

THE INFLUENCE OF MIGRATORY CONNECTIVITY AND SEASONAL
INTERACTIONS ON INDIVIDUAL- AND POPULATION-LEVEL DYNAMICS OF
A LONG DISTANCE MIGRATORY SONGBIRD

by

Michael T. Hallworth
A Dissertation
Submitted to the
Graduate Faculty
of
George Mason University
in Partial Fulfillment of
The Requirements for the Degree
of
Doctor of Philosophy
Environmental Science and Public Policy

Committee:

_____	Dr. Larry Rockwood, Dissertation Director
_____	Dr. Kevin Curtin, Committee Member
_____	Dr. Thomas Lovejoy, Committee Member
_____	Dr. Peter P. Marra, Committee Member
_____	Dr. T. Scott Sillett, Committee Member
_____	Dr. Albert Torzilli, Graduate Program Director
_____	Dr. Robert Jonas, Department Chairperson
_____	Dr. Donna M. Fox, Associate Dean, Office of Student Affairs & Special Programs, College of Science
_____	Dr. Peggy Agouris, Dean, College of Science

Date: _____ Summer Semester 2014
George Mason University
Fairfax, VA

The Influence of Migratory Connectivity and Seasonal Interactions on Individual- and
Population-Level Dynamics of a Long Distance Migratory Songbird

A Dissertation submitted in partial fulfillment of the requirements for the degree of
Doctor of Philosophy at George Mason University

by

Michael T. Hallworth
Master of Science
Plymouth State University, 2007
Bachelor of Science
Plymouth State University, 2004

Director: Larry Rockwood, Professor
Department of Environmental Science and Public Policy

Summer Semester 2014
George Mason University
Fairfax, VA



This work is licensed under a [creative commons attribution-noncommercial 3.0 unported license](https://creativecommons.org/licenses/by-nc/3.0/).

DEDICATION

To my late grandfather Perry A. Xenakis, who instilled in me at a young age the importance of knowledge and education. I also dedicate this to my family who have supported me every step of the way.

ACKNOWLEDGEMENTS

First I must thank Dr. Pete Marra who has been a great mentor over the past six years. He supported me throughout the process, added invaluable insight that drastically improved this dissertation and made me a better researcher/scientist along the way. Second, I would like to thank Dr. T. Scott Sillett for diligently working through previous drafts of this dissertation, forcing me to think critically and allowing me to talk through analyses and statistical hiccups I encountered throughout the process.

I am indebted to Dr. Larry Rockwood who was an excellent advisor and supervisor who helped me navigate George Mason University. Dr. Rockwood supported my growth as a student and as a teaching assistant throughout my tenure at George Mason. I will forever be grateful that he recruited me from an anatomy and physiology T.A. to become an ecology T.A. after my first semester. Dr. Kevin Curtin made me think critically about the approaches and techniques that I used within this dissertation and allowed me to sit in on lectures that helped with the spatial analyses found throughout this dissertation. I thank Dr. Tom Lovejoy for taking time out of his busy schedule to be part of my committee and for being supportive throughout the process.

Dr. Leonard Reitsma started me on this path many years ago and has served as a mentor and friend ever since. He introduced me to ecology, fieldwork and introduced me to the tropics and I haven't looked back since. For that I will be forever grateful.

I couldn't have completed this research without the help of many field technicians, R.E.U. students, friends and family members who helped in the field. I acknowledge the great fieldwork performed by Anne Bloomfield, C. Logan Bryant, April Costa, Vann Dwiggin, Malcolm Grant, Brian Lang, Katie Long, Desirée Narango, Robert Reitsma, Mark Thomas, and Joe Welklin. Dave Grunzel, Sara Kaiser and Nick Rodenhouse were exemplary roommates, friends and colleagues who I am grateful to have spent summers with at Hubbard Brook. I am grateful to Rebecca Marvin and José Avededo (Ito) who provided housing while I captured Ovenbirds in Puerto Rico. Jacob Marlin, Judy Dourson, Mick and Kathy Baisley and the staff at BFREE made our stay in Belize very enjoyable.

Finally, I want to thank my entire family who supported me throughout the graduate school process. I missed countless family events, outings, celebrations and holidays because of fieldwork and they were always understanding and supportive. I wouldn't have been able to do it without their support. I will forever be indebted to my best friend and future wife, Desirée Narango for the countless hours you spent helping me in the field, listening to and helping me work through ideas, providing comments on drafts, forcing me to think outside the box and see the bigger picture and for supporting me through this process and life in general.

TABLE OF CONTENTS

	Page
List of Tables	vi
List of Figures	vii
Abstract	viii
Chapter 1	1
Chapter 2	9
Chapter 3	47
Chapter 4	88
Chapter 5	127
Curriculum Vitae	155

LIST OF TABLES

Table	Page
Table 1	29
Table 2	30
Table 3	37
Table 4	70
Table 5	75
Table 6	76
Table 7	77
Table 8	78
Table 9	117
Table 10	146
Table 11	147
Table 12	148

LIST OF FIGURES

Figure	Page
Figure 1	31
Figure 2	32
Figure 3	33
Figure 4	38
Figure 5	40
Figure 6	71
Figure 7	72
Figure 8	73
Figure 9	79
Figure 10	80
Figure 11	81
Figure 12	113
Figure 13	114
Figure 14	115
Figure 15	149

ABSTRACT

THE INFLUENCE OF MIGRATORY CONNECTIVITY AND SEASONAL INTERACTIONS ON INDIVIDUAL- AND POPULATION-LEVEL DYNAMICS OF A LONG DISTANCE MIGRATORY SONGBIRD

Michael T. Hallworth, Ph.D.

George Mason University, 2014

Dissertation Director: Dr. Larry Rockwood

Determining the factors that influence population dynamics of migratory animals is complex in part because of the large spatial scales that these species occupy annually. The strength of migratory connectivity, the geographic link between breeding and non-breeding populations, may influence the way populations respond to selective pressures and influence how we conserve and protect such species. Furthermore, periods of the annual cycle interact and events during one period may affect subsequent stages of the life cycle. Using archival light-level geolocators I examined the degree of migratory connectivity and how carry-over effects influence individuals and the population growth rate of the Ovenbird (*Seiurus aurocapilla*) a long distance Neotropical migratory songbird. Ovenbirds exhibit strong migratory connectivity at broad spatial scales but connectivity within sub-populations ranged from moderate to weak. I found evidence of a strong carry-over effect during spring but no interaction resulting from breeding season

events during the fall. The presence of a strong carry-over effect in the spring was mediated via departure from the non-breeding grounds. Departure timing from the non-breeding and subsequent arrival to the breeding grounds influenced reproductive parameters at the individual level. As a result, early arriving individuals added significantly to the population while late arriving individuals did not. Indeed, the population growth rate decreased by 0.028 ± 0.003 for each day arrival to the breeding grounds was delayed. Overall, my findings suggest that seasonal interactions in the form of carry-over effects play a significant role in shaping individual and population-level dynamics of a migratory songbird. These findings highlight the importance of considering the entire annual-cycle of migratory animals when attempting to determine processes that regulate or limit migratory populations.

CHAPTER 1: INTRODUCTION

Determining the factors that influence population dynamics of migratory animals is complex in part because of the large spatial scales that these species occupy annually (Webster et al. 2002, Webster and Marra 2005). Migratory birds spend three to four months on the breeding grounds, one to two months in migration and six to seven months on non-breeding grounds (Rappole 1995). Multiple processes can operate at these different spatial and temporal scales that may influence fundamental processes controlling population growth rate (i.e., survival and reproduction) such as inter- and intra-specific competition (Marra et al. 1993, 1998, Sillett et al. 2004), predation, and food limitation (Sherry et al. 2005). Although these mechanisms likely function during breeding and non-breeding periods, over 75% of studies of long-distance migratory birds have focused on the breeding season despite the fact that many species spend the majority of their annual cycle on their non-breeding grounds in the tropics. Also important to consider is how events operating in different seasons might interact to influence events in subsequent stages of the life cycle (Marra et al. 1998, Norris et al. 2004, Betini et al. 2013). The strength of migratory connectivity, the degree to which breeding and non-breeding populations are geographically linked, may influence the way populations respond to selective pressures as well as influence how we conserve and protect such species (Marra et al. 2006, 2011). Moreover, processes or climatic changes that take

place in one geographic location may have significant impacts on either a specific sub-population or the population as a whole depending on the degree of migratory connectivity (Webster et al. 2002, Webster and Marra 2005).

Identifying the strength of migratory connectivity necessitates that individuals are tracked throughout the annual cycle. Our understanding of connectivity for the vast majority of migratory bird species is the result of over 100 years of capture-mark-recapture band recoveries (Ryder et al. 2011, Cohen et al. 2014). Not surprisingly, for many species the recapture rate of previously banded birds is very low, thus limiting our understanding of connectivity. Until recently, the small size of migratory songbirds precluded the use of extrinsic devices such as satellite transmitters, or Global Positioning System (GPS) tags to track individual movements throughout the year (Webster et al. 2002). The miniaturization of archival light-level geolocators (geolocators) has allowed researchers to track migratory birds as small as 16g and the technology is advancing rapidly (Stutchbury et al. 2009, Bridge et al. 2011, 2013). Previous to this advancement, intrinsic markers such as stable-hydrogen isotopes (Hobson 2005) and molecular markers (Clegg et al. 2003) were the only tools available to enumerate a large enough sample size to estimate migratory connectivity of small organisms such as songbirds.

Knowing the strength of migratory connectivity is critical to our understanding of migratory bird populations. as well as how events during one season influence subsequent seasons, Seasonal interactions are non-lethal events experienced by individuals that have residual effects on performance, survival or both during subsequent phases of the annual cycle (Runge and Marra 2005, O'Connor et al. 2014). Events during

the non-breeding season have been shown to carry-over and influence arrival date and reproductive success on the breeding grounds. Studies have demonstrated that habitat quality during the non-breeding season can have major impacts on departure dates for spring migration (Marra et al. 1998), arrival on the breeding grounds (Marra et al. 1998, Rockwell et al. 2012, McKellar et al. 2013), the number of offspring produced (Norris et al. 2004, Reudink et al. 2009), natal dispersal distances (Studds et al. 2008) and annual survival (Sillett and Holmes 2002). Currently, our understanding of seasonal interactions is limited to how events during the non-breeding season influence reproductive success, we know very little about how breeding season events carry-over and influence events during the non-breeding season (Stutchbury et al. 2011, Bogdanova et al. 2011).

OBJECTIVES

With this dissertation, I seek to improve our current understanding of migratory connectivity and how seasonal interactions throughout the year influence individuals and population-level dynamics using the Ovenbird (*Seiurus aurocapilla*), a long distance migratory songbird as a model organism. Toward that end, I use stable-hydrogen isotopes and geolocators to track individuals throughout the annual cycle. In chapter two, I compare the estimates of breeding ground origin derived using stable-hydrogen isotopes and geolocators of individuals captured at two non-breeding locations. In the next chapter (chapter 3), I identify the strength of migratory connectivity for Ovenbirds using geolocators deployed at two widely separated breeding and four non-breeding locations. I also create a metric to describe connectivity quantitatively as well as use data derived from citizen scientists to refine location estimates associated with geolocators.

The Ovenbird is a good model species because it is a large (~20g), insectivorous ground foraging warbler that breeds in deciduous and mixed-deciduous forests of northern North America and winters throughout the Caribbean basin and Central America (Porneluzi et al. 2011). In addition, Ovenbirds exhibit site-fidelity to both breeding and non-breeding sites; the population remains stable throughout its range (Sauer et al. 2014) and they are large enough to carry geolocators. Our knowledge of migratory connectivity for Ovenbirds is limited because only 0.15% of Ovenbirds banded (over 200,000 individuals) from 1914-2004 have been encountered (Bird Banding and Encounter Data 1914-2004, Patuxent Wildlife Research Center), thus the information regarding migratory connectivity is novel.

In chapter four, I investigate how seasonal interactions throughout the year influence individual- and population-level dynamics using a breeding population of Ovenbirds at Hubbard Brook Experimental Forest in central New Hampshire. Using a marked population over multiple years in combination with geolocators I determine how departure from the non-breeding and subsequent arrival to breeding grounds influences reproductive parameters. I then parameterize a population model using the data collected on reproductive performance while incorporating the impact of seasonal interactions on pairing success, and number of young fledged to elucidate how seasonal interactions influence the population growth rate.

For my final chapter, I determine how Ovenbirds select nest sites at two spatial scales and identify how habitat cues used in nest site selection influence daily nest survival. In combination, the chapters of this dissertation help fill gaps in our knowledge

and understanding of migratory connectivity as well as the importance of seasonal interactions on individual and population-level dynamics. This information is essential to make informed decisions regarding conservation and management of migratory bird populations.

LITERATURE CITED

- Betini, G. S., C. K. Griswold, and D. R. Norris. 2013. Carry-over effects, sequential density dependence and the dynamics of populations in a seasonal environment. *Proceedings of the Royal Society B: Biological Sciences* 280:20130110.
- Bogdanova, M. I., F. Daunt, M. Newell, R. A. Phillips, M. P. Harris, and S. Wanless. 2011. Seasonal Interactions in the Black-Legged Kittiwake, *Rissa Tridactyla*: Links Between Breeding Performance and Winter Distribution. *Proceedings of the Royal Society B: Biological Sciences* 278:2412–2418.
- Bridge, E. S., J. F. Kelly, A. Contina, R. M. Gabrielson, R. B. MacCurdy, and D. W. Winkler. 2013. Advances in tracking small migratory birds: a technical review of light-level geolocation. *Journal of Field Ornithology* 84:121–137.
- Bridge, E. S., K. Thorup, M. S. Bowlin, P. B. Chilson, R. H. Diehl, R. W. Fléron, P. Hartl, Roland Kays, J. F. Kelly, W. D. Robinson, and M. Wikelski. 2011. Technology on the Move: Recent and Forthcoming Innovations for Tracking Migratory Birds. *BioScience* 61:689–698.
- Clegg, S. M., J. F. Kelly, M. Kimura, and T. B. Smith. 2003. Combining genetic markers and stable isotopes to reveal population connectivity and migration patterns in a Neotropical migrant, Wilson's warbler (*Wilsonia pusilla*). *Molecular Ecology* 12:819–830.
- Cohen, E. B., J. A. Hostetler, J. A. Royle, and P. P. Marra. 2014. Estimating migratory connectivity of birds when re-encounter probabilities are heterogeneous. *Ecology and Evolution*.
- Hobson, K. A. 2005. Stable isotopes and the determination of avian migratory connectivity and seasonal interactions. *The Auk* 122:1037–1048.
- Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Pages 1884–1886. *American Association for the Advancement of Science*, 282.

- Marra, P. P., D. Hunter, and A. M. Perrault. 2011. Migratory connectivity and the conservation of migratory animals. *Envtl. L.* 41:317.
- Marra, P. P., D. R. Norris, S. M. Haig, M. S. Webster, and J. A. Royle. 2006. Migratory connectivity. Pages 157–183 in K. R. Crooks and M. A. Sanjayan, editors. *Connectivity conservation*. Cambridge University Press.
- Marra, P. P., T. W. Sherry, and R. T. Holmes. 1993. Territorial exclusion by a long-distance migrant warbler in Jamaica: a removal experiment with American Redstarts (*Setophaga ruticilla*). *The Auk* 110:565–572.
- McKellar, A. E., P. P. Marra, S. J. Hannon, C. E. Studds, and L. M. Ratcliffe. 2013. Winter rainfall predicts phenology in widely separated populations of a migrant songbird. *Oecologia* 172:595–605.
- Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences* 271:59–64.
- O'Connor, C. M., D. R. Norris, G. T. Crossin, and S. J. Cooke. 2014. Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. *Ecosphere* 5:art28.
- Porneluzi, P., M. A. Van Horn, and T. M. Donovan. 2011. Ovenbird (*Seiurus aurocapilla*). *The Birds of North America Online*.
- Rappole, J. H. 1995. *The ecology migrant birds. A Neotropical perspective*. Smithsonian Institution Press, Washington, DC (USA). 1995.
- Reudink, M. W., P. P. Marra, T. K. Kyser, P. T. Boag, K. M. Langin, and L. M. Ratcliffe. 2009. Non-breeding season events influence sexual selection in a long-distance migratory bird. *Proceedings of the Royal Society B: Biological Sciences* 276:1619–1626.
- Rockwell, S. M., C. I. Bocetti, and P. P. Marra. 2012. Carry-over effects of winter climate on spring arrival date and reproductive success in an endangered migratory bird, Kirtland's Warbler (*Setophaga kirtlandii*). *The Auk* 129:744–752.
- Runge, M. C., and P. P. Marra. 2005. *Modeling seasonal interactions in the population dynamics of migratory birds. Birds of two worlds: the ecology and evolution of migration*. Johns Hopkins University Press, Baltimore, Maryland, USA:375–389.

