation of additional parameters (Shumway and Stoffer 2006, Montgomery et al. 2008). However, differencing reduces the number of observations, and requires consecutive observations (i.e., missing data in either maternity or survival will further reduce the number of observations, especially if missing from different years). For the differencing approach, I subtracted the values for year $n+1$ from year n for both survival and maternity, and estimated the correlation between the differenced values (Shumway and Stoffer 2006, Montgomery et al. 2008). To detrend the data, I regressed both survival and maternity against time, and estimated the correlation between the residuals of regressions of survival against time and maternity against time (Shumway and Stoffer 2006, Montgomery et al. 2008).

I evaluated the temporal relationship between maternity in year n and maternity in year $n+1$ by estimating the correlation between these values from: 1) in all locations, 2) in only less disturbed locations, and 3) in only more disturbed locations.

Because within species analyses were performed on multiple species, I calculated the probability of significance (at level $\propto$) being obtained by chance K times out of N tests using a Bernoulli process, whereby $p=[N!(N-K)!K!] \times \propto^{K}(1-\propto)^{N-K}$ (Moran 2003).

Results

1) Trade-offs across species

Phylogenetic regression

When estimated across all locations, there was a negative relationship between survival and maternity across species (p=0.050, r^2=0.096; Table 4.1; Figure 4.3). The maximum likelihood estimate of Pagel's λ indicated no phylogenetic signal in the data (λ = 0), but was not significantly different from λ = 1 (a Brownian motion model of trait evolution). When Brownian motion was assumed (λ set to 1), the relationship between reproduction and survival was more strongly negative (p<0.001, r^2=0.344; Table 4.1; Figure 4.3). Considering locations with <50 housing units/km^2, the relationship between maternity and survival again revealed negative trend (Table 4.1; Figure 4.4). The maximum likelihood estimate of λ was again 0, and not significantly different from λ = 1. Considering a Brownian motion model of trait evolution led to a more strongly negative relationship between maternity and survival (p<0.001, r^2=0.302; Table 4.1; Figure 4.4). In locations with >100 housing units/km^2, there was no relationship between maternity and survival (Table 4.1; Figure 4.5). The maximum likelihood estimate of λ was 0.912, indicating phylogenetic signal in the data, and differed from λ = 0 (p=0.049). Considering a model where λ = 0, there was still no relationship.

The direction of the change in survival and maternity from less to more and disturbed locations differs across species (Figure 4.6). Some species appear to shift either survival or reproduction in response to disturbance to experience the same tradeoff as in less disturbed locations. Some species appear to be released from the tradeoff and increase in both survival and reproduction, and vice versa. Some experience a decline in one parameter but not the other, but are not shifted along the original slope of the survival-reproduction continuum.

Using data from all locations and a maximum likelihood estimate of λ, adding mean body mass or mean wing length explained more of the variance in survival (mean mass: p=0.030, r^2=0.185, λ = 0.55; mean wing length: p=0.009, r^2=0.259, λ = 0.489; Table 4.1). However, the

χ^2-values from the likelihood ratio test indicated that these models were not better than the model with maternity alone. In locations with <50 housing units/km^2, adding mean wing led explained more of the variance in survival ($p=0.024$, $r^2=0.199$, $\lambda = 0.523$; Table 4.1), although the χ^2-value from the likelihood ratio test again indicated that this model was not better than the model with maternity alone. In locations with >100 housing units/km^2, adding mean or variance of body mass or mean wing length did not improve models. Mean or variance of body metrics alone did not predict maternity.

Mixed-effects models

The direction of the relationship between maternity and survival using mixed-effects models was consistent with the direction of the relationships found in the phylogenetic regression. Across all locations and species, the relationship between maternity and survival showed a negative trend ($N=600$, $t=-1.64$; Figure 7; Table 4.2). The relationship was the same in locations with <50 housing units/km^2 ($N=433$, $t=-1.64$; Figure 4.7). There was no relationship between maternity and survival when considering only locations with >100 housing units/km^2 (Table 4.2; Figure 4.7).

Across all locations, models that included variance in body mass, wing length, or body condition had the lowest AIC values, though the *t*-value of maternity was not significant (Table 4.2). In locations with <50 housing units/km^2, including variance in mass yielded the lowest AIC value, and both maternity and mass predicted survival ($t_{\text{maternity}}=-2.01$, $t_{\text{mass}}=2.30$; Table 4.2). Maternity also predicted survival in a model including variance in body condition ($t_{\text{maternity}}=-2.04$; Table 4.2). Considering only locations with >100 housing units/km^2, models with maternity alone and models including mean mass, mean body condition, or variance in wing length had the lowest AIC values, but maternity did not predict survival in any model (Table 4.2).

Standardized major axis fit

The standardized major axis estimation confirmed the above trends of a negative relationship between survival and reproduction across all locations and in less disturbed locations. The trend in more disturbed locations was more positive with the standardized major axis fit (Figure 4.8).

2) Trade-offs within species

Across locations

House wren had a positive relationship between maternity and survival across all locations ($p=0.025$, $r=0.731$, $n=9$) and in locations with <50 housing units/km^2 ($p=0.010$, $r=0.833$, $n=8$). In locations with >100 housing units/km^2, no species showed a relationship. The probability of a single species having a relationship at the 0.05 significance level by chance alone was 0.369.

Temporal relationship between reproduction and survival

Only three species showed any relationship between current reproduction and future survival. Across all locations when differencing was used to remove within parameter temporal trends, Black-capped chickadee had a positive relationship between current reproduction and future survival ($p=0.019$, $r=0.579$, $n=16$). In disturbed locations when differencing was used to remove within parameter temporal trends, Ovenbird had a positive relationship between current reproduction and future survival ($p=0.001$, $r=0.739$, $n=16$). In disturbed locations when detrending was used to remove within parameter temporal trends, Gray catbird had a negative relationship between current reproduction and future ($p=0.047$, $r=-0.488$, $n=17$). The probability of three species having a relationship at the 0.05 significance level by chance alone was 0.086.

Temporal correlation in year-to-year reproduction

Nine species had a positive relationship between current and future maternity (Figure 9). The probability of nine species having a relationship at the 0.05 significance level by chance was 0.000001. Estimated across all locations and all species, maternity showed a significant, positive temporal correlation in eight species (Black-capped chickadee: $p=0.014$, $r=0.556$, $n=18$; Common yellowthroat: $p=0.002$, $r=0.691$, $n=17$; Gray catbird: $p=0.007$, $r=0.629$, $n=17$; Hermit thrush: $p=0.040$, $r=0.487$, $n=18$; Song Sparrow: $p=0.015$, $r=0.576$, $n=17$; Traill's flycatcher: $p=0.018$, $r=0.565$, $n=17$; Veery: $p=0.018$, $r=0.548$, $n=18$; Yellow warbler: $p=0.016$, $r=0.572$, $n=17$). The probability of eight species having a relationship at the 0.05 significance level by chance alone was 0.00001.

Estimated across only locations with <50 housing units/km^2 and all species, five species had a positive temporal correlation in maternity (Black-capped chickadee: $p=0.032$, $r=0.506$, $n=18$; Common yellowthroat: $p=0.005$, $r=0.651$, $n=17$; Song Sparrow: $p=0.010$, $r=0.606$, $n=17$; Traill's flycatcher: $p=0.046$, $r=0.490$, $n=17$; Yellow warbler: $p=0.004$, $r=0.665$, $n=17$). The probability of a five species having a relationship at the 0.05 significance level by chance alone was 0.005.

In locations with >100 housing units/km^2, two species had a positive temporal correlation in maternity (Gray catbird: $p=0.002$, $r=0.687$, $n=17$; Ovenbird: $p=0.027$, $r=0.535$, $n=17$). The probability of two species (out of 23) having a relationship at the 0.05 significance level by chance alone was 0.215.

Discussion

Trade-offs have been found in multiple taxa, and mechanisms behind these tradeoffs are a continuing focus of research (e.g., Harshman and Zera 2007, Monaghan et al. 2009, Hau et al. 2010, Travers et al. 2010, Pryke et al. 2012). While environmental heterogeneity is integrated into the foundation of life history theory (Kawecki and Stearns 1993), how trade-offs are influenced by human-disturbance has yet to be investigated. My findings suggest that the novel environments resulting from human disturbance may vary in their impact on species and potentially alter expected trade-offs. As expected from life history theory, I found support for the trade-off between survival and reproduction when all locations were included in analyses. However, separating the less and more disturbed locations, a negative trend remained only across the less disturbed locations. No trade-off was observed in more disturbed locations. The lack of a relationship between survival and reproduction in the more disturbed locations raises numerous questions regarding species' responses and the potential for adaptation to human disturbance.

Several lines of evidence support the trade-offs between survival and reproduction found in this study. The negative trend across all locations and in less disturbed locations was consistent across phylogenetic regressions, mixed-effects models, and using a standardized major axis fit, confirming the robustness of this result to the method and scale at which the data were aggregated. These patterns were further supported when body metrics were included in models. Including body metrics explained more of the variance in survival, and yielded the expected negative relationship between survival and reproduction, and positive relationship between survival and body size. The presence of this trade-off across species is consistent with a large empirical body of literature, for both birds and other taxa (e.g., Stearns 1989, Roff 1992, Martin et al. 1995, Ghalambor and Martin 2001).

The trade-off between survival and reproduction across species was not observed in disturbed environments, and likely reflects differences in species' responses to human disturbance. Some species may have more flexibility to adapt, some may be released from environmental pressures upon entering more disturbed areas, and some species may incur greater threats to survival, reproduction, or both. If factors known to drive life history evolution in birds, such as nest predation or food limitation (Martin 1987, Martin 1995, Ghalambor and Martin 2001), are altered in disturbed environments, then the relationship between survival and reproduction may no longer be observable across species. Some species may have enough phenotypic plasticity to respond to human disturbances or may be able to evolve quickly to new environments (e.g., Diamond 1986, Møller 2008). In these cases, the species' location along the survival-reproduction life history continuum may shift and the trade-off will not be altered. Other species may benefit from supplemental feeding by humans (Robb et al. 2008a, 2008b), or a potential reduction in predation risk (Shochat et al. 2006, Newhouse et al. 2008, Fischer et al. 2012, but see Lepczyk et al. 2004, Beckerman et al. 2007, van Heezik et al. 2010), and no longer experience a trade-off. Lastly, some species may be unable to adjust their reproduction or survival in response to novel threats imposed by human-disturbed, and may be of particular conservation concern. The lack of a relationship between survival and reproduction across species in more disturbed locations may be temporary, and over a longer period of time as species come to equilibrium with their environment (Bell 1980), a trade off between survival and reproduction may become apparent. Given the data at hand, it is not possible to distinguish between these, and perhaps additional explanations for the lack of a relationship in more disturbed locations. However, regardless of the mechanism, the change in this well-supported life history trade-off with human disturbance begs further investigation.

I did not find the expected relationship between survival and reproduction within species across locations or across time. Finding no relationship between life history parameters within populations using data from observational studies is far from uncommon (Van Noordwijk and Dejong 1986, Stearns 1992). The simplest explanation for the lack of this relationship within species is that too much variation exists between individuals within populations, and not enough variation among populations (i.e., locations) or across time. This variation may be caused by the fact that volunteers sampled the data across a large geographic region. Nonetheless, the lack of a relationship between reproduction and survival could also have a biological explanation, though additional data would be required to evaluate different alternatives. First, because birds must procure a certain level of reserves before they will breed, a physiological trade-off due to food limitation may not be apparent (Drent and Dann 1980, Stearns 1992). If only physiologically fit individuals reach breeding condition, any cost of reproduction on survival in breeding individuals may not be distinguishable from non-breeding individuals which could have decreased survival because they already have lower body condition. Second, all individuals may not reproduce with equal effort each year. For instance, an individual with high reproductive success in a previous breeding attempt may have low success in the current attempt, and vice versa. The temporal mismatch in successful breeding attempts across individuals in a population could average out across individuals, resulting in no relationship between survival and reproduction at the population level.

Although the expected life history trade-offs between survival and reproduction were not found at the population level, a positive relationship between current and future reproduction was detected. A positive relationship in productivity across years may be a result of site fidelity, if individuals to return to sites where productivity is high (Haas 1998). The relationship could also reflect broader climatic trends that lead to higher productivity across years with similar environmental conditions. In addition, years with more individuals born into the broader population would be followed by years with more individuals breeding, not accounting for effects of density dependence and competition. Further investigation of these positive relationships in a few species with high abundance and recapture rates across time and within sites of varying degrees of disturbance may uncover more informative results. Documenting relationships within a few species would not yield general evidence of effects of human disturbance on life history trade-offs, but would begin to illuminate the potential effect of disturbance on this trade-off.