- Ryder, T. B., J. W. Fox, and P. P. Marra. 2011. Estimating migratory connectivity of gray catbirds (*Dumetella carolinensis*) using geolocator and mark–recapture data. *The Auk* 128:448–453.
- Sauer, J. R., J. E. Hines, J. E. Fallon, Pardieck, K. L., Ziolkowski, D. J., and Link, W. A. 2014, February. The North American Breeding Bird Survey, Results and Analysis 1966-2012. Version 02.19.2014. USGS Patuxent Wildlife Research Center, Laurel, MD.
- Sherry, T. W., M. D. Johnson, and A. M. Strong. 2005. Does winter food limit populations of migratory birds? *Birds of the two worlds: the ecology and evolution of migration*:414–425.
- Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296–308.
- Sillett, T. S., N. L. Rodenhouse, and R. T. Holmes. 2004. Experimentally reducing neighbor density affects reproduction and behavior of a migratory songbird. *Ecology* 85:2467–2477.
- Studds, C. E., T. K. Kyser, and P. P. Marra. 2008. Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory songbird. *Proceedings of the National Academy of Sciences* 105:2929.
- Stutchbury, B. J. ., E. A. Gow, T. Done, M. MacPherson, J. W. Fox, and V. Afanasyev. 2011. Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. *Proceedings of the Royal Society B: Biological Sciences* 278:131.
- Stutchbury, B. J. ., S. A. Tarof, T. Done, E. Gow, P. M. Kramer, J. Tautin, J. W. Fox, and V. Afanasyev. 2009. Tracking long-distance songbird migration by using geolocators. *Science* 323:896.
- Webster, M. S., and P. P. Marra. 2005. The importance of understanding migratory connectivity and seasonal interactions. *Birds of the two worlds: the ecology and evolution of migration*:199–209.
- Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution* 17:76–83.

CHAPTER 2: DO ARCHIVAL LIGHT-LEVEL GEOLOCATORS AND HYDROGEN STABLE ISOTOPES PROVIDE COMPARABLE ESTIMATES OF BREEDING GROUND ORIGIN?

Michael T. Hallworth,^{1,2,4} Colin E. Studds,^{1,3} T. Scott Sillett,¹ and Peter P. Marra¹

¹Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, MRC 5503, Washington, D.C. 20013, USA;

²College of Science, George Mason University, 4100 Patriot Drive, Fairfax, Virginia 22030, USA;

³ARC Centre of Excellence for Environmental Decisions, the NERP Environmental Decisions Hub, Centre for Biodiversity and Conservation Science, University of Queensland, Brisbane, Queensland 4072, Australia

⁴E-mail: mhallwor@masonlive.gmu.edu

This chapter was published in *The Auk* in its current state

Abstract.—Migratory connectivity for small migratory passerines has been quantified primarily with stable hydrogen isotopes in feathers ($\delta^2\text{H}_\text{F}$) because, until recently, we lacked the technology to track small organisms over long distances. Direct tracking of small passerines throughout the annual cycle is now possible with archival light-level geolocators. Our objective was to evaluate whether $\delta^2\text{H}_\text{F}$ and geolocators produce similar breeding-origin assignments for the same individual birds sampled during the non-breeding season. We estimated breeding origin with geolocators and $\delta^2\text{H}_\text{F}$ and validated those estimates using a population of Ovenbirds (*Seiurus aurocapilla*) from a known breeding location at Hubbard Brook Experimental Forest, New Hampshire. We also deployed geolocators on Ovenbirds in Jamaica and Florida during March 2010–2011. We performed stable hydrogen isotope analysis on feathers of birds whose geolocators we recovered (Jamaica: $n = 9$; Florida: $n = 3$). Probabilistic assignments of $\delta^2\text{H}_\text{F}$ that accounted for regional variation in feather-isotope discrimination predicted breeding origins that agreed with kernel density estimates of origin derived from geolocators. By contrast, assignments of $\delta^2\text{H}_\text{F}$ using the common assumption of a consistent feather-isotope discrimination across space predicted breeding origins that overlapped minimally with those from geolocators. Finally, Bayesian analyses that incorporated prior information of Ovenbird abundance across the breeding range yielded more accurate assignments for both site-independent and site-specific discrimination factors. Our findings suggest that creating more detailed feather isoscapes by increasing the number of validation locations and sampling underrepresented portions of species

distributions could increase the accuracy of geographic assignments using $\delta^2\text{H}_\text{F}$. *Received 27 February 2013, accepted 15 March 2013.*

Key words: Bayesian, deuterium, discrimination, migratory bird, Ovenbird, *Seiurus aurocapilla*, solar geolocator, stable isotopes.

Long-distance migration is a common avian behavior, yet the degree to which populations are geographically linked throughout the annual cycle remains poorly understood for thousands of species (Webster et al. 2002, Marra et al. 2006). Such uncertainty impairs our capacity to study and manage migratory bird populations and, thus, emphasizes the need for accurate information about migratory connectivity (Marra et al. 2011). Progress has been especially challenging with passerines because the small body size of most species precludes the use of satellite telemetry (Clegg et al. 2003, Robinson et al. 2009). In addition, the value of long-term band-recovery data sets has been limited by low recapture rates (e.g., Ryder et al. 2011).

Our understanding of migratory connectivity in passerines was revolutionized by the analysis of stable hydrogen isotope ($\delta^2\text{H}$) ratios in feathers (Chamberlain et al. 1997, Hobson and Wassenaar 1997). These ratios, which are incorporated into growing feathers from local food webs and become metabolically inert, have been used to estimate both breeding (e.g., Kelly et al. 2005, Boulet et al. 2006) and non-breeding (e.g., Pain et al. 2004, Mazerolle et al. 2005) locations. However, this approach has three important constraints. First, although $\delta^2\text{H}$ in growing-season precipitation ($\delta^2\text{H}_\text{P}$) is strongly

correlated with latitude in many parts of the northern hemisphere, it does not show a clear relationship with longitude (Hobson 1999, Bowen et al. 2005), which limits geographic inferences based on $\delta^2\text{H}$ in feathers ($\delta^2\text{H}_\text{F}$) alone. Second, the heavy fraction of hydrogen in nature varies in relation to other factors, including elevation (Clark and Fritz 1997, Hobson et al. 2003), diet (Lott et al. 2003), distance from coastlines (Hobson et al. 2000, Lott et al. 2003), foraging guild (Hobson et al. 2012), bird age, and habitat type (Haché et al. 2012), all of which can complicate assignment of origin. Lastly, some birds molt at multiple times and locations each year (Butler et al. 2002, Leu and Thompson 2002, Rohwer et al. 2005), which can further confound geographic assignment. Accurately assigning individuals to breeding origin using $\delta^2\text{H}$ requires an understanding of the relationship between $\delta^2\text{H}_\text{P}$ and $\delta^2\text{H}_\text{F}$. Currently, much of our understanding of migratory connectivity comes from assignments based on $\delta^2\text{H}_\text{F}$ where the relationship between $\delta^2\text{H}_\text{P}$ and $\delta^2\text{H}_\text{F}$ is assumed to be similar throughout the breeding range (e.g., Kelly et al. 2005, Hobson et al. 2012). In addition, it is clear that various factors can influence the magnitude of isotopic discrimination between long-term average $\delta^2\text{H}_\text{P}$ and $\delta^2\text{H}_\text{F}$ (Hobson et al. 2012), but these discrimination relationships require further refinement.

Direct tracking of birds throughout their annual cycle is the most accurate way to quantify migratory connectivity and has recently become possible for small passerines with the advent and miniaturization of archival light-level geolocators (e.g., Shaffer et al. 2006, Stutchbury et al. 2009). Geolocators provide much-improved spatial resolution in both latitude and longitude compared with $\delta^2\text{H}_\text{F}$ but are expensive per bird compared with

isotope analyses. Moreover, geolocators have a low recovery rate, require that individuals be recaptured, and may alter behavior and survival (Bowlin et al. 2010).

Direct and indirect tracking methods therefore remain valuable tools for assessing migratory connectivity. The accuracy of geographic assignments derived from $\delta^2\text{H}_\text{F}$ measurements, however, has not been fully validated. Here, we compare assignments of breeding-ground origin determined by $\delta^2\text{H}_\text{F}$ values and geolocators for the Ovenbird (*Seiurus aurocapilla*), a small Neotropic–Nearctic migratory passerine. The Ovenbird is well suited for our study because it is widely distributed throughout North America during the breeding season and throughout the Caribbean Basin during the non-breeding season (Van Horn and Donovan 1994). Also, it annually molts its flight feathers before fall migration (Pyle 1997) and is large enough to carry a geolocator. We captured Ovenbirds in the eastern United States during the breeding season to validate the relationship between estimates of origin derived through $\delta^2\text{H}_\text{F}$ values and breeding estimates provided by geolocator data at a known breeding location. We then captured individuals on Caribbean non-breeding areas to compare the agreement between $\delta^2\text{H}_\text{F}$ values and geolocator data in assigning overwintering birds to unknown breeding locations.

METHODS

Field work was conducted from 2010 to 2012 on the breeding grounds at the Hubbard Brook Experimental Forest (HBEF) in central New Hampshire (41°30'N, 71°73'W), in Everglades National Park in southern Florida (25°13'N, 80°95'W), and at Font Hill Nature Preserve, St. Elizabeth Parrish, Jamaica (18°04'N, 77°94'W). We

captured Ovenbirds with simulated territorial intrusions and passive mist-netting techniques (Faaborg and Arendt 1984, Hobson et al. 2004), fit archival light-level geolocators (British Antarctic Survey, models MK12 [1.0 g] and MK20SALT [0.9 g]) to individuals whose mass was ≥ 19.0 g using a leg-harness technique (Naef-Daenzer 2007), and plucked a single tail feather (rectrix R3) for stable isotope analysis. A single tail feather was sampled from each Ovenbird captured to determine whether individuals with geolocators were representative of the capture population. We deployed 51 geolocators on Ovenbirds breeding at HBEF (2010, $n = 17$ [16 males and 1 female]; 2011, $n = 34$ [all male]) and 46 geolocators on birds on the non-breeding areas in Florida ($n = 18$ [12 males, 1 female, and 5 of unknown sex]) and Jamaica (total $n = 28$; 2010, $n = 11$ [4 males, 3 females, and 4 of unknown sex; 2011, $n = 17$ [10 males, 1 female, and 6 of unknown sex]). We recaptured returning birds in subsequent years, removed geolocators (HBEF: $n = 20$ [all male]; Florida: $n = 3$ [all male]; Jamaica: $n = 9$ [5 males, 2 females, and 2 of unknown sex]; Table S1, available with the online version of this article; see Acknowledgments), and collected another tail feather (rectrix R3) for stable isotope analysis.

Geolocator analysis.—Light data were transformed into latitude and longitude using BASTrack, versions 18 and 19 (British Antarctic Survey). Each sunrise and sunset was scored by the same observer (M.T.H.) using a threshold of 5, with TransEdit software (British Antarctic Survey). Light transition events from stationary geolocators indicated smooth transitions during sunrise and sunset. Transition events that indicated smooth transitions were scored as high-quality transitions (69 ± 9 SE of 190 transitions

between 1 May and 31 July; $36.1 \pm 0.10\%$), whereas those that included shading during light transitions were scored as low-quality and were removed from all analyses (McKinnon et al. 2013). These low-quality transition events were excluded because they would have increased uncertainty associated with sunrise and sunset estimates used to generate location data. Both midnight and noon locations were used to estimate breeding location. Locations within 15 days of spring and fall equinox were excluded from analyses (spring equinox period = 5 March–4 April; fall equinox period = 7 September–8 October) because of unreliable location data due to day length being similar everywhere. Sun elevation angles were determined by locator aid (BASTrack) using the latitude and longitude of deployment for geolocators recovered at HBEF and by using calibration from stationary geolocators placed on the forest floor at HBEF (-1.82°) as well as geolocators deployed on Ovenbirds at HBEF ($-1.75 \pm 0.14^\circ$). For all geolocators recovered during the non-breeding season, our analyses assumed a sun elevation angle of -1.75° based on 1,034 transition events prior to fall migration collected from 20 geolocators on Ovenbirds breeding at HBEF. A single sun elevation angle was used for all geolocators recovered during the non-breeding season because the true sun elevation angle at the breeding location was unknown and the variation in sun elevation angle between geolocators deployed at the same location and between individual geolocators was small (HBEF: $-1.75 \pm 0.14^\circ$, $n = 20$; Florida: $-3.31 \pm 0.07^\circ$, $n = 3$; Jamaica: $-3.53 \pm 0.13^\circ$, $n = 9$).

Geocator location data collected during the breeding season were used for direct comparison with $\delta^2\text{H}_\text{F}$ values to validate both tools. A longitudinal range for the months

of June and July was created for every bird captured in Jamaica and Florida. A longitudinal range was created because arrival information from HBEF indicated that all birds are present before 1 June if they attempt to breed (M. T. Hallworth et al. unpubl. data); however, the true breeding location was not known for Jamaica and Florida birds. Location data were classified as breeding locations once the geolocator locations fell within the June–July longitudinal range (arrival date range: 2–23 May), at which point we assumed that migration had ceased and individuals attempted to breed. The longitudinal range was used to determine when individuals arrived at breeding locations because changes in latitude could result from migratory movements or uncertainty associated with sunrise and sunset transitions caused by a number of factors (Lisovski et al. 2012). For geolocators recovered from HBEF, location points generated during July of the deployment year, and those generated between the date of arrival at HBEF and the date of recapture during the subsequent recovery year, were used to test the accuracy of geolocators for estimating the breeding location of birds at HBEF.

Stable hydrogen isotopes.—Isotope analysis was performed at the Smithsonian Institution’s Stable Isotope Mass Spectrometry Laboratory in Suitland, Maryland. Tail feathers were washed of debris and surface oils with a 2:1 chloroform:methanol solution and air dried for 48 h under a fume hood. Feathers were allowed to equilibrate with the local atmosphere at the laboratory for 72 h. A small distal sample (non-breeding: 0.345 ± 0.005 mg, $n = 151$, HBEF: 0.346 ± 0.003 mg, $n = 92$) of feather was clipped and loaded into a silver capsule. The feather samples were combusted in an elemental analyzer (Thermo TC/EA; Thermo Scientific, Waltham, Massachusetts) and introduced to an

isotope ratio mass spectrometer (Thermo Scientific Delta V Advantage) via a ConFlo IV interface. One in-house standard was run for every two unknowns to measure the accuracy and precision during sampling. Analytical error (\pm SD) was 2‰, based on replicate analysis of the same feather ($n = 20$). The non-exchangeable hydrogen was determined by linear regression with calibrated in-house keratin standards (spectrum keratin: $-121.6 \pm 0.88\text{‰}$, $n = 20$; CBS: $-197.3 \pm 1.20\text{‰}$, $n = 20$, KHS: $-54.1 \pm 0.91\text{‰}$, $n = 20$; Wassenaar and Hobson 2003). To minimize any potential systematic errors caused by exchangeable hydrogen, we ran all samples within 7 days of one another and included an approximately equal number of samples from Florida and Jamaica for each run (Wassenaar and Hobson 2003). We report isotope ratios for non-exchangeable hydrogen in δ notation in relation to Vienna Standard Mean Ocean Water.

The $\delta^2\text{H}_\text{P}$ values were determined using the interpolated amount-weighted mean $\delta^2\text{H}$ during the growing season from the Global Network of Isotopes in Precipitation database (Bowen et al. 2005). We used two approaches to convert from this $\delta^2\text{H}_\text{P}$ isoscape to a $\delta^2\text{H}_\text{F}$ isoscape that accounted for isotopic differences between precipitation, Ovenbird prey, and feathers. First, adult (after-second-year) breeding Ovenbirds were captured throughout the eastern portion of their breeding range in Maryland ($n = 5$), Michigan ($n = 5$), Missouri ($n = 5$), New Hampshire ($n = 10$), North Carolina ($n = 5$), Vermont ($n = 5$), and West Virginia ($n = 5$). We used a linear mixed model that included capture location as a random intercept to determine a site-specific discrimination equation (hereafter $\delta^2\text{H}_{\text{Fsite-specific}}$) that allowed for potential regional variation in isotopic discrimination (Table 1). Second, we converted $\delta^2\text{H}_\text{P}$ values into $\delta^2\text{H}_\text{F}$ values using the

calibration relationship derived by Hobson et al. (2012) for ground-foraging Neotropical migratory birds (hereafter $\delta^2\text{H}_{\text{Fsite-independent}}$). The site-specific intercept was determined using location data obtained with geolocators. If the 75% kernel density estimate (KDE) derived from geolocators (see below) deployed during the non-breeding season overlapped one of the sampling locations used to create the site-specific calibration relationship ($n = 10$), we chose the intercept for that site to convert $\delta^2\text{H}_\text{P}$ into $\delta^2\text{H}_\text{F}$ (Table 2). None of the 75% KDEs overlapped more than one sampling location. A site-specific intercept was not used when a KDE did not overlap any of the sampling locations ($n = 2$ birds, 1 in Florida and 1 in Jamaica), and those individuals were excluded from analyses comparing assignment accuracy of site-specific intercepts versus site-independent intercepts. For birds breeding at HBEF, we used the site-specific intercept for New Hampshire to determine $\delta^2\text{H}_{\text{Fsite-specific}}$.

Statistical analyses.—To compare $\delta^2\text{H}_\text{F}$ of Ovenbirds with and without geolocators and between non-breeding locations, we used a two-way analysis of variance including individual as a random effect. We used a normal probability density function (Royle and Rubenstein 2004) to determine breeding origin, where the likelihood that each $\delta^2\text{H}_\text{F}$ value, y^* , originates from a given location is:

$$f(y^*|\mu_b, \sigma_b) = \frac{1}{\sqrt{2\pi}\sigma_b} \exp\left[-\frac{1}{2\sigma_b^2}(y^* - \mu_b)^2\right]$$

where μ_b is the specific cell in a given feather isoscape and σ_b is the standard deviation of the residuals from the calibration equation. We used $\sigma_b = 16.40\text{‰}$ for both feather isoscapes because the standard deviation of residuals for calibration relationships were

similar and it was the most conservative. We then incorporated Ovenbird abundance from Breeding Bird Survey routes sampled between 2006 and 2010 (Sauer et al. 2011) as prior information using Bayes's rule:

$$f(b|y) = \frac{f(y|b)f(b)}{\sum_{b=1}^B f(y|b)f(b)}$$

where $f(y|b)$ is the likelihood of assignment to breeding locations and $f(b)$ is the probability that Ovenbirds occur in each breeding location throughout their breeding range. Breeding Bird Survey data were obtained from Patuxent Wildlife Research Center's website. We reclassified each raster cell (approximately 35×35 km) within the breeding-origin assignments into likely (1) or unlikely (0) origin using a 3:1 odds ratio (Chabot et al. 2012). Breeding assignments based on $\delta^2\text{H}_\text{F}$ values were created and reclassified into binary assignments using the "raster" package (Hijmans and van Etten 2011) in R (R Development Core Team 2012).