The relationships between reproduction and survival or between current and future reproduction found in this study are meaningful in light of the fact that a cost of reproduction may be difficult to detect in observational studies (Roff 1992). Detecting trade-offs in natural populations can generate and refute hypotheses regarding factors affecting populations, and may improve our understanding of species responses to human disturbance. Life history theory is a classic subject in ecology and evolutionary biology, but theories have largely been developed through study of wild populations, assuming constant environments or natural disturbances. Some have argued that classic ecological theories can be used to understand processes occurring in urban areas (Niemelä 1999), while others argue for a theory of urban ecology (Pickett et al. 2008). As these urban theories begin to emerge (Mugerauer 2010), life history should be included as an important evolutionary driver of responses to humans, and the patterns revealed may be explainable using classic life history theory. Given that urbanization and deforestation are huge threats worldwide, understanding differences in trade-offs in response to human disturbance in species with very different life histories may allow better prediction of species vulnerability. Life history theory and exploration of trade-offs in urbanizing environments presents a wide-open field for investigation with a strong foundation in the classic literature, and many questions left unanswered.

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Table 4.1. Statistics for phylogenetic regressions of survival on maternity. Models include maternity alone as a predictor variable, and maternity plus body metrics. In models with maternity alone, maximum likelihood was used to estimate phylogenetic signal (λ_{ML}), then λ was set to 0 or 1 (depending on which was most different from the λ_{ML} estimate) to obtain the range of possible relationships between maternity and survival, given small sample size (N<30). Models with body metrics used a maximum likelihood estimate of λ.

Location	**Parameter**	**Maternity alone** (λ_{ML})	**Maternity + mean mass**	**Maternity + mean wing**	**Maternity + var. mass**	**Maternity + var. wing**	**Maternity alone** (λ=1 or 0)
All (N=24)	Maternity: t (p-value)	-1.86 (0.077)•	-2.26 (0.035)*	-2.08 (0.050)*	-1.83 (0.086)•	-1.70 (0.10)	-3.61(0.002)*
	λ	λ_{ML}=0	λ_{ML}=0.553	λ_{ML}=0.489	λ_{ML}=0	λ_{ML}=0	1
	p-value λ=0, λ=1	1, 0.127	1, 0.138	0.545, 0.072•	1, 0.105	1, 0.113	–
	log(body mass): t (p-value)	–	1.42 (0.168)	–	0.884 (0.387)	–	–
	log(wing length): t (p-value)	–	–	2.13 (0.046)*	–	0.657 (0.518)	–
	Model p-value	0.050*	0.030*	0.009*	0.131	0.162	0.0002*
	Model r^2	0.096	0.185	0.259	0.087	0.072	0.3437
	Model likelihood	35.24	35.65	36.92	35.68	35.48	34.08
	LRT χ^2 (p-value)	–	0.845 (0.358)	3.36 (0.067)•	0.877 (0.349)	0.489 (0.485)	–
<50 housing units/km^2 (N=24)	Maternity: t (p-value)	-1.46 (0.157)	-1.92 (0.07)•	-1.85 (0.08)•	-1.40 (0.175)	-1.35 (0.192)	-3.31 (0.003)*
	λ	λ_{ML}=0	λ_{ML}=0.564	λ_{ML}=0.523	λ_{ML}=0	λ_{ML}=0	1
	p-value λ=0, λ=1	1, 0.186	1, 0.186	0.412, 0.063•	1, 0.156	1, 0.140	–
	log(body mass): t (p-value)	–	1.07 (0.298)	–	0.497 (0.624)	–	–
	log(wing length): t (p-value)	–	–	1.95 (0.065)•	–	1.07 (0.296)	–
	Model p-value	0.141	0.097•	0.024*	0.349	0.208	0.0005*
	Model r^2	0.047	0.108	0.199	0.014	0.054	0.302
	Model likelihood	31.02	31.08	32.45	31.16	31.66	30.14
	LRT χ^2 (p-value)	–	0.129 (0.720)	2.86 (0.091)•	0.281 (0.596)	0.275 (0.259)	–
>100 housing units/km^2 (N=23)	Maternity: t (p-value)	-0.173 (0.864)	0.122 (0.904)	0.492 (0.628)	0.171 (0.866)	-0.201 (0.843)	0.577 (0.570)
	λ	λ_{ML}=0.912	λ_{ML}=0.901	λ_{ML}=0.897	λ_{ML}=0.926	λ_{ML}=0.907	0
	p-value λ=0, λ=1	0.049*, 0.222	0.08•, 0.202	0.067•, 0.196	0.053, 0.320	0.047*, 0.204	–
	log(body mass): t (p-value)	–	0.948 (0.354)	–	1.27 (0.220)	–	–
	log(wing length): t (p-value)	–	–	1.50 (0.150)	–	-0.395 (0.697)	–
	Model p-value	0.970	0.712	0.359	0.498	0.964	0.720
	Model r^2	-0.046	-0.051	0.012	-0.016	-0.090	-0.031
	Model likelihood	17.73	18.23	18.94	18.60	17.81	15.80
	LRT χ^2 (p-value)	–	1.00 (0.317)	2.43 (0.119)	1.76 (0.185)	0.178 (0.674)	–

*indicates a significant relationship; •indicates a nearly significant relationship

Table 4.2. AIC and *t*-values for mixed-effects model regressions of survival on maternity, with and without including body metrics. *T*-values ≥|2.00| are considered significant.