Kernel density estimates (50%, 75%, and 95%) were created using geolocator location data for each individual during the breeding season, using least-squares cross validation (Barg et al. 2005) to estimate the bandwidth or smoothing parameter with Geospatial Modelling Environment software (Beyer 2012). From these three KDEs, we chose the 75% KDE for subsequent analyses because 19 of 20 individuals (95%) overlapped the true breeding origin with this approach when the breeding location was known (i.e., HBEF: 50% KDE = 14 of 20 [70%]; 95% KDE = 20 of 20 [100%]). Moreover, the 75% KDE was directly comparable with the probability of correct assignment for $\delta^2\text{H}_\text{F}$ under a 3:1 odds ratio. In addition, a single KDE (75% KDE) was created using geolocator data from all birds captured at HBEF. We used Fisher's exact

test to evaluate whether the two methods of assignment using $\delta^2\text{H}_\text{F}$ predicted the same origin estimated using geolocators. The amount of overlap between geolocators and assignment using $\delta^2\text{H}_\text{F}$, both site-independent and site-specific discrimination equations, was quantified in two ways. First, if the 75% KDE produced from geocator data overlapped any portion of the reclassified posterior probability using a 3:1 odds ratio, it was classified as overlapping. Second, the percentage of the 75% KDE that overlapped the reclassified posterior probability was enumerated. The percentage of overlap was classified into >25% and <25% overlap to be consistent with both the 3:1 odds ratio reclassification of $\delta^2\text{H}_\text{F}$ and the 75% KDE produced with geocator data. All statistical analyses were conducted in R, version 2.15.0 (R Development Core Team 2012). Results are presented as means \pm SE.

RESULTS

Twenty geolocators (40%) were recovered from Ovenbirds breeding at HBEF (deployed in 2010: $n = 3$; deployed in 2011: $n = 17$). Forty-six percent of Ovenbirds with geolocators returned to HBEF, which is similar to return rates of Ovenbirds without geolocators ($53 \pm 1.85\%$; Hallworth et al. unpubl. data); three individuals returned carrying geolocators but could not be recaptured (2011: $n = 1$; 2012: $n = 2$), and one returned during 2011 without a geocator attached. The mean number of locations used to determine breeding-origin estimates for birds captured at HBEF was 34 ± 4 ($54.5 \pm 0.6\%$ of location points). Mean $\delta^2\text{H}_\text{F}$ values of Ovenbirds known to have bred at HBEF varied among years (2010: $-70.4 \pm 1.7\text{‰}$; 2011: $-67.4 \pm 1.2\text{‰}$; 2012: $-61.3 \pm 3.0\text{‰}$). The $\delta^2\text{H}_\text{F}$ profiles of individual birds captured in multiple years also showed annual

variation (2010–2011: mean difference = 4.54‰, $t = 2.11$, $df = 28$, $P = 0.044$; 2011–2012: mean difference = 8.60‰, $t = 3.46$, $df = 18$, $P = 0.003$; 2010–2012: mean difference = 12.86‰, $t = 4.03$, $df = 9$, $P = 0.003$). The δ^2H_F values did not differ between birds with geolocators and those without geolocators breeding at HBEF ($t = 0.17$, $df = 45$, $P = 0.86$).

The 75% KDE for 19 of 20 birds (95%) with geolocators breeding at HBEF overlapped HBEF, indicating that the 75% KDE accurately predicted true breeding origin and, thus, provided an unbiased baseline for evaluating the accuracy of assignments made with δ^2H_F for individuals captured during the non-breeding season (Fig. 1). Assignments of δ^2H_F done with a site-specific intercept in the feather-isotope discrimination equation showed strong concordance with 75% KDEs derived from geolocators (Table 2 and Figs. 2, S1, and S2; Figs. S1 and S2 are supplemental materials available with the online version of this article; see Acknowledgments). By contrast, δ^2H_F assignments made with the commonly used site-independent fractionation equation (i.e., Lott et al. 2003, Mazerolle et al. 2005, VanWilgenburg and Hobson 2011) overlapped minimally with KDEs from geolocators. Bayesian analyses that incorporated prior information of Ovenbird abundance across the breeding range yielded posterior probabilities of assignment that more closely matched 75% KDEs calculated from geolocator data for both site-independent and site-specific discrimination factors (Table 2 and Figs. 2, S1, and S2).

We deployed 46 geolocators during the non-breeding seasons of 2010 and 2011. Twelve geolocators were recovered (Florida, 2011: 3 [17%]; Jamaica, 2010: 3 [27%]; 2011: 6 [35%]), 8 from males, 2 from females, and 2 from individuals of unknown sex.

The number of geolocator fixes used to estimate breeding origin between May and 31 July ranged from 44 to 95 (69 ± 9 , $36.1 \pm 0.1\%$).

In general, $\delta^2\text{H}_\text{F}$ assignments of overwintering birds in Florida and Jamaica to unknown breeding origins were similar to the geolocator assignments under both site-specific and site-independent discrimination equations, although the mean $\delta^2\text{H}_\text{F}$ values of Ovenbirds captured in Florida differed from those sampled in Jamaica (Florida: $-45.6 \pm 2.5\text{‰}$; Jamaica: $-52.1 \pm 1.4\text{‰}$; $t = -2.76$, $\text{df} = 108$, $P = 0.007$). Similarly, the $\delta^2\text{H}_\text{F}$ values of birds fitted with geolocators did not differ from those without geolocators at the same non-breeding capture location ($t = -1.18$, $\text{df} = 14$, $P = 0.26$). Both site-specific and site-independent methods produced overlap with 75% KDEs of breeding origin in the same individuals (Table 2), but the site-specific discrimination factor overlapped with more 75% KDEs than the conventional site-independent approach, although the difference was not statistically significant (Table 2). For birds overwintering in Jamaica, the site-specific discrimination resulted in a higher probability of assignment to breeding locations predicted by geolocators in 5 of 8 individuals (Figs. 2 and S1), and for Florida birds, the site-specific discrimination relationship indicated a higher probability of assignment to breeding origins suggested by geolocators in 2 of 3 individuals (Fig. S2). Bayesian assignment of $\delta^2\text{H}_\text{F}$ values that incorporated range-wide variation in Ovenbird abundance reduced the differences in predicted breeding origin made using the site-independent and site-specific discrimination relationship by 50% and 30%, respectively.

DISCUSSION

Although archival light-level geolocators represent an important advance in our ability to track movement and destinations of migratory birds, indirect methods, such as stable isotopes, continue to provide valuable information and are likely to remain in the migratory-connectivity toolbox for many years. Validating the use and assumptions of these indirect techniques to infer breeding origins is therefore essential. We examined how geolocators and stable hydrogen isotopes compared in their ability to assign Ovenbirds to known and unknown breeding origins, and our results indicate that (1) breeding-origin assignments that use $\delta^2\text{H}_\text{F}$ values of unknown origin would be improved substantially by incorporating $\delta^2\text{H}_\text{F}$ values of known breeding birds sampled from the area of potential origin, because of regional differences in isotopic discrimination between $\delta^2\text{H}_\text{P}$ and $\delta^2\text{H}_\text{F}$; and (2) incorporating relative abundance of breeding birds into probabilistic origin assignments using a Bayesian approach (Royle and Rubenstein 2004) provided more accurate breeding assignments than using probabilistic assignments alone. Below, we discuss the implications of these findings.

Accurately assigning individuals to breeding origin using $\delta^2\text{H}_\text{F}$ values depends on the ability of feather isoscapes to encompass sources of the heavy fraction of hydrogen variation in nature. Assignments to breeding origin done with $\delta^2\text{H}_\text{F}$ values are characterized by a high degree of uncertainty because the discrimination between $\delta^2\text{H}_\text{P}$ and $\delta^2\text{H}_\text{F}$ varies in relation to diverse factors (Lott et al. 2003; Hobson et al. 2000, 2012; Haché et al. 2012). Despite rigorous feather-sampling efforts across the breeding range, isoscape values are interpolated across substantial geographic areas and, therefore, may not accurately depict local isotopic variation. Consistent with this idea, we found that the

site-independent discrimination equation, the approach commonly used to assign $\delta^2\text{H}_\text{F}$ values to breeding origin (i.e., Lott et al. 2003, Kelly et al. 2005, Mazerolle et al. 2005, VanWilgenburg and Hobson 2011), led to assignments that differed markedly from the geolocator estimates of breeding origin. Conversely, the site-specific discrimination equation, which accounted for regional differences in discrimination, led to assignments that were more concordant with geolocator estimates.

Geolocators enabled us to incorporate site-specific discrimination equations into $\delta^2\text{H}_\text{F}$ assignments. Although location estimates from geolocators can have high uncertainty because of variation in habitat features, bird behavior, and weather (Fudickar et al. 2012, Lisovski et al. 2012), our geolocator estimates for Ovenbirds encompassed the true breeding location for 95% of individuals when deployed and recovered from a known breeding location at HBEF. Geolocators also provided longitudinal estimates of breeding origin, unlike $\delta^2\text{H}_\text{F}$. However, other intrinsic markers such as genetic markers provide longitudinal information (e.g., Kelly et al. 2005, Chabot et al. 2012) and, in combination with $\delta^2\text{H}_\text{F}$, may improve assignment.

Developing a calibration relationship between $\delta^2\text{H}_\text{P}$ and $\delta^2\text{H}_\text{F}$ to create feather isoscapes with general linear models may be misleading because of regional differences in isotopic discrimination. Instead, building in random effects for different sites (Wunder et al. 2005), like the approach we applied here, may be necessary to determine the accurate origin for individual feathers using $\delta^2\text{H}_\text{F}$. Assigning single individuals to breeding origin may not reflect the origins of an entire population. Here, however, it was necessary to assign individuals to compare the estimates of origin derived from $\delta^2\text{H}_\text{F}$ and

geolocators for the same individual. The site-independent discrimination may not have performed as well as the site-specific equation because few validation locations were used to create the isotopic basemap of the area where our sample population bred (Hobson et al. 2012). In addition, a coastal effect (Lott et al. 2003) may have influenced $\delta^2\text{H}_\text{F}$ values, especially for individuals breeding east of the Appalachian Mountains in North America. Coastal areas are known to have higher $\delta^2\text{H}_\text{F}$ values and relationships between $\delta^2\text{H}_\text{F}$ and $\delta^2\text{H}_\text{P}$ that differ from those found inland because of the marine influence on the prey base (Lott et al. 2003, Kelly et al. 2005). Refining feather isoscapes for individual species by increasing the number of validation locations will likely increase the accuracy of assignments to breeding origin. In addition, including other intrinsic markers that provide longitudinal information such as genetic markers (i.e., Kelly et al. 2005, Chabot et al. 2012) in combination with $\delta^2\text{H}_\text{F}$ may also improve assignment.

Consistent with the results of Royle and Rubenstein (2004), our findings suggest that incorporating breeding bird abundance into probability-based assignments may alleviate the need to incorporate site-specific intercepts when validation locations do not occur throughout the entire breeding range or when prior knowledge of breeding location is not known. Specifically, incorporating breeding bird abundance increased the accuracy of origin assignments, especially where Ovenbirds are abundant. Assignments that incorporated breeding bird abundance accurately assigned 100% of birds when using a site-specific discrimination and 91.7% when the site-independent discrimination was used. In comparison, only 70% and 41.7% of birds were accurately assigned when using

the site-specific and site-independent discrimination, respectively, without accounting for spatial variation in breeding bird abundance. Unfortunately, few isotopic studies have incorporated variation in breeding bird abundance into probabilistic breeding assignments (Royle and Rubenstein 2004, Norris et al. 2006).

A major assumption of assigning breeding origin with $\delta^2\text{H}_\text{F}$ is that birds molt where they breed (e.g., Chabot et al. 2012, Studds et al. 2012), which occurs frequently but may not always be the case (Butler et al. 2002, Leu and Thompson 2002). One of our Ovenbirds equipped with a geolocator (male captured in Jamaica 2011) made a long-distance movement (~800 km) in the middle of the summer, perhaps to a southern staging area or to a second breeding location (Fig. 3; also see Rohwer et al. 2009). Consistent with the geolocator data, the $\delta^2\text{H}_\text{F}$ value suggests that it molted at the second, more southerly location. Relying solely on $\delta^2\text{H}_\text{F}$ would have resulted in missing the first location completely, even though the individual arrived at the northern location on 3 May and departed for the southerly location on 9 July, providing enough time at the more northerly location to reproduce successfully (Van Horn and Donovan 1994, M. T. Hallworth et al. unpubl. data). Although sample sizes are generally small for studies that use geolocators (e.g., Ryder et al. 2011, Stutchbury et al. 2011), our results suggest that the use of stable hydrogen isotopes alone may miss some rare, large-scale movements within the breeding season. Individuals that molt in areas different from those used by the rest of the population will increase variation of $\delta^2\text{H}_\text{F}$ sampled during the non-breeding season. As a consequence, increased variation in $\delta^2\text{H}_\text{F}$ within a non-breeding population will reduce the precision and accuracy of probabilistic assignments when assigning non-

breeding populations to breeding origin. We were not able to assess how often such broad-scale movements occur during the breeding season, given our small sample size of geolocators recovered from Ovenbirds. Even if large-scale movements during the breeding season are rare, they will likely have important implications for interpretations of the ecology and evolution of migratory birds, such as the possibility of “double breeding” (Rohwer et al. 2009) or dispersal dynamics. Further direct comparisons between stable isotopes and geolocators may provide additional insights into the frequency of this phenomenon.

Conclusions.—Our geocator- and isotope-based estimates of origin were not statistically different (Table 2), despite low overlap of estimates for most birds (Figs. 1, 2, S1, and S2). This discrepancy is due in part to the uncertainty of site-independent and site-specific location estimates, even after incorporating range-wide relative Ovenbird abundance into our assignment models. Converting probabilistic, $\delta^2\text{H}_\text{F}$ -based assignments of location into binary assignments and using a 3:1 odds ratio (Chabot et al. 2012) yielded low statistical power to detect differences between geocator and isotope methods, despite our relatively large sample size. Indeed, >85% of our birds would have to have been misclassified for this Fisher’s exact test to have acceptable power (i.e., $1 - \beta \geq 0.8$; $\alpha = 0.05$) to detect a statistically significant difference between assignment methods (Cohen 1988). Therefore, using only $\delta^2\text{H}_\text{F}$ values to assign breeding origin, especially with a site-independent isoscape model, could have led to an erroneous interpretation of migratory connectivity for the Ovenbird. Additional studies that

compare geolocator and $\delta^2\text{H}_\text{F}$ assignments of origin are needed to determine the generality of our findings for other migratory bird species.

ACKNOWLEDGMENTS

Supplemental materials are available at dx.doi.org/10.1525/auk.2013.13037. We thank N. Cooper, J. Gautreaux, D. Narango, R. Reitsma, L. Rowse, R. Terrill, M. Thomas, and C. Tonra for assistance with field work; K. Hobson and S. Van Wilgenburg for providing valuable comments on the manuscript; and E. McKinnon and K. Fraser for organizing and inviting us to present at the Beyond Connectivity: Using Geolocators to Explore Bird Migration Strategies symposium at the North American Ornithological Conference in Vancouver, British Columbia, in 2012. We also thank A. Jahn and two anonymous reviewers for their comments on the manuscript. This research was supported by the James Bond Fund at the Smithsonian Institution (M.T.H. and P.P.M.), the U.S. National Science Foundation (P.P.M. and T.S.S.), and the Cosmos Club (M.T.H.). Ovenbird Breeding Bird Survey data were obtained from Patuxent Wildlife Research Center's relative abundance shapefiles for geographic analysis webpage (www.mbr-pwrc.usgs.gov/bbs/shape_ra10.html).

Table 1. Site-specific discrimination intercepts used for converting $\delta^2\text{H}_\text{P}$ to $\delta^2\text{H}_\text{F}$ isoscapes for geographic assignment of Ovenbirds to breeding origin. Geographic coordinates (latitude, longitude) of the study locations are given for the states in which Ovenbirds were captured. Site-specific intercepts were determined using a linear mixed model incorporating capture site as a random variable. Feather isoscapes were created using a site-independent ($\delta^2\text{H}_\text{Fsite-independent} = -27.09 + 0.95 * \delta\text{H}_\text{P}$; Hobson et al. 2012) and a site-specific ($\delta^2\text{H}_\text{Fsite-specific} = \text{site-specific intercept} + 1.15 * \delta\text{H}_\text{P}$) discrimination equation.

Table 1

Capture location	Coordinates	Site-specific intercept	95% CI
Maryland	38.54, -73.20	11.92	07.95 to 15.87
Michigan	44.65, -84.13	-23.38	-27.34 to -19.42
Missouri	38.35, -93.55	-09.69	-13.65 to -05.73
New Hampshire	43.30, -71.73	21.35	17.40 to 25.32
North Carolina	35.49, -82.99	06.55	02.59 to 10.52
Vermont	44.54, -73.20	-14.76	-18.72 to -10.80
West Virginia	44.65, -84.13	08.01	04.04 to 11.97

Table 2. The amount of overlap between breeding $\delta^2\text{H}_\text{F}$ assignments reclassified using a 3:1 odds ratio for site-independent and site-specific discrimination equations and geolocator estimates of Ovenbirds captured in Jamaica and Florida. The amount of overlap was quantified in two ways: (1) a binary approach, whereby the 75% KDE determined by geolocators was classified as either overlapping or not overlapping any portion of the 3:1 odds ratio assignment (see supplemental materials with the online version of this article); and (2) a percentage of overlap, whereby the 3:1 odds ratio assignment was classified as overlapping >25% or <25% of the 75% KDE determined by geolocators. The observed (Obs.) and expected (Exp.) numbers of individuals using a 3:1 odds ratio are shown for each scenario. The *P* value from a Fisher's exact test is indicated under the corresponding data.

Table 2

	Without breeding bird densities				With breeding bird densities			
	Site-independent		Site-specific		Site-independent		Site-specific	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Overlap	11	9	10	7.5	12	9	10	7.5
No overlap	1	3	0	3.5	0	3	0	2.5
Significance	<i>P</i> = 0.59		<i>P</i> = 0.47		<i>P</i> = 0.22		<i>P</i> = 0.47	
>25%	5	9	7	7.5	11	9	10	7.5
<25%	7	3	3	2.5	1	3	0	2.5
Significance	<i>P</i> = 0.21		<i>P</i> = 0.99		<i>P</i> = 0.59		<i>P</i> = 0.47	

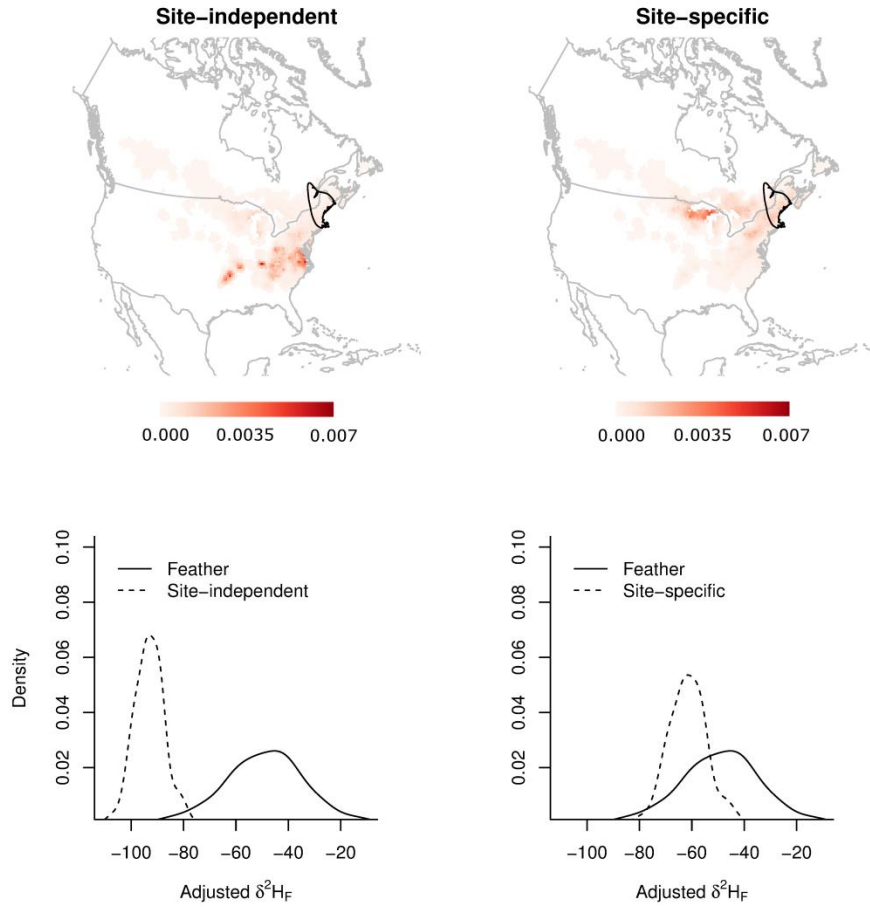


Figure 1

Fig. 1: Posterior probability of origin using δ^2H_F and bird relative abundance with site-independent and site-specific discrimination equations for Ovenbirds breeding at Hubbard Brook Experimental Forest (HBEF), New Hampshire. The 75% kernel density estimate (KDE), represented by the black polygon, includes locations from all 20 geolocators recovered during the breeding season. The color ramp indicates the posterior probability of assignment using δ^2H_F and bird relative abundance. The bottom panels show the normal distribution around the mean δ^2H_F value of birds fitted with geolocators breeding at HBEF (solid line) with a standard deviation of 16.40%, which was used to create breeding assignments. The density of values under the curve is represented by the y-axis. The adjusted δ^2H_F value after including breeding bird density in assignment under the 75% KDE using the site-independent and site-specific discrimination equations to create the feather isoscape (dotted line) is also shown. The map projection is North American Lambert Conformal Conic.

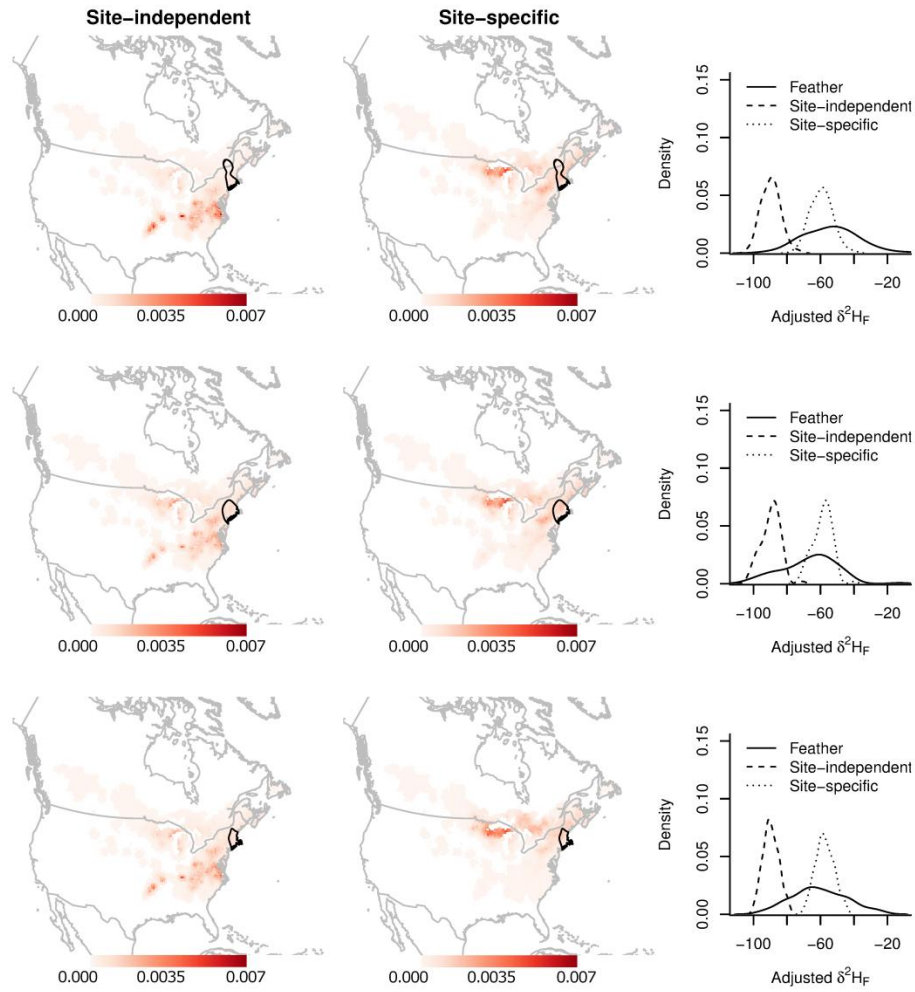


Figure 2

Fig. 2. Posterior probability of origin using $\delta^2\text{H}_F$ and bird relative abundance with site-independent and site-specific discrimination equations for 3 of 9 birds fitted with geolocators captured at Font Hill Nature Preserve, St. Elizabeth Parish, Jamaica, during the non-breeding season (see Fig. S1, available with the online version of this article). Each row corresponds to a different individual fitted with a geolocator. The right column shows the normal distribution around the mean $\delta^2\text{H}_F$ value from feathers collected upon recapture (solid line; $\text{SD} = 16.40\text{‰}$), which was used to create breeding assignments (see Fig. 1 caption). The adjusted $\delta^2\text{H}_F$ value after including relative abundance of breeding birds in assignment under the 75% kernel density estimate using site-independent discrimination equation (hashed line) and site-specific discrimination equation (dotted line) to create the feather isoscape is also shown. The map projection is North American Lambert Conformal Conic.

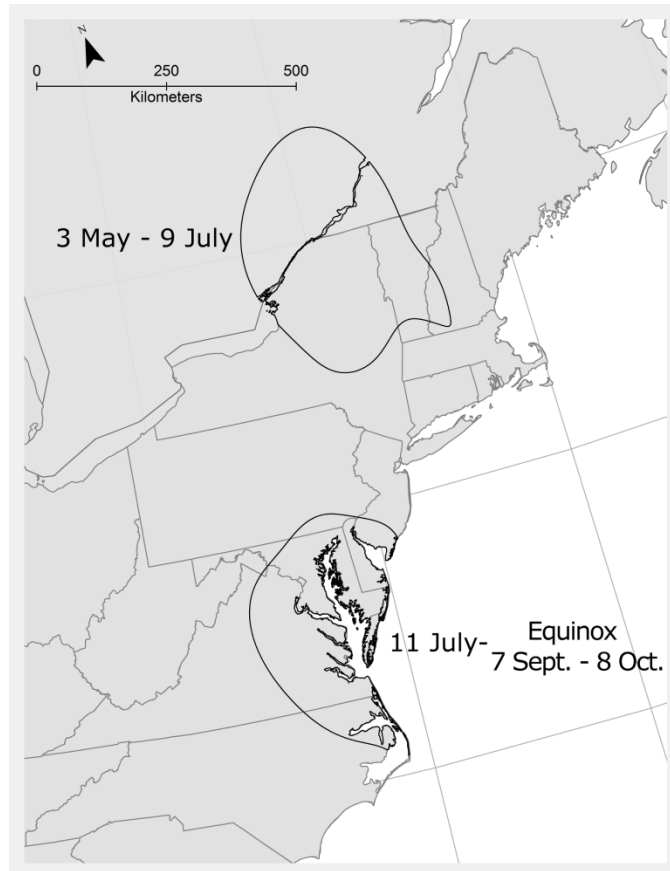


Figure 3

Fig. 3. Movement of a male Ovenbird, determined by geolocator data during the summer of 2011. The polygons represent the 75% kernel density estimate of geolocator points during generated from 3 May until 31 July. The bird arrived at the northern location on 3 May and migrated to the second location on 10 July, where it remained until the period around fall equinox (7 September–8 October) where latitude estimates determined by geolocators are not reliable (see text).

Online Supplemental Information

METHODS

Sex.—Ovenbirds (*Seiurus aurocapilla*) are monomorphic and cannot be reliably sexed when captured during the non-breeding season. A subset of individuals captured at Font Hill Nature Preserve, St. Elizabeth Parish, Jamaica, were sexed genetically using blood samples taken from the brachial artery (C. Tonra et al. unpubl. data). The morphological data (tarsus, wing, tail, bill length from tip to nares, bill width, and bill depth measured at the nares) of genetically sexed individuals captured in Jamaica as well as morphometric data from individuals breeding at Hubbard Brook Experimental Forest (HBEF) were used as prior probabilities in a discriminant function analysis using leave-one-out cross validation (Dechaume-Moncharmont et al. 2011) to determine the sex of Ovenbirds captured in Jamaica and Florida. We assigned a sex to an individual if the posterior probability was >80%; we classified the individual as “sex unknown” if the posterior probability was <80%. The number of individuals that were reliably sexed (posterior probability >80%) using a discriminant function analysis based on morphometric data was 117 of 193 individuals (61%; Jamaica: $n = 41$ males, $n = 33$ females; Florida: $n = 40$ males, $n = 3$ females).

Geolocator.—Light data were transformed into latitude (stationary) and longitude using BASTRACK software (British Antarctic Survey). Both noon and midnight locations were used to determine breeding locations. Ovenbirds were assumed to remain on their territory during the breeding season; thus, locations should not have been affected by either diurnal or nocturnal movements during the breeding season. Transition events were

inspected for smooth light transitions during sunrise and sunset. Transition events that encompassed shading events, were abrupt or shallow, or exhibited “peaks” prior to sunrise were considered low-quality transitions (McKinnon et al. 2013). Low-quality transitions increase the uncertainty associated with the time of sunrise and sunset, which are used to determine geographic location; thus, they were removed from the analysis. The amount of low-quality transitions was due to a large number of shading events during transitions, particularly during sunrise. Ovenbirds inhabit deciduous and mixed-deciduous coniferous forests. Their domed nests are located on the ground, and they forage primarily on the forest floor (Van Horn and Donovan 1994), all of which likely increased the number of shading events during transition events.

Stable isotopes.—We used a general linear mixed model to determine the discrimination relationship between $\delta^2\text{H}_\text{P}$ and $\delta^2\text{H}_\text{F}$ of adult Ovenbirds sampled at validation locations throughout the eastern portion of their breeding distribution. We included validation location as a random intercept in the model to allow for regional differences in the discrimination relationship between $\delta^2\text{H}_\text{P}$ and $\delta^2\text{H}_\text{F}$. We created one site-specific feather isoscape for each validation location using the equation $\delta\text{H}_{\text{Fsite-specific}} = \text{site-specific intercept} + 1.15 * \delta\text{H}_\text{P}$ (Table 2). We used geolocator breeding estimates to determine which site-specific isoscape to use for assigning origin using $\delta^2\text{H}_\text{F}$. If the 75% kernel density estimate (KDE) produced from geolocator data overlapped one of our validation locations ($n = 10$ of 12 birds), we used that site-specific isoscape to determine breeding origin using $\delta^2\text{H}_\text{F}$. The standard deviation of the residuals from the general linear mixed model that included validation site as a random intercept was used to

determine origin using the spatially explicit normal probability density function (Royle and Rubenstein 2004). The spatially explicit normal probability density function was then normalized by dividing by the sum of the density function across the surface. This produced a spatially explicit, probability-based map of origin.

Ovenbird relative abundance determined from breeding-bird survey data (Sauer et al. 2011) was transformed into a probability surface by dividing each cell within the raster by the sum of the raster layer. The resulting probability surface of Ovenbird abundance was used as a prior probability in a Bayesian framework to determine a bird's origin using δ^2H_F . Following the formula for Bayes's rule, the product of the Ovenbird abundance and the spatially explicit normal probability density function produced the posterior probability of breeding origin based on δ^2H_F values. The posterior probability of origin was then reclassified into a binary surface of likely (1) and unlikely (0) origin using a 3:1 odds ratio (Chabot et al. 2012), where the upper 75% of the posterior probability was reclassified as likely origin.

Fisher's exact tests were used to determine the degree of overlap between origin estimates produced by geolocators and δ^2H_F . The amount of overlap between the two methods was quantified in two ways (see text). The number of overlapping raster cells was not used because each 75% KDE was a different size and overlapped a different number of raster cells. The percentage of overlap was classified into >25% and <25% overlap to be consistent with both the 3:1 odds ratio reclassification of δ^2H_F and the 75% KDE produced with geolocator data.

Table S1. Sex of Ovenbirds that received geolocators. Sex was determined using a discriminant function analysis (see supplemental Methods) using morphometric measurements from individuals of known sex captured at Hubbard Brook Experimental Forest (HBEF), New Hampshire, and genetically sexed individuals captured in Jamaica as prior probabilities.