Locations	Model	*N*	AIC	*t*-value
All	maternity	600	–	maternity = -1.64•
All	maternity	500	1201.6	maternity = -1.32
All	maternity + mean mass	500	1205.1	maternity = -1.43 mass = 1.20
All	maternity + mean wing length	500	1202.0	maternity = -1.38 wing length = 1.59
All	maternity + mean condition index	500	1203.8	maternity = -1.23 condition index = -0.916
All	maternity + variance of mass	500	**1195.4**	maternity = -1.54 var. mass = 1.26
All	maternity + variance of wing length	500	**1195.4**	maternity = -1.46 var. wing length = 0.239
All	maternity + variance of condition index	500	**1195.8**	maternity = -1.47 var. condition index = -0.469
<50 housing units/km^2	maternity	433	–	maternity = -1.64•
<50 housing units/km^2	maternity	357	888.0	maternity = -1.90•
<50 housing units/km^2	maternity + mean mass	357	890.2	maternity = -1.94• mass = 1.43
<50 housing units/km^2	maternity + mean wing length	357	886.8	maternity = -1.86• wing length = 1.86•
<50 housing units/km^2	maternity + mean condition index	357	890.0	maternity = -1.81• condition index = -0.945
<50 housing units/km^2	maternity + variance of mass	357	**880.2**	maternity = -2.01* var. mass = 2.30*
<50 housing units/km^2	maternity + variance of wing length	357	883.8	maternity = -1.98• var. wing length = 0.510
<50 housing units/km^2	maternity + variance of condition index	357	884.6	maternity = -2.04* var. condition index = 0.161
>100 housing units/km^2	maternity	121	–	maternity = 0.378
>100 housing units/km^2	maternity	104	**252.5**	maternity = 0.781
>100 housing units/km^2	maternity + mean mass	104	256.5	maternity = 0.773 mass = 0.042
>100 housing units/km^2	maternity + mean wing length	104	**254.4**	maternity = 0.768 wing length = -0.218
>100 housing units/km^2	maternity + mean condition index	104	**254.2**	maternity = 0.622 condition index = 0.592
>100 housing units/km^2	maternity + variance of mass	104	255.0	maternity = 0.838 var. mass = -0.664
>100 housing units/km^2	maternity + variance of wing length	104	**254.2**	maternity = 0.803 var. wing length = 0.065
>100 housing units/km^2	maternity + variance of condition index	104	254.7	maternity = 0.815 var. condition index = -0.325

*indicates a significant relationship; •indicates a nearly significant relationship

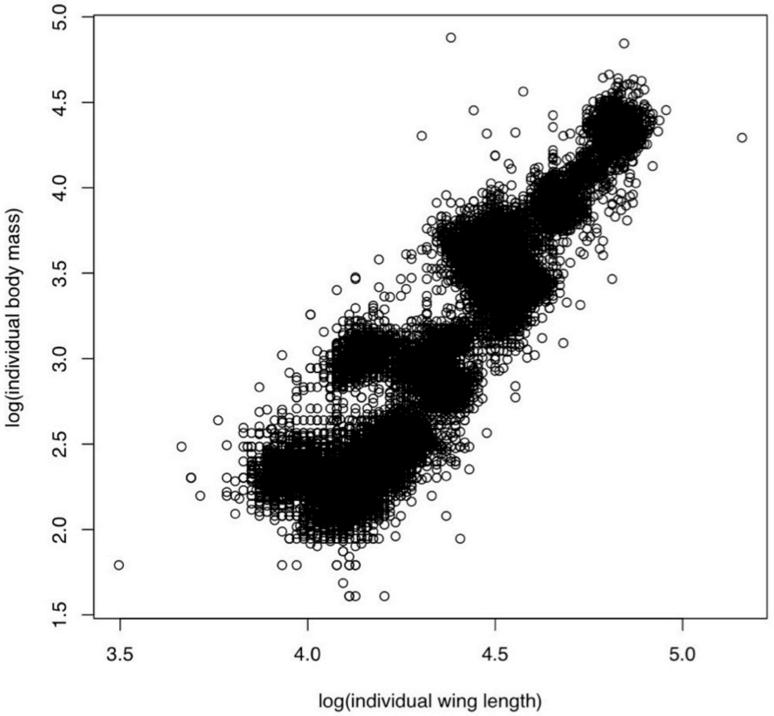


Figure 4.1. Relationship between wing length and body mass used to estimate body condition index for mixed-effects model regressions ($p<2.5\text{x}10^{16}$, $r^2=0.844$, $df=24{,}695$).

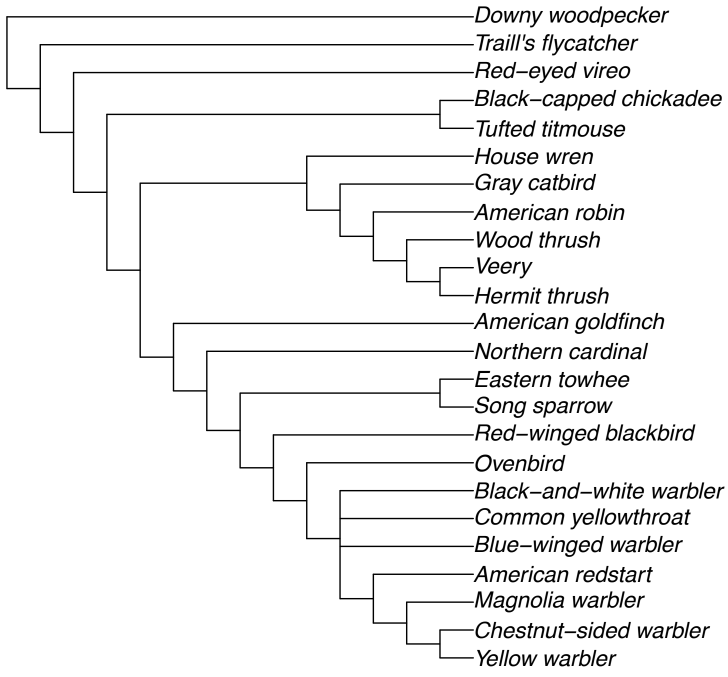


Figure 4.2. Phylogenetic relationships among species. Tree built from Jonsson and Fjeldsa (2006), and Lovette et al. (2010), used for phylogenetic regressions.