Table 3

	2010		2011		
	HBEF	Jamaica	HBEF	Jamaica	Florida
Male	16	4	34	10	12
Female	1	3	0	1	1
Unknown sex	0	4	0	6	5
<i>n</i>	17	11	34	17	18

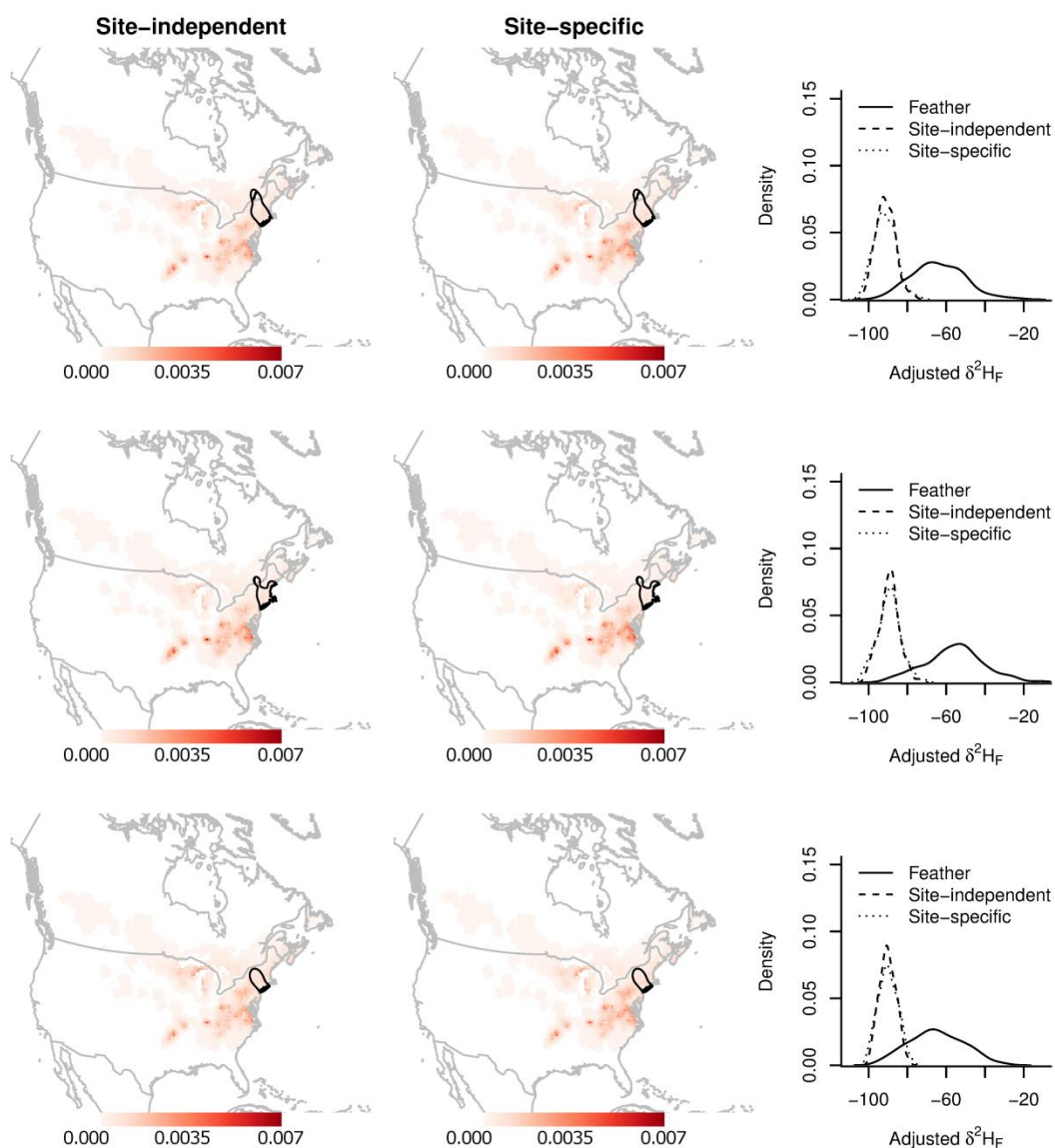


Figure 4

Fig. S1. Posterior probability of origin using δ^2H_F and bird relative abundance with site-independent and site-specific discrimination equations for the 9 birds fitted with geolocators captured at Font Hill Nature Preserve, St. Elizabeth Parish, Jamaica, during the non-breeding season (see Fig. 2 caption).

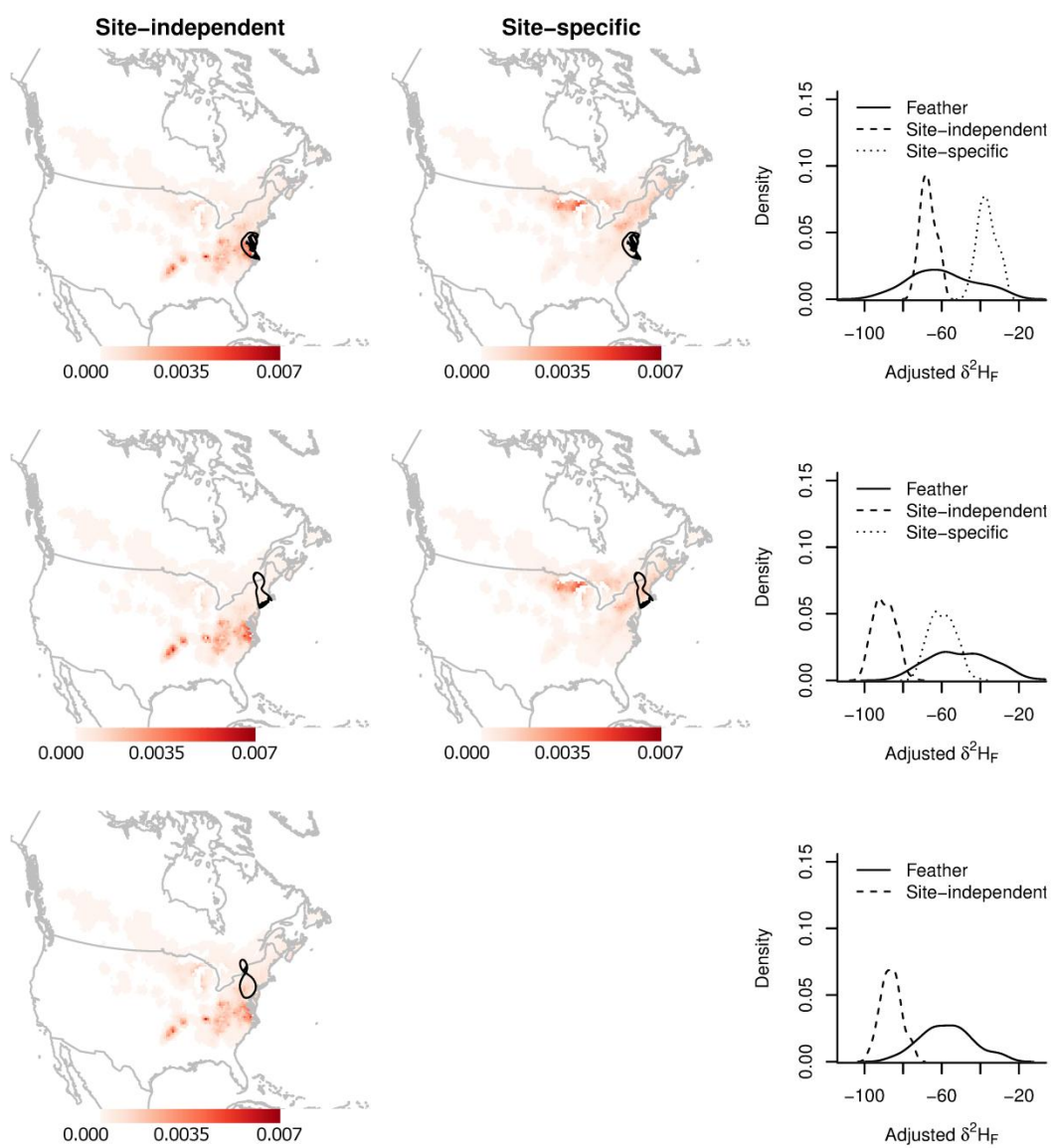


Fig. S1. continued

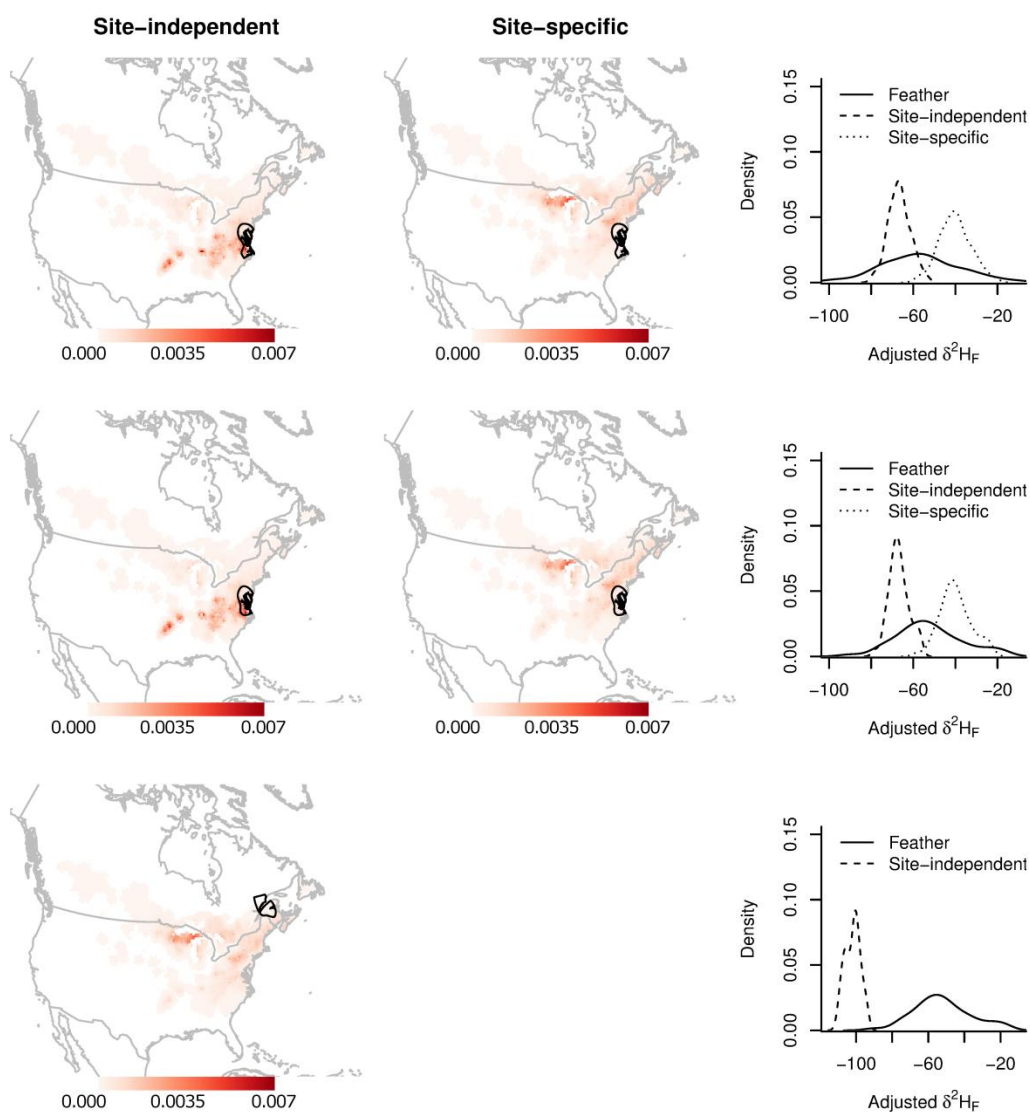


Figure 5

Fig. S2. Posterior probability of origin using δ^2H_F and bird relative abundance with site-independent and site-specific discrimination equations for birds captured in Everglades National Park, Florida, during the non-breeding season (see Fig. 2 caption).

LITERATURE CITED

- Barg, J. J., J. Jones, and R. J. Robertson. 2005. Describing breeding territories of migratory passerines: Suggestions for sampling, choice of estimator, and delineation of core areas. *Journal of Animal Ecology* 74:139–149.
- Beyer, H. L. 2012. Geospatial Modelling Environment, version 0.7.1.0. Available online at www.spatialecology.com/gme.
- Boulet, M., H. L. Gibbs, and K. A. Hobson. 2006. Integrated analysis of genetic, stable isotope, and banding data reveal migratory connectivity and flyways in the Northern Yellow Warbler (*Dendroica petechia*; *aestiva* group). Pages 29–78 in *Patterns of Migratory Connectivity in Two Nearctic-Neotropical Songbirds: New Insights from Intrinsic Markers* (M. Boulet and D. R. Norris, Eds.). Ornithological Monographs, no. 61.
- Bowen, G. J., L. I. Wassenaar, and K. A. Hobson. 2005. Global application of stable hydrogen and oxygen isotopes to wildlife forensics. *Oecologia* 143:337–348.
- Bowlin, M. S., P. Henningsson, F. T. Muijres, R. H. E. Vleugels, F. Liechti, and A. Hedenström. 2010. The effects of geolocator drag and weight on the flight ranges of small migrants. *Methods in Ecology and Evolution* 1:398–402.
- Butler, L. K., M. G. Donahue, and S. Rohwer. 2002. Molt-migration in Western Tanagers (*Piranga ludoviciana*): Age effects, aerodynamics, and conservation implications. *Auk* 119:1010–1023.
- Chabot, A. A., K. A. Hobson, S. L. Van Wilgenburg, G. J. McQuat, and S. C. Loughheed. 2012. Advances in linking wintering migrant birds to their breeding-ground origins using combined analyses of genetic and stable isotope markers *PLoS ONE* 7(8):e43627.
- Chamberlain, C. P., J. D. Blum, R. T. Holmes, X. Feng, T. W. Sherry, and G. R. Graves. 1997. The use of isotope tracers for identifying populations of migratory birds. *Oecologia* 109:132–141.
- Clark, I. D., and P. Fritz. 1997. *Environmental isotopes in hydrogeology*. Lewis Publishers, New York, New York.

- Clegg, S. M., J. F. Kelly, M. Kimura, and T. B. Smith. 2003. Combining genetic markers and stable isotopes to reveal population connectivity and migration patterns in a Neotropical migrant, Wilson's Warbler (*Wilsonia pusilla*). *Molecular Ecology* 12:819–830.
- Cohen, J. 1988. *Statistical Power Analysis for the Behavioral Sciences*, 2nd ed. Lawrence Erlbaum, Hillsdale, New Jersey.
- Faaborg, J., and W. J. Arendt. 1984. Population sizes and philopatry of winter resident warblers in Puerto Rico. *Journal of Field Ornithology* 55:376–378.
- Fudickar, A. M., M. Wikelski, and J. Partecke. 2012. Tracking migratory songbirds: Accuracy of light-level loggers (geolocators) in forest habitats. *Methods in Ecology and Evolution* 3:47–52.
- Haché, S., K. A. Hobson, M.-A. Villard, and E. M. Bayne. 2012. Assigning birds to geographic origin using feather hydrogen isotope ratios ($\delta^2\text{H}$): Importance of year, age, and habitat. *Canadian Journal of Zoology* 90:722–728.
- Hijmans, R. J., and J. van Etten. 2012. Raster: raster: Geographic data analysis and modeling. R package, version 2.0-41. Available online at CRAN.R-project.org/package=raster.
- Hobson, K. A. 1999. Tracing origins and migration of wildlife using stable isotopes: A review. *Oecologia* 120:314–326.
- Hobson, K. A., R. B. Brua, W. L. Hohman, and L. I. Wassenaar. 2000. Low frequency of “double molt” of remiges in Ruddy Ducks revealed by stable isotopes: Implications for tracking migratory water-fowl. *Auk* 117:129–135.
- Hobson, K. A., S. L. Van Wilgenburg, L. I. Wassenaar, and K. Larson. 2012. Linking hydrogen ($\delta^2\text{H}$) isotopes in feathers and precipitation: Sources of variance and consequences for assignment to isoscapes. *PLoS ONE* 7:e35137.
- Hobson, K. A., and L. I. Wassenaar. 1997. Linking breeding and wintering grounds of Neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. *Oecologia* 109:142–148.
- Hobson, K. A., L. I. Wassenaar, and E. Bayne. 2004. Using isotopic variance to detect long-distance dispersal and philopatry in birds: An example with Ovenbirds and American Redstarts. *Condor* 106:732–743.

- Hobson, K. A., L. I. Wassenaar, B. Milá, I. Lovette, C. Dingle, and T. B. Smith. 2003. Stable isotopes as indicators of altitudinal distributions and movements in an Ecuadorean hummingbird community. *Oecologia* 136:302–308.
- Kelly, J. F., K. C. Ruegg, and T. B. Smith. 2005. Combining isotopic and genetic markers to indentify breeding origins of migrant birds. *Ecological Applications* 15:1487–1494.
- Leu, M., and C. W. Thompson. 2002. The potential importance of migratory stopover sites as flight feather molt staging areas: A review for Neotropical migrants. *Biological Conservation* 106:45–56.
- Lisovski, S., C. M. Hewson, R. H. G. Klaassen, F. Korner-Nievergelt, M. W. Kristensen, and S. Hahn. 2012. Geolocation by light: Accuracy and precision affected by environmental factors. *Methods in Ecology and Evolution* 3:603–612.
- Lott, C. A., T. D. Meehan, and J. A. Heath. 2003. Estimating the latitudinal origins of migratory birds using hydrogen and sulfur stable isotopes in feathers: Influence of marine prey base. *Oecologia* 134:505–510.
- Marra, P. P., D. Hunter, and A. M. Perrault. 2011. Migratory connectivity and the conservation of migratory animals. *Environmental Law* 41:317–354.
- Marra, P. P., D. R. Norris, S. M. Haig, M. Webster, and J. A. Royle. 2006. Migratory connectivity. Pages 157–183 *in* *Connectivity Conservation* (K. R. Crooks and M. Sanjayan, Eds.). *Conservation Biology*, no. 14.
- Mazerolle, D. F., K. A. Hobson, and L. I. Wassenaar. 2005. Stable isotope and band-encounter analyses delineate migratory patterns and catchment areas of White-throated Sparrows at a migration monitoring station. *Oecologia* 144:541–549.
- McKinnon, E. A., C. Q. Stanley, K. C. Fraser, M. M. MacPherson, G. Casbourn, P. P. Marra, C. E. Studds, N. Diggs, and B. J. M. Stutchbury. 2013. Estimating geolocator accuracy for a migratory songbird using live ground-truthing in tropical forest. *Animal Migration* 1:31–38.
- Naef-Daenzer, B. 2007. An allometric function to fit leg-loop harnesses to terrestrial birds. *Journal of Avian Biology* 38:404–407.
- Norris, D. R., P. P. Marra, G. J. Bowen, L. M. Ratcliffe, J. A. Royle, and T. K. Kyser. 2006. Migratory connectivity of a widely distributed songbird, the American Redstart (*Setophaga ruticilla*). Pages 14–28 *in* *Patterns of Migratory Connectivity in Two Nearctic-Neotropical Songbirds: New Insights from Intrinsic Markers* (M. Boulet and D. R. Norris, Eds.). *Ornithological Monographs*, no. 61.

- Pain, D. J., R. E. Green, B. Gießing, A. Kozulin, A. Poluda, U. Ottosson, M. Flade, and G. M. Hilton. 2004. Using stable isotopes to investigate migratory connectivity of the globally threatened Aquatic Warbler *Acrocephalus paludicola*. *Oecologia* 138:168–174.
- Pyle, P. 1997. Identification Guide to North American Birds, part 1. Slate Creek Press, Bolinas, California.
- R Development Core Team. 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
- Robinson, W. D., M. S. Bowlin, I. Bisson, J. Shamoun-Baranes, K. Thorup, R. H. Diehl, T. H. Kunz, S. Mabey, and D. W. Winkler. 2009. Integrating concepts and technologies to advance the study of bird migration. *Frontiers in Ecology and the Environment* 8:354–361.
- Rohwer, S., L. K. Butler, and D. R. Froehlich. 2005. Ecology and demography of east–west differences in molt scheduling of Neotropical migrant passerines. Pages 87–105 in *Birds of Two Worlds: The Ecology and Evolution of Migration* (R. Greenberg and P. P. Marra, Eds.). Johns Hopkins University Press, Baltimore, Maryland.
- Rohwer, S., K. A. Hobson and V. G Rohwer. 2009. Migratory double breeding in Neotropical migrant birds. *Proceedings of the National Academy of Sciences U.S.A.* 106:19050–19055.
- Royle, J. A., and D. R. Rubenstein. 2004. The role of species abundance in determining breeding origins of migratory birds with stable isotopes. *Ecological Applications* 14:1780–1788.
- Ryder, T. B., J. W. Fox, and P. P. Marra. 2011. Estimating migratory connectivity of Gray Catbirds (*Dumetella carolinensis*) using geolocator and mark–recapture data. *Auk* 128:448–453.
- Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2011. The North American Breeding Bird Survey, Results and Analysis 1966–2010. Version 12.07.2011. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland.
- Shaffer, S. A., Y. Tremblay, H. Weimerskirch, D. Scott, D. R. Thompson, P. M. Sagar, H. Moller, G. A. Taylor, D. G. Foley, B. A. Block, and D. P. Costa. 2006. Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an

endless summer. *Proceedings of the National Academy of Sciences USA* 103:12799–12802.

Studds, C. E., K. P. McFarland, Y. Aubry, C. C. Rimmer, K. A. Hobson, P. P. Marra, and L. I. Wassenaar. 2012. Stable-hydrogen isotope measures of natal dispersal reflect observed population declines in a threatened migratory songbird. *Diversity and Distributions* 18:919–930.

Stutchbury, B. J. M., E. A. Gow, T. Done, M. MacPherson, J. W. Fox, and V. Afanasyev. 2011. Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. *Proceedings of the Royal Society of London, Series B* 278:131–137.

Stutchbury, B. J. M., S. A. Tarof, T. Done, E. Gow, P. M. Kramer, J. Tautin, J. W. Fox, and V. Afanasyev. 2009. Tracking long-distance songbird migration by using geolocators. *Science* 323:896.

Van Horn, M. A., and T. M. Donovan. 1994. Ovenbird (*Seiurus aurocapilla*). In *The Birds of North America*, no. 88 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Van Wilgenburg, S. L., and K. A. Hobson. 2011. Combining stable-isotope (δD) and band recovery data to improve probabilistic assignment of migratory birds to origin. *Ecological Applications* 21:1340–1351.

Wassenaar, L. I., and K. A. Hobson. 2003. Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. *Isotopes in Environmental and Health Studies* 39:211–217.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: Unraveling migratory connectivity. *Trends in Ecology & Evolution* 17:76–83.

Wunder, M. B., C. L. Kester, F. L. Knopf, and R. O. Rye. 2005. A test of geographic assignment using isotope tracers in feathers of known origin. *Oecologia* 144:607–617.

SUPPLEMENTAL-

Chabot, A. A., K. A. Hobson, S. L. Van Wilgenburg, G. J. McQuat, and S. C. Loughheed. 2012. Advances in linking wintering migrant birds to their breeding-ground

origins using combined analyses of genetic and stable isotope markers PLoS ONE 7(8):e43627.

Dechaume-Moncharmont, F.-X., K. Monceau, and F. Cézilly. 2011. Sexing birds using discriminant function analysis: A critical appraisal. *Auk* 128:78–86.

McKinnon, E. A., C. Q. Stanley, K. C. Fraser, M. M. MacPherson, G. Casbourn, P. P. Marra, C. E. Studds, N. Diggs, and B. J. M. Stutchbury. 2013. Estimating geolocator accuracy for a migratory songbird using live ground-truthing in tropical forest. *Animal Migration* 1:31–38.

Royle, J. A., and D. R. Rubenstein. 2004. The role of species abundance in determining breeding origins of migratory birds with stable isotopes. *Ecological Applications* 14:1780–1788.

Van Horn, M. A., and T. M. Donovan. 1994. Ovenbird (*Seiurus aurocapilla*). In *The Birds of North America*, no. 88 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

CHAPTER 3: MIGRATORY CONNECTIVITY OF A NEOTROPICAL MIGRATORY SONGBIRD REVEALED BY ARCHIVAL LIGHT-LEVEL GEOLOCATORS

Michael T. Hallworth^{1,2,5}, T. Scott Sillett¹, Steven L. VanWilgenburg^{3,4}, Keith A.
Hobson³, and Peter P. Marra¹

¹Migratory Bird Center, Smithsonian Conservation Biology Institute, National
Zoological Park, MRC 5503, Washington DC 20013

²College of Science, George Mason University, 4400 Patriot Drive, Fairfax VA.
22030

³Environment Canada, 11 Innovation Blvd., Saskatoon, SK, Canada, S7N 3H5.

⁴Environment Canada, 115 Perimeter Road., Saskatoon, SK, Canada, S7N 0X4

⁵E-mail: mhallwor@masonlive.gmu.edu

This chapter was submitted to Ecological Applications in its current state

ABSTRACT

Understanding migratory connectivity is critical for interpreting population dynamics, seasonal interactions and for the implementation of conservation strategies of migratory species. To date, research on migratory connectivity of small birds has mostly been conducted from breeding locations. We evaluated the migratory connectivity of a Neotropical migratory songbird, the Ovenbird (*Seiurus aurocapilla*) using archival light-level geolocators deployed at two breeding and four non-breeding locations while incorporating Ovenbird abundance as prior information using Bayes' Rule. We also included band recoveries submitted to the United States Geological Survey's Bird Banding Laboratory to assess connectivity of areas where geolocators were not deployed. We created a probabilistic map of origin for each capture site and mapped spring migration routes between non-breeding and breeding locations. We found a complete separation of eastern and western populations of Ovenbirds throughout the annual cycle. Breeding Ovenbirds from western Canada spent the non-breeding season throughout Central America and migrated through central North America during spring migration. Birds breeding in northeastern United States were distributed throughout the central Greater Antilles in the Caribbean and migrated through eastern North America during spring migration. Fall migration routes were not included because the timing of migration coincided with fall equinox when latitudinal estimates are unreliable. Ovenbirds with geolocators attached in Jamaica bred in the northeastern United States with the highest posterior probability of origin found in Massachusetts, while Ovenbirds captured in Florida and Puerto Rico bred primarily in the mid-Atlantic. Incorporating Ovenbird

abundance as a prior into geolocator estimates decreased the area of origin by $90.37\% \pm 1.05\%$ for the breeding season and $62.30\% \pm 1.69\%$ for the non-breeding season, compared to geolocator estimates alone. Ovenbirds exhibited strong migratory connectivity between breeding and non-breeding season which has important implications for various aspects of the ecology, evolution and conservation.

KEYWORDS

Bayesian, Caribbean Basin, Conservation biogeography, Geo-logger, Migration, Movement ecology, Ovenbird (*Seiurus aurocapilla*), Probability of origin, Spatial-distribution

INTRODUCTION

Elucidating patterns of migratory connectivity, the degree to which breeding and non-breeding populations of migratory species are geographically linked, is essential for advancing our understanding of most facets of the ecology and evolution of these species as well as for prioritizing conservation efforts (Webster et al. 2002, Marra et al. 2006, 2011). Identifying the strength of migratory connectivity has been especially difficult for small migratory organisms such as songbirds because of the geographic scales over which they occur annually and because their small size generally precluded the attachment of tracking devices.

The miniaturization of archival light-level geolocators (hereafter geolocators) has facilitated the tracking of individual songbirds as they move between breeding and non-breeding locations (Stutchbury et al. 2009, Ryder et al. 2011, Renfrew et al. 2013,

Laughlin et al. 2013). Geolocators provide temporally and spatially explicit estimates of geographical location that include approximate latitudinal and longitudinal coordinates. Although geolocators have drawbacks, including cost, the need to recapture individuals, often low recovery rates related to potential effects on survival and behavior (Gómez et al. 2013., Arlt et al. 2013, Costantini and Møller 2013), and uncertainty in assigning light transition events to latitude and longitude (Lisovski et al. 2012), geolocators have increased our understanding of migratory connectivity for several species (e.g., Stutchbury et al. 2009, Heckscher et al. 2011, Ryder et al. 2011, Stanley et al. 2012, Renfrew et al. 2013, Contina et al. 2013).

Because passive extrinsic markers like geolocators only provide information on individuals initially marked, they must be deployed in multiple locations throughout a species' range to gain a broader understanding of migratory connectivity. The majority of geocator studies have thus far been conducted during the breeding season (Stutchbury et al. 2009, Heckscher et al. 2011, Ryder et al. 2011) and usually at a small number of deployment locations limited to only a small portion of a species range. Thus, with few exceptions (Stanley et al., 2012; McKinnon et al., 2013), our understanding of migratory connectivity is biased towards where breeding populations spend the non-breeding season.

Here, we examine the migratory connectivity of a small (~18g) passerine, the Ovenbird (*Seiurus aurocapilla*), throughout its breeding and non-breeding range. Ovenbirds are a widely distributed species in both the breeding and non-breeding seasons and are capable of carrying geolocators throughout the annual cycle (Hallworth et al.

2013), making them an ideal species for quantifying migratory connectivity. We deployed geolocators at two widely separated (>2700 km) locations during the breeding season and four locations throughout the non-breeding range to determine the strength of migratory connectivity. We predicted that breeding populations of Ovenbirds in eastern and western North America would correspondingly spend the non-breeding season in the eastern and western parts of their non-breeding range. Similarly, we predicted that Ovenbirds captured in eastern, central and western portions of the Caribbean basin would breed in eastern, central and western North America and migrate through eastern, central, and mid-western North America, respectively. We also predicted that Ovenbirds captured in the northern portion of their non-breeding distribution would breed further south than birds captured in the southern extent of their non-breeding distribution, consistent with leapfrog migration (Langin et al. 2009).

METHODS

Breeding season fieldwork was conducted at the Hubbard Brook Experimental Forest (HBEF), New Hampshire, USA (43.93° N, 71.93° W) and Prince Albert National Park, Saskatchewan, CA (53.89° N, 106.16° W). During the non-breeding season, we conducted field work in Everglades National Park, Florida, USA (25.13° N, 80.94° W) Guanica Dry Forest, Puerto Rico (17.97° N, 66.87° W), Fonthill Nature Preserve, St. Elizabeth Parish, Jamaica (18.04° N, 77.94° W), and at the Belize Foundation for Education and the Environment, Toledo District, Belize (16.55° N, 88.69° W). At two breeding and four non-breeding locations, Ovenbirds were captured using simulated

territorial intrusions and passive mist-netting techniques (Faaborg and Arendt 1984). We attached geolocators (British Antarctic Survey, Models MK12 [1.0g] and MK20SALT [0.9g]) to individuals >19.0g with a leg harness technique (Naef-Daenzer 2007). We deployed 51 on birds breeding at HBEF in 2010 (n = 17) and 2011 (n = 34) and 46 on birds breeding at Prince Albert National Park, Canada in 2011. Eighteen geolocators were attached to Ovenbirds in Everglades National Park, Florida, USA during the 2010-2011 non-breeding season. Twenty-eight geolocators were deployed during the 2009-2010 (n = 11) and 2010-2011 (n = 17) non-breeding seasons in Jamaica, while 18 and 21 were attached in Puerto Rico and Belize respectively during the 2011-2012 non-breeding season. We attempted to recapture these individuals during the subsequent year to retrieve the geolocators.

Geolocator data analysis-

Light data were transformed into estimated positions (latitude and longitude) using BASTRACK version 19.0 (British Antarctic Survey, Cambridge, UK; www.birdtracker.co.uk). Transitions were determined using TRANSEDIT (British Antarctic Survey) with a threshold value of 5. We set the minimum dark period to 4 hours and removed any transitions that were less than 4 hours apart; transition data were used to determine the sun elevation angle of the different capture locations (Table 1). To ensure that the sun elevation angle was representative of the capture location, only transitions that occurred while at the capture site were used (Non-breeding: Deployment date – 31 March and 1 Dec – re-capture date; Breeding: Deployment date – 31 July and Arrival date (if known or 1 June if unknown) – re-capture date). We used two sun

elevation angles to determine individual locations during the breeding and non-breeding seasons. The sun elevation angle of the capture location was used to determine either the breeding or non-breeding season locations (McKinnon et al. 2013). We then used the mean sun elevation angle for the other portion of the year (breeding: -1.335° , non-breeding: -3.409°) to determine locations because sun elevation angles were similar between individuals at the same capture location (Hallworth et al. 2013) and the true sun elevation angle was unknown. A third sun elevation angle was used to identify the non-breeding location of two individuals breeding at Prince Albert National Park, Saskatchewan because the mean non-breeding season sun elevation angle (-3.409°) identified the non-breeding exclusively over the Gulf of Mexico. The sun elevation angle from a reference geolocator placed near the forest floor in Belize (1.194° , Table 1) was used instead for these two Ovenbirds.

Geographic locations can be determined from archived light intensity levels to estimate sunrise and sunset times and thereby calculate day length and the time of midday giving latitude and longitude respectively for two location estimates per 24 hour period (Hill 1994). Non-breeding locations were identified as estimated positions occurring between 1 November and 31 March. All data collected during the spring equinox (3 March – 4 April) were removed because latitude is not reliably estimated during that timeframe as day length is similar everywhere. Breeding locations were identified as geolocator positions that occurred between 1 June and 31 July. The first of June was used as the start of the breeding to avoid positions obtained during migration.

To determine probable breeding and non-breeding locations of individuals, we separately fit kernel density estimates (KDE) to geolocator positions for each individual. We used least-squares cross validation (LSCV) to estimate bandwidth (Gaussian smoothing parameter) (Barg et al. 2005) for each KDE, which were generated using all breeding (1 June-31 July) and non-breeding (1 Nov-31 March) locations. KDEs did not include locations that occurred during the period around spring equinox (3 March – 4 April). Precision in geolocator estimates was similar for geolocators deployed during breeding (median = 521,506 km², 95% CI: 401,189 - 641,823 km²) and non-breeding (median = 565,115 km², 95% CI: 225,019 - 905,211 km²) seasons.

We further refined probable breeding and non-breeding locations of individuals using Ovenbird abundance as prior probabilities in a Bayesian framework (Royle and Rubenstein 2004, Norris et al. 2006). Ovenbird abundance during the breeding (Sauer et al. 2012) or non-breeding season (see below), depending on capture location, were used as prior probabilities in Bayes' Rule:

$$f(b|y) = \frac{f(y|b)f(b)}{\sum_{b=1}^B f(y|b)f(b)}$$

where $f(y|b)$ is the kernel density estimate determined from geolocators and $f(b)$ is the probability of being randomly drawn from the population given Ovenbird abundance.

The abundance of Ovenbirds was estimated from Breeding Bird Survey data (Sauer et al. 2012) for the breeding season, and from eBird checklists (Avian Knowledge Network accessed 16 March 2013) reported from the Ovenbirds non-breeding range (see Ridgely et al. 2003).

Non-breeding Abundance-

Non-breeding abundance maps were created from eBird checklists that reported observer effort, every species detected, provided the number of Ovenbirds detected, and were collected between 1 November –31 March 2010-2013. The number of eBird checklists submitted within the wintering distribution of Ovenbirds between 1 November and 31 March has increased exponentially since 2009 (Figure S1). Checklists submitted between 2010-2013 were pooled to increase the likelihood that sites were sampled multiple times between 1 November and 31 March. To maximize the amount of coverage across the non-breeding distribution we assumed no change in abundance between 2010 and 2013. Encounter histories were structured by month between November and March resulting in five sampling occasions at 17,103 sites. Geolocator data suggest that some individuals arrive to non-breeding sites during the month of October and begin northward migration during April. Therefore, we excluded October and April to maintain the assumption of population closure (MacKenzie et al. 2002). The total number of Ovenbirds seen at a location during the encounter intervals was used to estimate abundance. Ovenbirds were assumed absent if no Ovenbirds were observed and all species were reported for a particular checklist. Longitude, elevation and the mean difference of Normalized Difference Vegetation Index (NDVI) between March and November of locations were used as covariates in the candidate model set. We considered models with main effects and included models with up to second order polynomial (quadratic) terms for longitude and elevation. Longitude was included in the candidate model set to test whether abundance was highest in the center of the non-breeding distribution. Elevation was included to determine whether Ovenbird abundance changes

along an elevation gradient. The difference between March and November NDVI values were included in the candidate model set as a proxy for habitat type (values < 0 indicate browning, values $= 0$ indicates no change, values > 0 indicate greening). The digital elevation model was obtained from databasin.org

(<http://databasin.org/datasets/d2198be9d2264de19cb93fe6a380b69c>, accessed on 1 April 2013). Monthly NDVI values (November – March) were obtained from National Aeronautics and Space Administration's Earth Observations (NASA's NEO) website (<http://neo.sci.gsfc.nasa.gov/Search.html>, accessed on 28 March 2013).