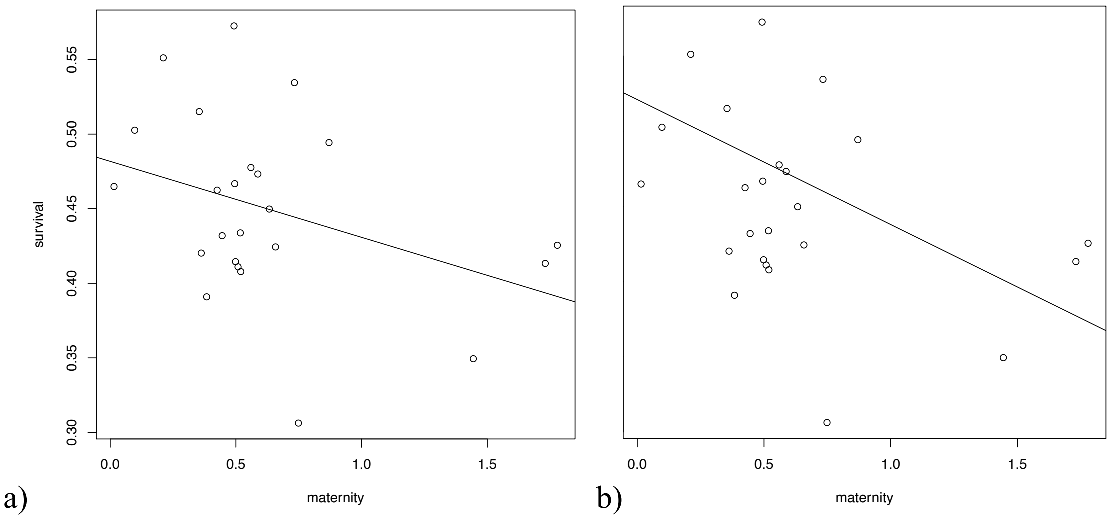


Figure 4.3. Relationship between survival and maternity across species across all locations (each point represents a species), estimated using a) maximum likelihood estimate of lambda (p=0.0499, r^2=0.10; lambda estimated by model to be 0), and b) Brownian motion model of evolution in which lambda=1 (p=0.0002, r^2=0.34).

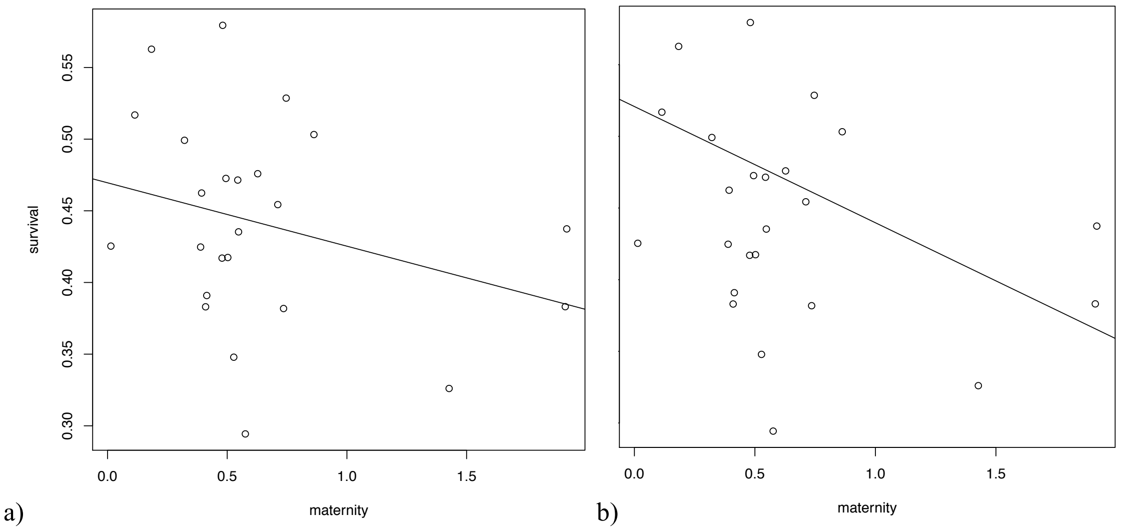
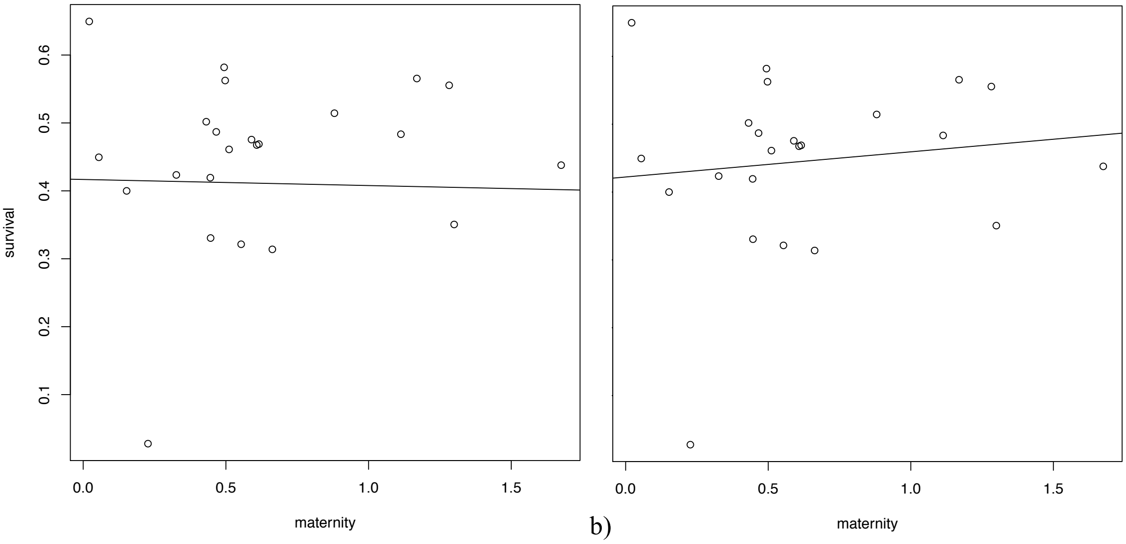


Figure 4.4. Relationship between survival and maternity across species (each point represents a species) in locations with <50 housing units/km^2, estimated using a) maximum likelihood estimate of lambda (estimated by model to be 0), and b) Brownian motion model of evolution in which lambda=1 (p=0.0005, r^2=0.30).



a) b)

Figure 4.5. Relationship between survival and maternity across species (each point represents a species) in locations with >100 housing units/km^2, estimated using a) maximum likelihood estimate of lambda (estimated by model to be 0.912), and b) a model in which lambda=0.

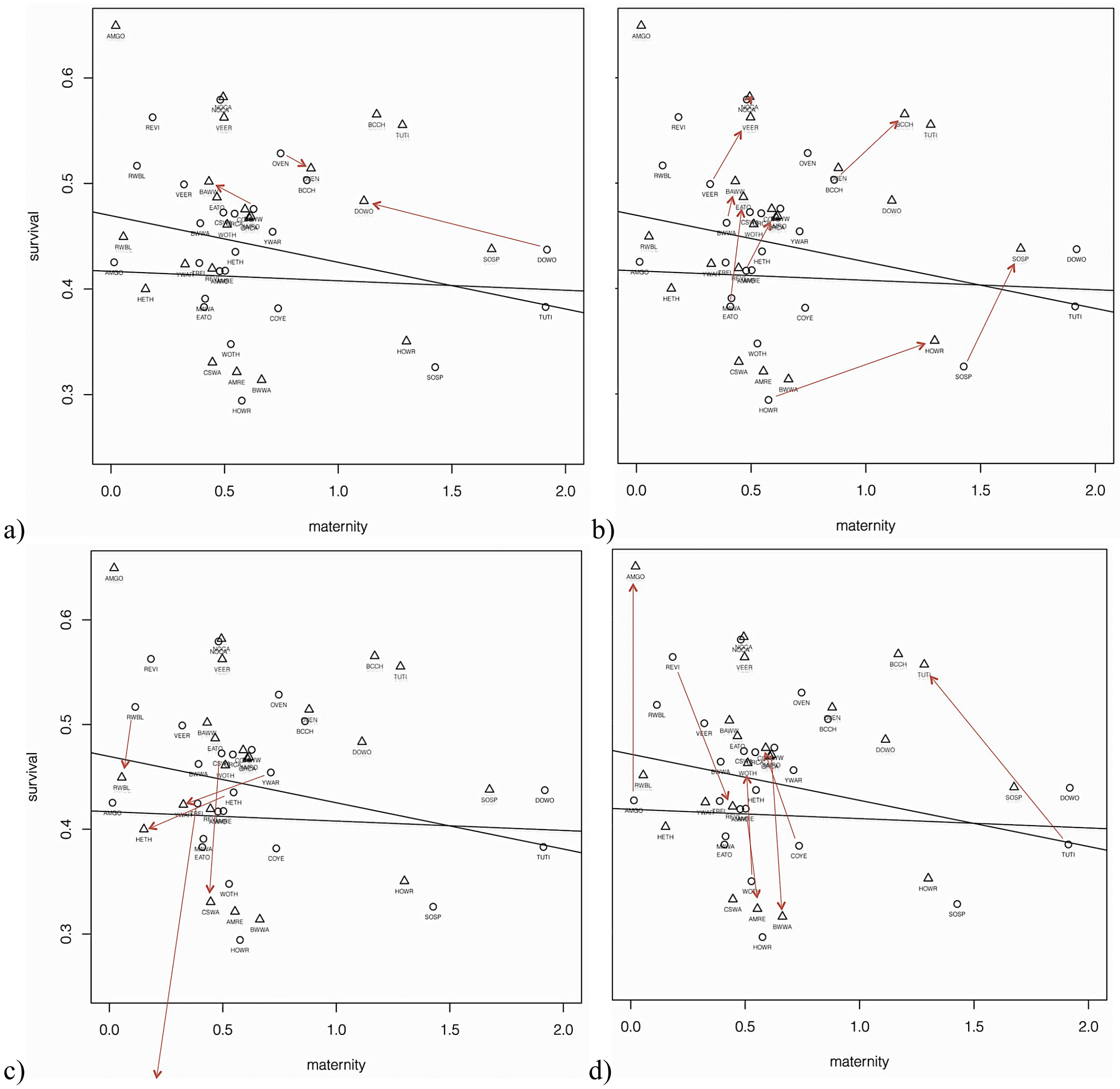


Figure 4.6. The direction of the change (indicated by arrows) in the relationship between survival and maternity from less disturbed to more disturbed locations across species: a) These species that may shift their location along the survival-reproduction continuum by moving along the original slope (represented by the negative trendline) in response to disturbance (flat line represents slope in disturbed locations), b) Species that increase in both survival and reproduction in response to human disturbance, c) Species that decrease in both survival and reproduction in response to human disturbance, d) Species that increase or decrease in only one parameter, but not along the original slope of less disturbed locations.