We modeled Ovenbird abundance from eBird checklist data by selecting amongst Poisson, zero inflated Poisson and negative binomial N-mixture models (Royle and Dorazio, 2008) to determine the distribution that best fit the data. The negative binomial distribution had the lowest Akaike Information Criterion (AIC) value (Table S1) and thus the negative binomial distribution was used to model Ovenbird abundance during the non-breeding season using N-mixture models (Royle and Dorazio, 2008). Relative abundance of Ovenbirds during the non-breeding season were modeled using the 'pcount' function in the 'unmarked' (Fiske and Chandler 2011) package and the predictions were mapped using the 'raster' (Hijmans and van Etten 2012) package in R (R Core Team 2013). We considered multiple competing models for non-breeding abundance of Ovenbirds in which we modeled counts as a function of the change in NDVI, latitude, elevation and squared terms for both elevation and latitude. In order to account for imperfect detection we selected amongst competing models in which detection probability was modeled as either a constant or in which the total amount of time (count

minutes) and the number of checklists submitted (number counts) during each month were included as observation covariates.

Ovenbird abundance during the breeding season was obtained via the Breeding Bird Survey which incorporated mean Ovenbird counts on survey routes from 2006-2010 using the start of the 39.43 km sampling route as the sampling location. Abundance was then interpolated using inverse distancing weighting to create a contour map of estimated mean abundance across the survey area (Sauer et al. 2012). Further details on how the Ovenbird breeding season abundance map was generated using Breeding Bird Survey data can be found at <http://www.mbr-pwrc.usgs.gov/bbs/ramapin10.html>.

Migratory connectivity-

To assess the strength of migratory connectivity, we created a probability of origin map for each breeding and non-breeding capture location. We depicted the probable origins for multiple individuals within a given geographic sample (e.g. HBEF, etc) by summing the individual posterior probability surfaces and dividing by the sample size to derive a mean probability of origin map for the sample. The resulting probability of origin map is spatially explicit and depicts error associated with geolocator estimates unlike point-based measures of connectivity such as nearest neighbor (Fraser et al. 2012), graph theory (Iwamura et al. 2013) or a Mantel test (Ambrosini et al. 2009, Cormier et al. 2013). To compare the strength of migratory connectivity between capture locations, we scaled the probability of origin using:

$$\frac{\text{Pr}(\text{origin}) - 1/n}{E - 1/n}$$

where $\text{Pr}(\text{origin})$ is the maximum posterior probability of origin when incorporating Ovenbird abundance as prior information in a Bayesian framework, n is the number of geolocators recaptured at each sample location and E , the maximum posterior probability of origin for a known capture location. In theory, the posterior probability of origin for a known capture location should equal 1. However, geolocator error meant that the probability of origin for a known location was < 1 (see Table S2). The resulting scaled connectivity values ranged between 0, indicating no overlap of individual geolocator estimates, and 1, where all individual geolocator estimates overlap entirely in the subsequent season. We categorized scaled migratory connectivity values between 0-0.333, 0.334-0.666 and 0.667-1.00 as weak, moderate and strong migratory connectivity respectively.

We also used band recoveries submitted to the United States Geological Survey's Bird Banding Laboratory to assess migratory connectivity of Ovenbirds from a broader geographic area and to include locations where geolocators were not deployed (Ryder et al. 2011). Ovenbird encounter data were obtained from the Bird Banding Laboratory and included all Ovenbird encounters up until February 2011. Ovenbirds that were banded between 1 June - 31 July and encountered between 1 November and 31 March, or banded between 1 November and 31 March and encountered between 1 June and 31 July were used to avoid individuals encountered during migration.

Migration-

Spring migration routes were estimated from the two geolocator locations generated daily from time of relative 'noon' (sunrise to sunset) and 'midnight' (sunset to

sunrise). Only ‘noon’ locations were used to determine migration routes because ‘midnight’ locations may be influenced by the Ovenbird’s nocturnal migratory behavior. Fall migration routes were not considered because the timing of fall migration for Ovenbirds corresponds with fall equinox when latitude is not reliably estimated. To generate migration routes, we assumed that the error associated with location data was similar during both stationary and migratory periods. We incorporated longitude and latitude error into each model (Sibert et al. 2012) by estimating the error around the known capture location. We used individual error estimates for birds captured during the breeding season, and the mean error for birds captured during the non-breeding season due to the relatively small change in day length at tropical latitudes. To determine the starting (if captured during the breeding season) or ending (if captured during the non-breeding season) location, which were included in the model as known locations, we used the mean location of geolocator estimates weighted by the posterior probability surface created using Ovenbird abundance as prior probabilities and KDEs with Bayes’ rule (see above) calculated with Spatial Analyst in ArcMap 10.0 (ESRI 2011). The beginning of migration was determined by longitudinal movements that exited the non-breeding posterior probability surface. The arrival date to the breeding grounds was identified as the first location that fell within the breeding posterior probability surface (Hallworth et al 2013). The most probable migration route and 95% confidence intervals (CI) were generated using the ‘kfttrack’ package (Sibert et al. 2012) in R version 2.15.0.

RESULTS

Forty-four (24.7%) geolocators were recovered from six locations throughout the Ovenbird's breeding and non-breeding ranges. Sixteen (18.9%) were recovered during the non-breeding season (Jamaica: 2010 n=3, 2011 n=6, Everglades: 2011 n=3, Puerto Rico: 2012 n = 4, Belize: 2012 n = 0), and 29 (29.8%) were recovered during the breeding season (HBEF 2010, n = 3; 2011 n = 18; western Canada, 2011 n = 8). Apparent survival rates did not differ between Ovenbirds with (0.675 ± 0.06) and without (0.549 ± 0.08) geolocators breeding at HBEF (Supplemental methods, Hallworth et al. unpublished data). We did not attempt to relocate birds during the non-breeding season that were captured but did not meet the weight requirement ($>19.0\text{g}$) to carry a geocator, and no birds were marked with only bands at the Canadian site. Hence, we are unable to compare survival rates of birds with and without geolocators during the non-breeding season or for the Canadian breeding location.

Incorporating Abundance –

We built our non-breeding season abundance map using 74,838 eBird checklists from 17,103 locations submitted between 1 November – 31 March, 2010-2013; 1493 checklists (2%) submitted from 563 locations detected at least 1 Ovenbird. The mean number of Ovenbird observations per location was 1.33. The most parsimonious model included the effect of elevation² and the mean difference in NDVI scores between March and November (Table S2 & Figure S2 & S3) on Ovenbird abundance and detection probability varying as a function of total count minutes (Figure S2). Ovenbird abundance was highest in dry, low elevation locations. Beta estimates from the most parsimonious model were used to create a spatially explicit Ovenbird abundance map during the non-

breeding season. This map was converted to a probability surface by dividing it's summation across the surface.

Incorporating Ovenbird abundance as a prior probability using Bayes' rule decreased the potential area of origin by $90.37 \% \pm 1.05 \%$ during the non-breeding and $62.30 \% \pm 1.69 \%$ during the breeding season compared to the potential area of origin using 95% KDEs of geolocator positions alone. The area of potential origin during the non-breeding season was reduced by $26.88 \% \pm 1.78\%$ (mean \pm SE) even after accounting for the removal of open water encompassed by the KDE. Our Bayesian analyses also decreased the 75% and 50% KDE by $21.89 \% \pm 4.02 \%$ and $35.28 \% \pm 5.04 \%$ respectively during the non-breeding season and by $56.50 \% \pm 2.30\%$ and $61.63 \% \pm 2.89\%$ during the breeding season.

Migratory connectivity-

The strength of migratory connectivity for Ovenbirds varied between and among capture locations. Connectivity between eastern and western breeding populations were completely non-overlapping during the non-breeding season (Figure 1). Individuals breeding in western Canada spent the non-breeding season in Central America with the maximum posterior probability of origin occurring in Mexico, followed by Nicaragua, El Salvador, and Honduras. Ovenbirds breeding at HBEF spent the non-breeding season in the Caribbean with the highest posterior probability of origin occurring in the Dominican Republic, followed by Haiti, Bahamas, Cuba, and Jamaica. In contrast, birds with geolocators attached on non-breeding areas exhibited overlap in breeding areas (with the exception of Jamaica). Ovenbirds captured in Everglades National Park, Florida, USA

had the largest posterior probability of origin in the mid-Atlantic region of the United States, followed by the northeastern United States and southeastern Canada. Ovenbirds captured in Jamaica exhibited the largest posterior probability of origin in the northeastern United States. Individuals captured in Puerto Rico also bred along the eastern United States with the highest probability of origin found in the mid-Atlantic region followed by the northeastern United States (Figure 2).

The scaled strength of within-population connectivity ranged from weak to moderate. Ovenbirds captured in Jamaica exhibited the strongest connectivity (0.635) followed by HBEF (0.525), Everglades (0.360), Puerto Rico (0.336), and western Canada (0.213).

We contrasted banding encounters submitted to the Bird Banding Laboratory with geolocator data to determine migratory connectivity across a broad geographic range. A total of 252,688 Ovenbirds were banded between 1960 and 2011, 360 ($< 0.14\%$) Ovenbirds were re-encountered between 1922 and 2011. However, only 3 (0.001%) recapture events matched our criteria. Band recovery data appeared concordant with connectivity patterns determined by geolocators (Figure 1).

Migration –

We recovered data from 43 geolocators from five capture locations; the batteries of two (4.54%) geolocators failed during the non-breeding season prior to migration. Individuals with geolocators captured at HBEF ($n = 20$), Everglades National Park, FL ($n = 3$), Puerto Rico ($n=4$) and Jamaica ($n =9$) all migrated along the Atlantic coast during spring migration (Figure 3). Two individuals captured in Canada migrated around the

Gulf of Mexico and six flew over the Gulf, but all migrated along the Mississippi River valley before moving west towards their breeding location. Fall migration routes were not considered because fall equinox coincides with Ovenbird migration when latitude is not reliably estimated.

DISCUSSION

Understanding the patterns and strengths of migratory connectivity is essential for interpreting population dynamics, life history strategies, seasonal interactions (Marra et al. 1998, Rockwell et al. 2012, Miller et al. 2012), responses to climate change (Wilson et al. 2011, Fraser et al. 2012, Small-Lorenz et al. 2013, McKellar et al. 2013, Iwamura et al. 2013) as well as the development and implementation of conservation plans for migratory species (Marra et al. 2011). To assess the strength of migratory connectivity, multiple populations throughout breeding and non-breeding distributions need to be tracked. Our results suggest that Ovenbirds exhibit a strong east-west separation. Furthermore, individuals breeding within the eastern and western portions of the species' range overwinter in different regions in the Caribbean and Central America, respectively.

Patterns of migratory connectivity can be influenced by a variety of factors acting throughout the annual cycle. Barriers to migration such as mountain ranges (Delmore et al. 2012), inhospitable environments (i.e. deserts) and large bodies of water (Tøttrup et al. 2008, 2012, Åkesson et al. 2012) may influence connectivity. Conditions experienced by individuals during the non-breeding season, at least first-year birds, may also contribute to natal dispersal distances (Studds et al. 2008) ultimately influencing the connectivity of

populations. Inferring natal dispersal using geolocators is only possible if 1) natal origin is inferred using intrinsic markers such as stable isotopes (Studds et al. 2008) and 2) geolocators are deployed on individuals during their first non-breeding season. Only three (Puerto Rico, $n = 2$, Jamaica, $n = 1$) of our 16 recaptured birds were originally captured during their first non-breeding season and we did not determine their natal origin, thus we were unable to address the influence of dispersal on connectivity.

Here, we found that Ovenbirds breeding at the Hubbard Brook Experimental Forest, NH spent the non-breeding season exclusively in the Caribbean Basin, while birds breeding in western Canada spent the non-breeding season in Central America. Our results suggest that the segregation between breeding populations using the Caribbean Basin versus Central America may occur along the Mississippi river valley. Genetic analysis of other Neotropical migratory songbirds has revealed strong segregation between eastern and western breeding populations (e.g., Boulet et al. 2006, Irwin et al, 2011). However, these genetic differences indicate the Rocky Mountains in western North America as the divide between the eastern and western populations (Clegg et al. 2003, Boulet et al. 2006, Rundel et al. 2013). Our findings also suggest segregation between eastern and western populations. However, the split between the populations is east of the Rocky Mountains and may be the result of behavior rather than a physical barrier. Spring migration routes suggest that eastern and western populations migrate along different non-overlapping migratory flyways which may have led to the broad scale connectivity patterns exhibited by Ovenbirds.

Other studies have shown differences in non-breeding locations of individuals from within the same breeding population of Neotropical migrant bird species (Heckscher et al. 2011, Delmore et al. 2012). However, our findings suggest that the non-breeding locations of birds breeding along the Atlantic coast are more similar to each other than to birds breeding in the western portion of their distribution. These findings suggest that changes in ecological conditions or habitat within the Caribbean and Central America could impact Ovenbirds in the eastern or western portion of their distribution, respectively. Further research is needed to identify more subtle patterns of connectivity within each of these regions as well as the underlying mechanisms causing the divide between eastern and western populations.

We devised a probability of origin map to quantitatively measure migratory connectivity of a population that incorporates error associated with geolocator estimates. We used the probability of origin maps for each capture location as an index of the strength of migratory connectivity. Using these maps, we determined that connectivity within sample populations ranged from weak to moderate. This metric provides a quantitative, spatially explicit prediction of where breeding and/or non-breeding populations originate. In addition, mapping probability of origin in a Bayesian framework for each capture location allowed us to incorporate the uncertainty into origin estimates unlike point-based measures of connectivity such as nearest neighbor (Fraser et al. 2012), graph theory (Iwamura et al. 2013) or Mantel tests (Ambrosini et al. 2009, Cormier et al. 2013).

Archival light-level geolocators have increased our knowledge of migratory connectivity dramatically and rapidly; however, the level of uncertainty associated with location data gathered from geolocators leads to large areas of potential origin. Statistical techniques that reduce and incorporate the uncertainty in location estimates are needed to refine our understanding of migratory connectivity for migratory populations (Bridge et al. 2013). As has been used previously in studies based on assignments using stable isotopes (Royle and Rubenstein 2004, Wunder and Norris 2008, González-Prieto et al. 2011, Hallworth et al. 2013, Flockhart et al. 2013) we incorporated Ovenbird abundance, which assumes the probability of origin to be affected only by the population density during the breeding or non-breeding season, into location estimates using Bayes' rule to reduce the potential area of origin generated by geocator estimates alone. Incorporating prior probabilities based upon bird abundance into posterior probability of origin estimates reduced the potential area of origin during both the breeding and non-breeding season by $90.37 \% \pm 1.05\%$ and $62.30 \% \pm 1.69\%$, respectively. Using abundance estimates in conjunction with geocator data could help identify areas of special concern or where to focus conservation efforts for species of concern. Here, we relied on Breeding Bird Survey data (Sauer et al. 2012) and eBird checklists submitted by citizen scientists to create abundance maps during breeding and non-breeding seasons, respectively. To date, eBird checklists within the non-breeding distribution of many Neotropical migrants are concentrated in highly travelled areas (e.g. Costa Rica) and lacking in locations with limited accessibility (e.g. Cuba, high elevations (Snäll et al. 2011)) which may encompass large areas of a species' distribution. Thus, using

abundance estimates derived using eBird checklists may only be useful for species with large distributions. Observer differences and species detection may also limit the use of eBird data for species that are difficult to identify and/or are cryptic. In addition, common species may not be reported or get overlooked (Snäll et al. 2011) adding to the uncertainty in the estimates for common species. Despite the limitations mentioned above, eBird data are the only range-wide abundance data available for migratory birds during the non-breeding season (Figure 1 & 2).

Our findings suggest that the strength of migratory connectivity depends upon on the spatial scale of interest. We found strong overall migratory connectivity at broad spatial scales but weaker patterns within sub-populations, although some locations, particularly Jamaica and New Hampshire, exhibited moderate connectivity. Our measure of connectivity was corrected for the number of individuals captured; however, our power to assess the degree of connectivity may increase if our sample size was larger. Our assessment of connectivity may be biased by the amount of land area in different portions of the non-breeding season, with strong connectivity in areas with limited land area (i.e. Caribbean) and weak connectivity in areas with large land masses (i.e. Central America). In addition, the uncertainty in geolocator estimates increases towards the equator potentially leading to weak connectivity estimates for populations captured during the breeding season. However, geolocators were deployed during the breeding season for one of the two populations that exhibited moderate connectivity (HBEF) and Ovenbirds from all capture locations spent the non-breeding season at approximately the

same latitude (Figure 1) minimizing the influence of uncertainty in geolocator estimates between capture locations.

The creation of probabilistic maps of origin may help predict how populations respond to changes during subsequent seasons as the probability of originating from a particular geographic region can be determined. Our findings suggest that the breeding population at Hubbard Brook Experimental Forest in N.H. could be impacted by events, such as large disturbances like hurricanes on the island of Hispaniola. Similarly, large-scale disturbance in Jamaica will likely impact Ovenbirds breeding in the northeastern United States. In contrast, locations such as Puerto Rico that exhibit weak connectivity would likely be unaffected by localized pressures during the breeding season as individuals originate from a wider array of breeding locations. Probability of origin maps could be used to focus conservation efforts as well as predict the influence of disturbances on specific populations.