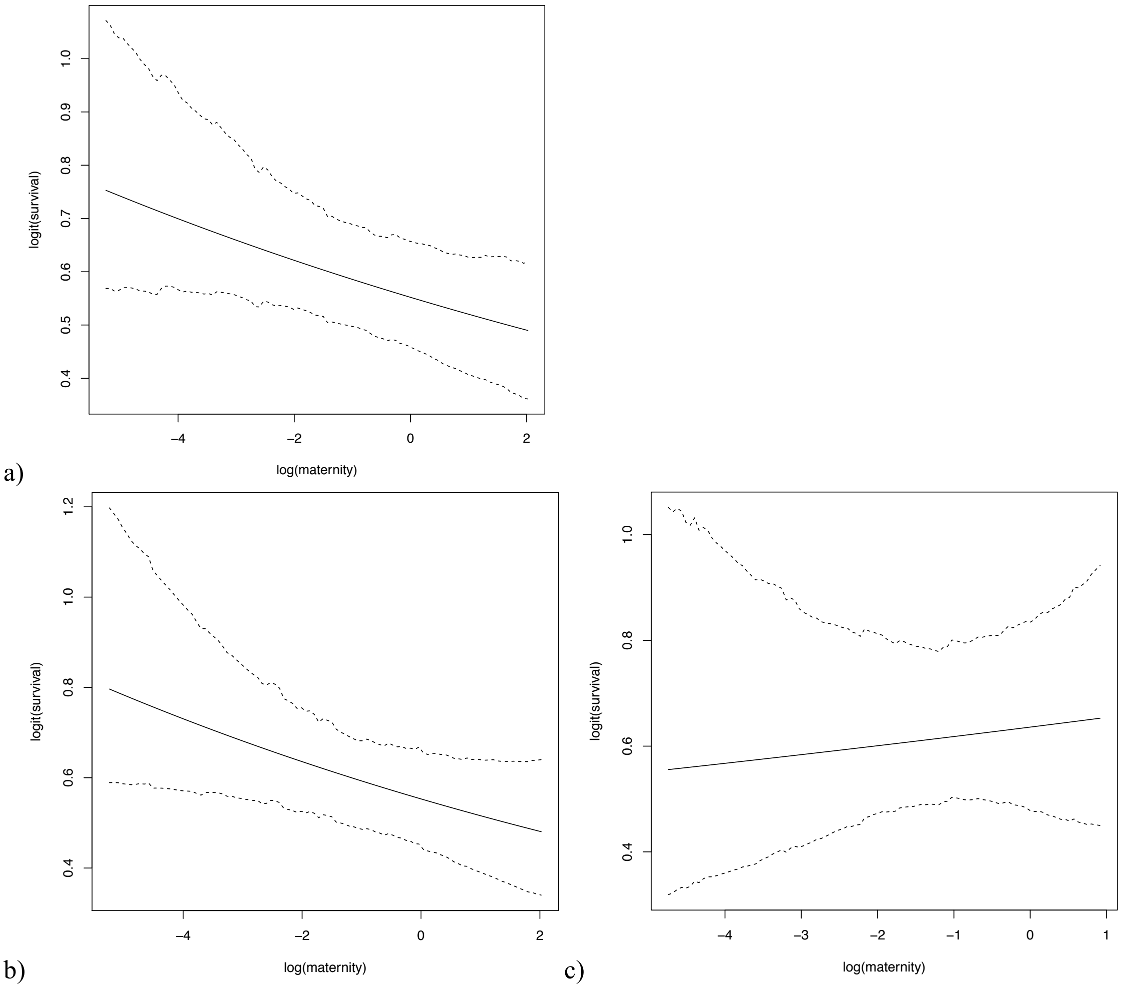


Figure 4.7. Relationship between survival and maternity from mixed-effects models using data from all species at a) all sites (*t*=-1.64), b) only sites with <50 housing units/km^2 (*t*=-1.64), and c) only sites with >100 housing units/km^2 (*t*=0.378).

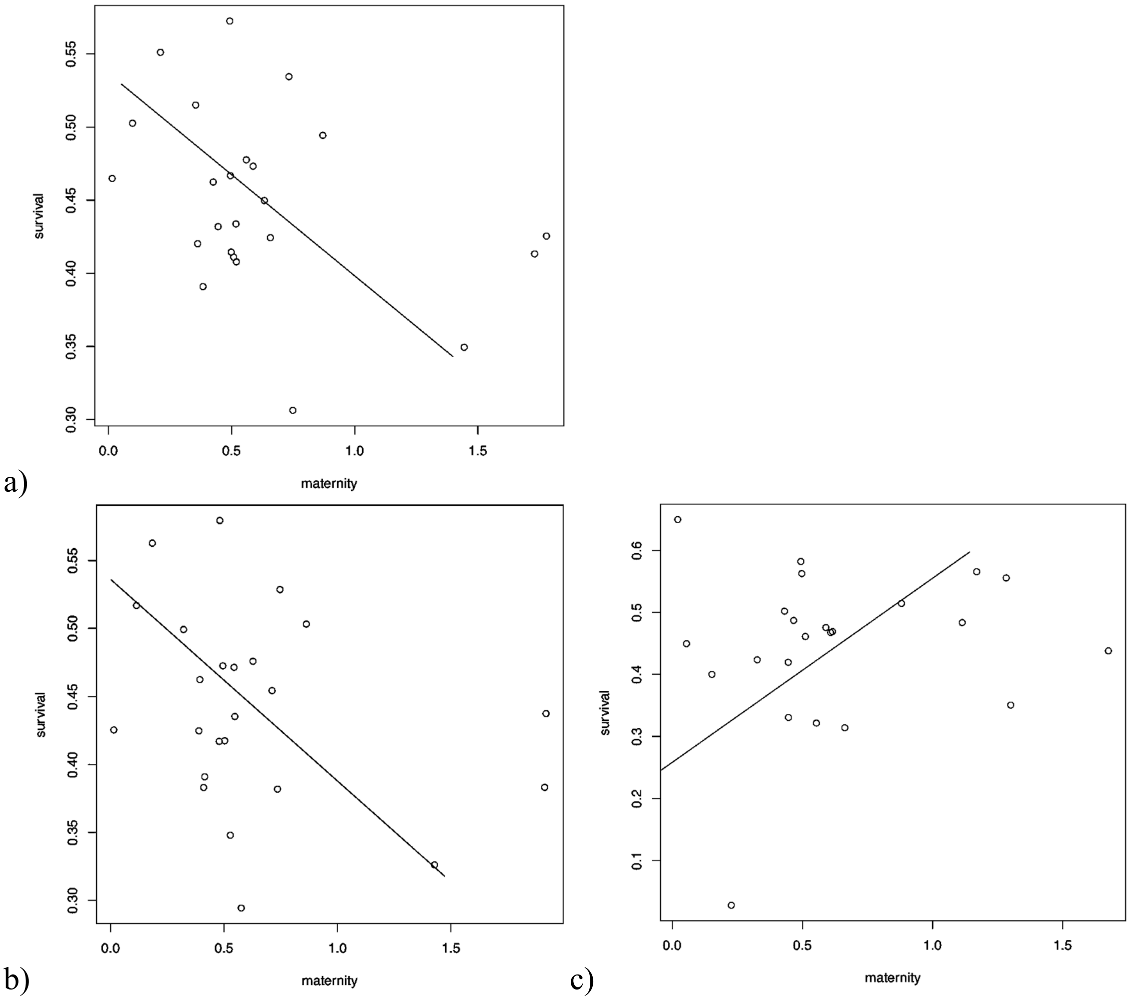


Figure 4.8. Direction of the relationship between survival and maternity using standardized major axis estimation among species at a) all locations, b) locations with <50 housing units/km^2, and c) locations with >100 housing units/km^2.

Chapter 5:
Effects of human disturbance on birds populations of the northeastern United States: Discussion and future directions

Summary of the dissertation

In this dissertation, I assessed the effect of human disturbance on survival, reproduction and population growth of breeding bird populations in the northeastern United States. I found evidence for an influence of human disturbance on demographic parameters across multiple species, and I was able to confirm, challenge, and generate several generalizations about species' responses to disturbance based on life history characteristics. In addition, I found that disturbance appeared to mediate the expected trend of a cost of reproduction across species. By including multiple species in my research, I addressed a lack of multi-species studies in the literature, and was able to investigate the impacts of human disturbance on demographic parameters and life history in a comparative framework. Further, by evaluating multiple demographic parameters simultaneously instead of a single parameter, I was able to compare the effects of disturbance on different components of life history, an important and often neglected approach. Below I summarize results of the broad questions addressed in my thesis.

Is there evidence across a range of species for a general negative response to human disturbance? At the species level, I found support for the influence of human disturbance on several breeding bird species in the northeastern United States. While disturbance alone was rarely the single most important predictor of demographic parameters, human disturbance in combination with land cover or climate variables was important in predicting demographic parameters in nearly three-quarters of the studied species. This alone is not particularly surprising, as much research has focused on responses of bird populations to human disturbance and has documented negative effects. However, I found that the direction and strength of an effect of human disturbance, classified here as intensity of human-developed land cover, on demographic parameters varied across species. There are several reasons that not all species may be negatively affected, especially if they are able to use amenities provided by humans. However, when measures of species' responses to human disturbance are based on single-species studies or use a single demographic parameter, the results may not provide a complete picture of the interacting components of population growth or decline. The results of this chapter uncover interesting trends in population dynamics across a number of species, and raise questions about the ways in which species' responses to disturbance are quantified. Specifically, a general tendency not to publish negative results may lead to the conclusion from the literature that there is more often than not an effect of human disturbance on birds. Multi-species studies investigating multiple demographic parameters can reveal variability in responses not gleaned from single- or few- species studies alone. These also provide a more controlled approach to evaluating species-wide responses to disturbance than permitted by a synthesis of results obtained from studies using incongruent methods to quantify disturbance and species' responses.

Can we make generalizations about species' responses based on life history characteristics? At the trait-level, I was able to make some generalizations about the relationship between species' characteristics, demographic parameters, and responses to human disturbance. Specifically, differences in nest location, food preference, and migratory strategy influenced demographic parameter values, and human disturbance interacted with mass, food preference, habitat preference, and migratory strategy. However, these relationships were not entirely consistent with my predictions based on patterns documented in the literature. In addition, where a relationship between life history characteristics and demographic parameters was found, reproduction was most often affected. In some cases the effect of species' characteristics on demographic parameters was not altered by human disturbance, and in general the relationship between species' characteristics and demographic parameters (e.g., those conferring highest versus lowest mean values) was not necessarily indicative of vulnerability to human disturbance. Importantly, the relationship between species' characteristics and human disturbance may be more complex than can be inferred from studies of abundance or richness alone. Recently-developed integrated population modeling methods (Shaub and Abadi 2011) that combine measures of abundance and demographic parameters can provide an innovative approach to understanding of processes linking responses to human disturbance, but were beyond the scope of this study.

Does disturbance mediate or exacerbate costs of reproduction? In assessing the costs of reproduction within and across species, I was able to test expectations from a fundamental theory in ecology and evolution across locations with high and low levels of human development. I found a negative trend between survival and reproduction across species, across all locations and across undisturbed locations. This negative trend was robust to the modeling approach used to evaluate the relationship, and consistent with an expected cost of reproduction. However, in locations with high disturbance, there was no longer a cost of reproduction. The fact that a relationship was present in undisturbed but not in disturbed locations indicates that disturbance is affecting species differently. In particular, where some species had high reproduction and low survival, survival may not be as compromised in disturbed areas. In addition, maternity increased for some species, also alleviating a visible cost of reproduction. Within species, there was no evidence of a trade-off between reproduction and survival across time or across populations in more and less disturbed environments. However, there was a positive relationship between current and future reproduction in several species, and this relationship was positive regardless of the level of disturbance. The extent to which human disturbance alters the relationship between demographic parameters, e.g., between survival and reproduction, likely has implications for population growth or decline. While there may have been too much within-species variation for a tradeoff within species to be apparent, the across-species relationships indicate that disturbance may alter expected life history tradeoffs. An application of fundamental principles in life history theory can aid in understanding why these relationships may be altered, and suggest new avenues of research to test existing hypotheses.

General trends and implications

Collating results of the above work, a few general trends are worth nothing. At the species level, human disturbance was important in predicting of survival in more species than were reproduction or population growth. However, at the trait-level, reproduction was most often influenced by human disturbance. While these may seem conflicting results, adult dispersal influences apparent survival rates and is often caused by reproductive failure (Greenwood and Harvey 1982, Haas 1998). Therefore, the effect of human disturbance on survival at the species-level may be in part related to a broader effect of human disturbance on maternity that is more apparent at the trait-level. The positive relationship between current and future reproduction further supports the idea that individuals are more likely to return to sites where they have higher reproductive success, and move away from sites where they have lower reproductive success. These results also underscore the importance of measuring more than a single demographic parameter, as a combination of parameters may yield different insights into population processes. However, if only survival or reproduction can be measured, a measure of survival that includes estimation of dispersal may be the best choice in populations where reproductive success is known to affect site fidelity.

Regarding the aims of this research, first, I do not wish to argue against single-species studies, as these may in fact achieve a greater level of detail than possible with multi-species studies. However, extrapolations from single-species studies to a broader set of species should be done with caution, if at all. Next, it is often useful to make generalizations for conservation management purposes, but these should be carefully evaluated across multiple population parameters. Multi-species studies of abundance and species' richness may point to expected patterns, but these should be combined using a mechanistic approach that integrates several measures of species' responses to understand the documented patterns. Lastly, only a handful of fundamental theories in ecology and evolution have been tested in urbanizing environments. Where possible, hypotheses generated by fundamental theories should be tested to see if they are broadly applicable across both human-disturbed and undisturbed areas, where they can be revised, and where or if a general theory of urban ecology is necessary. This would both benefit conservation and facilitate advancements in the field of ecology.

Conclusions

In addition to being adored by nature lovers, birds provide several ecosystem services (Sekercioglu 2006), and may serve as environmental indicators (Naccari et al. 2009, Morrissey et al. 2010, Butler et al. 2012). As the human population grows and human-developed land cover exceeds that put into parks and natural reserves (McKinney 2002), long term-monitoring programs offer a window into understanding the effects of humans on wildlife populations. Combined, these programs allow evaluation of both patterns and processes in response to human disturbance, and can improve implementation of conservation management plans. The results of this dissertation contribute to a growing body of literature documenting the effects of human disturbance on breeding bird populations of the United States, and call for more multi-species studies measuring several demographic parameters simultaneously to confirm or refute the results found here. The use of data from a continent-wide mark-recapture bird-banding program to complete this dissertation further illustrates the potential for these data to be used to address numerous questions in ecology and conservation, and their value far beyond the hands of the thousands of volunteers generously dedicated to their collection.

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