We were able to identify the strength of migratory connectivity at a broad spatial scale with the use of archival light-level geolocators deployed at multiple locations within the Ovenbirds' distribution. Understanding how the strength of migratory connectivity impacts life history strategies, population dynamics, seasonal interactions and a populations' response to selective pressures, requires an understanding of migratory connectivity at both broad and local spatial scales. Currently, the uncertainty associated with geolocator estimates precludes their use for determining local scale connectivity information. In an attempt to reduce the uncertainty of geolocator estimates and provide more detailed location information we refined the geolocator estimates using bird

abundance. In addition, we created probabilistic origin maps and identified migration routes between subsequent seasons which are critical for assessing how populations respond to things such as habitat alteration, weather events and climate change throughout their range. Although our findings have improved our understanding of migratory connectivity for the Ovenbird, further research is needed to determine 1) the utility of using eBird data to provide abundance estimates of Neotropical migrants during the non-breeding season, and 2) additional sampling locations are needed to locate where the divide between eastern and western populations of Ovenbirds occurs and identify the underlying mechanisms for the divide.

ACKNOWLEDGEMENTS –

We acknowledge N. Cooper, W. Garcia, M. Thomas, C. Tonra, R. Reitsma, D. Narango, R. Terrill, J. Gautreaux, L. Rowse, and L. Pop for assisting in field work. We thank R. Harvey and J. Avecedo for generously donating accommodations during field work. Field work in Canada was facilitated by a research permit and accommodations provided by Parks Canada (Prince Albert National Park) to KAH. J. Smith provided helpful insight on the use of NDVI maps. Funding was provided by grants from the U.S. National Science Foundation's Long-term Research in Environmental Biology program (PPM, TSS), the Smithsonian Institution's Bond Fund (MTH and PPM), Cosmos Scholars (MTH), and the American Ornithological Union (MTH). Funding for the Canadian component of the study was provided by an operating grant to KAH from Environment Canada.

Table 1. Sun elevation angles used to calculate latitude and longitude from light transition data obtained with archival light-level geolocators. Ovenbirds were captured across a broad geographic range throughout the breeding and non-breeding distribution. We used the mean breeding and non-breeding sun elevation angles to locate individuals when captured during the non-breeding and breeding seasons, respectively. The number of geolocators and transition events (sunrise or sunset) used to calculate sun elevation angles are also shown.

Table 4

Capture Location	Sun Elevation Angle (°) (Mean \pm SE)	Geolocators (<i>n</i>)	Transition events (<i>n</i>)	Geographic Coordinates
Breeding	-1.335 \pm 0.15	28	2664	
Canada	-2.233 \pm 0.10	8	469	53°90'N 106°18'E
New Hampshire	-0.976 \pm 0.62	20	2195	43°93'N 73°71'E
Non-breeding	-3.409 \pm 0.11	16	1511	
Florida	-3.559 \pm 0.37	3	134	25°13'N 80°94'E
Jamaica	-3.369 \pm 0.54	9	719	18°04'N 77°93'E
Puerto Rico	-3.384 \pm 0.34	4	658	17°97'N 66°86'E
Belize*	1.194	1	59	16°55'N 88°71'E

*reference geocator placed near the forest floor

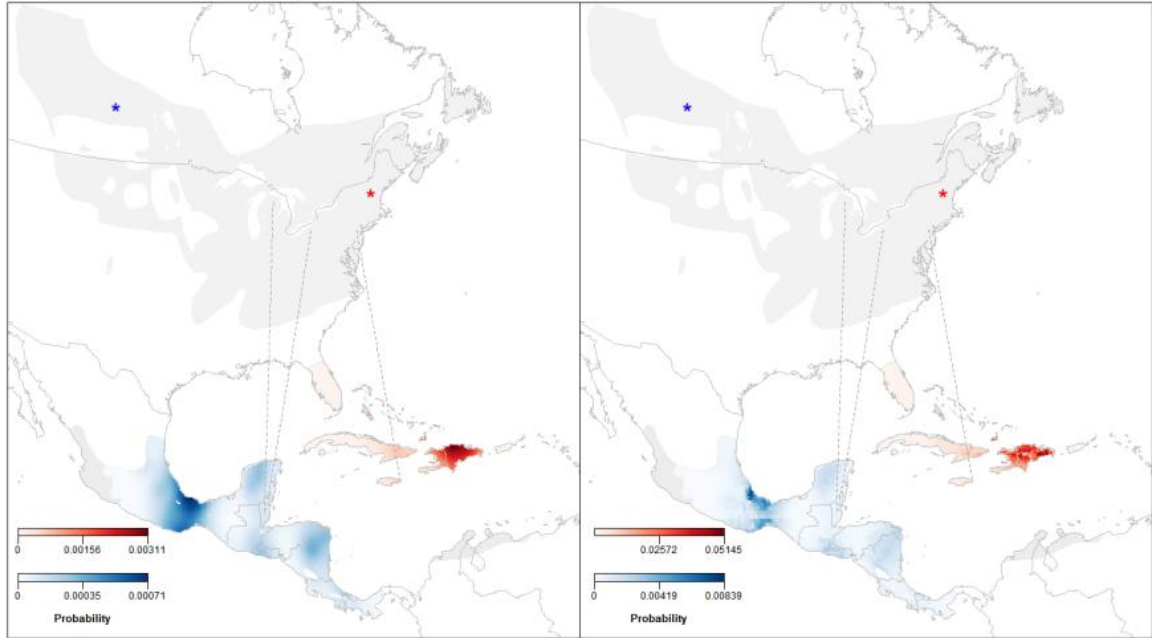


Figure 6

Figure 1. Ovenbirds captured during the breeding season exhibited non-overlapping non-breeding distributions between east and west populations, which were supported by three band encounters (gray dotted lines, see methods for selection criteria). Ovenbirds breeding in Saskatchewan, CA (Blue asterisks) spent the non-breeding season in Central America with the highest probability of origin (blue color ramp) found in southern Mexico. Geolocators recovered from New Hampshire, USA indicate Ovenbirds wintered exclusively in the Caribbean with the highest probability of origin found on the island of Hispaniola (red color gradient). Darker colors indicate a higher probability of origin for a specific breeding location. The probability of origin was calculated using geolocator estimates from all geolocators recovered from a single capture location (panel A) and Ovenbird abundance derived using eBird data (panel B). Both breeding and non-breeding distributions of Ovenbirds are shown in light gray.

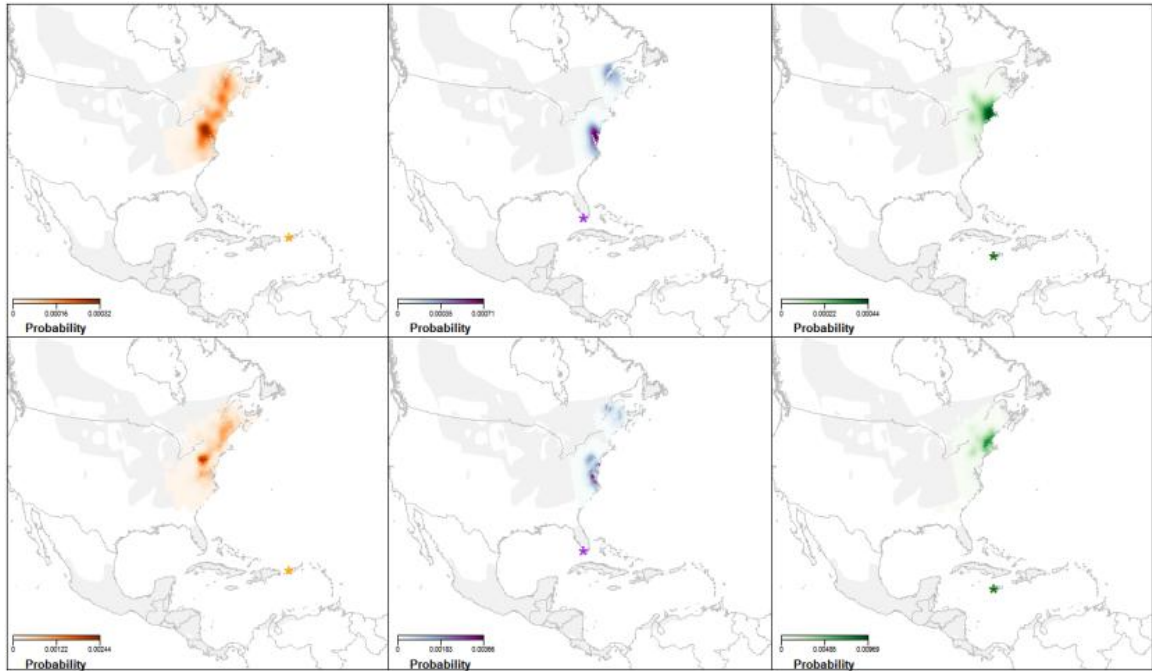


Figure 7

Figure 2. Ovenbirds captured during the non-breeding season had overlapping breeding locations. Ovenbirds wintering in Puerto Rico (Orange asterisks, Panel A) exhibited weak connectivity and breed along the entirety of the Atlantic coast with the highest probability of origin located along the mid-Atlantic region. Similarly, Ovenbirds wintering in Everglades National Park (Blue asterisks, Panel B) exhibited weak connectivity with the highest probability of origin in the mid-Atlantic region. Conversely, Ovenbirds captured in Jamaica (Green asterisks, Panel C) exhibited moderate connectivity with the highest probability of origin found in northeastern United States. Darker colors indicate a higher probability of origin for a specific wintering location (see Figure 1 legend). The probability of origin was calculated using geolocator estimates from all geolocators recovered from a single capture location (top panel) and Ovenbird abundance obtained from the Breeding Bird Survey (Sauer et al. 2012, bottom panel). Both breeding and non-breeding distributions of Ovenbirds are shown in light gray.

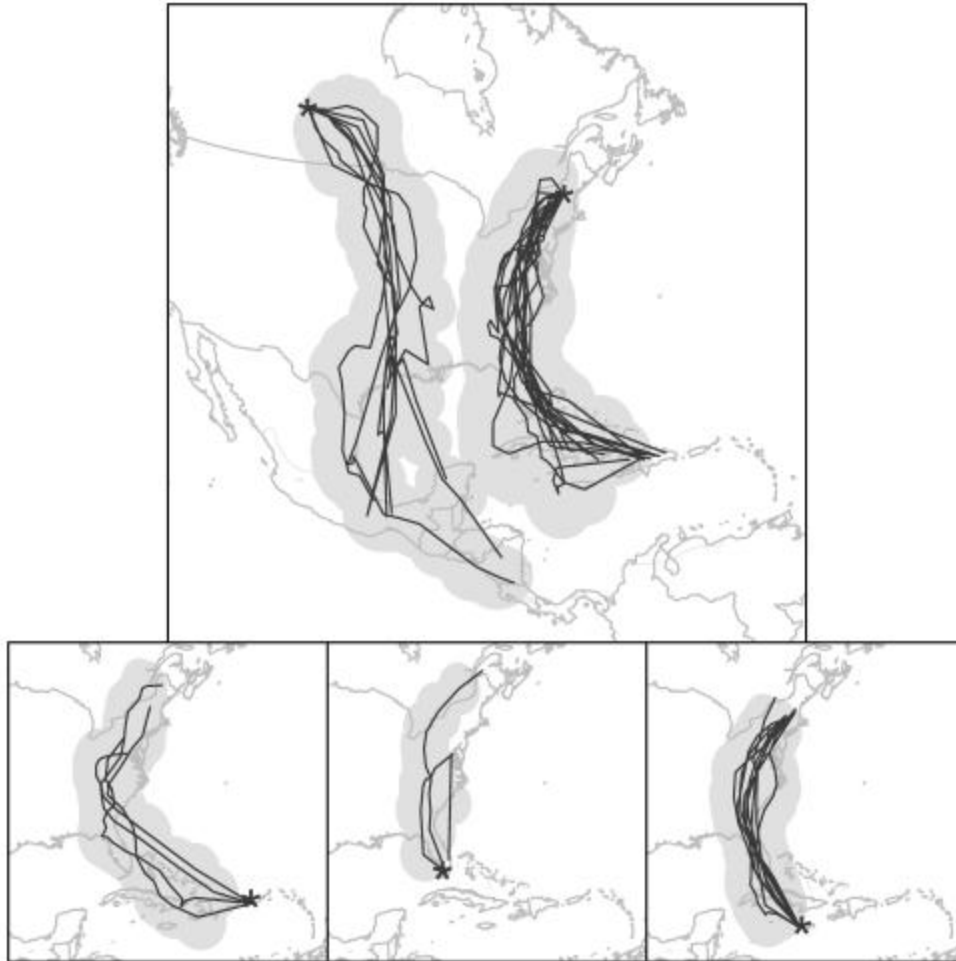


Figure 8

Figure 3. The most probable spring migration routes (lines) and 95% confidence intervals (shaded area) of Ovenbirds ($n = 43$) captured at five locations across a broad geographic distribution determined using 'noon' locations obtained with archival light-level geolocators. Ovenbirds captured in the eastern portion of their distribution migrate within the Atlantic flyway while individuals captured in the west migrate within the Mississippi flyway during spring migration. Capture locations are illustrated with asterisks. Fall migration was not considered because the Ovenbird migration overlaps with the fall equinox when latitudinal location estimates are not reliable.

SUPPLEMENTAL MATERIAL-

METHODS-

Apparent Survival- Apparent survival was estimated from annual capture-mark and recapture / re-sight data of male Ovenbirds from Hubbard Brook Experimental Forest, NH between 2010-2012 using Cormack-Jolly-Seber (CJS) models analyzed with RMark (Laake 2013). We incorporated geolocator as a covariate to determine whether geolocators influenced apparent survival and/or detection probabilities. We also ran models that allowed survival and detection probabilities to vary through time as well as a null model that assumed constant survival and detection probabilities. The candidate model set was then assessed using Akaike's Information Criterion (AIC).

RESULTS-

Apparent Survival- The most parsimonious model that influenced apparent survival and detection probabilities included geolocator as a covariate (Table S4). However, the apparent survival for individuals with geolocators ($n=66$; 0.675 ± 0.06) was higher than individuals without geolocators ($n=148$; 0.549 ± 0.08). Detection probability was also higher for individuals with geolocators (0.939 ± 0.06) than individuals without (0.665 ± 0.11).

Table S1. eBird checklists were used to determine the non-breeding season abundance of Ovenbirds modeled using N-mixture models with the ‘unmarked’ package in R. Model selection was used to determine which distribution best fit the eBird abundance data when abundance (λ) and detection probability (Ψ) were held constant.

Table 5

Distribution	K	AIC	Δ AIC	Model Weight	Cumulative Model Weight
Negative Binomial	3	8676.59	0.00	1.00	1.00
Zero inflated Poisson	3	9817.31	1140.72	0.00	1.00
Poisson	2	14021.30	5344.71	0.00	1.00

Table S2. Values used to scale the strength of migratory connectivity. The number of geolocators captured at each location (n), the expected posterior probability of origin if there was no overlap of individuals during subsequent seasons ($1/n$) and the maximum posterior probability of origin at a known capture location (Location Error). In theory, the maximum posterior probability of origin should be equal to 1, however because of the uncertainty associated with geolocator estimates the maximum posterior probability of origin was less than 1. The strength of connectivity was scaled (see methods) using the values in the table.

Table 6

Capture Location	n	$1/n$	Location Error
Breeding Season			
HBEF	21	0.0476	0.7830
Canada	8	0.1250	0.8580
Non-breeding Season			
Everglades	3	0.3333	0.9344
Jamaica	9	0.1111	0.7741
Puerto Rico	4	0.2500	0.9875

Table S3. eBird checklists were used to determine the non-breeding season abundance of Ovenbirds modeled using N-mixture models with the 'pcount' function in 'unmarked' package in R. Model selection was used to determine which parameters influenced Ovenbird abundance during the non-breeding season. The model most parsimonious model included elevation² and the change in normalized difference vegetation index (NDVI) between November and March on abundance, while the sum of count minutes (Mins) for each month influenced detection. Beta estimates from the most parsimonious model were used to create an abundance map during the non-breeding season.

Table 7

Model	K	AIC	ΔAIC	Model Weight	Cumulative Model Weight
$\lambda(\text{Elevation}^2 + \text{NDVI})$ $p(\text{Mins})$	6	8242.74	0.00	0.86	0.86
$\lambda(\text{NDVI}) p(\text{Mins})$	5	8246.37	3.63	0.14	1.00
$\lambda(.) p(\text{Mins})$	4	8269.57	26.83	0.00	1.00
$\lambda(\text{Elevation}) p(\text{Mins})$	5	8271.54	28.80	0.00	1.00
$\lambda(.) p(\text{Counts})$	4	8380.39	137.65	0.00	1.00
$\lambda(\text{Elevation}^2 + \text{NDVI})$ $p(\text{NDVI})$	6	8618.22	375.47	0.00	1.00
$\lambda(\text{Elevation}^2 + \text{NDVI}) p(.)$	5	8653.27	410.53	0.00	1.00
$\lambda(\text{NDVI}) p(.)$	4	8657.42	414.68	0.00	1.00
$\lambda(\text{Elevation} + \text{NDVI}) p(.)$	5	8659.27	416.53	0.00	1.00
$\lambda(.) p(.)$	3	8676.59	433.85	0.00	1.00
$\lambda(\text{Longitude}^2) p(.)$	4	8678.41	435.67	0.00	1.00
$\lambda(\text{Longitude}^2 + \text{Elevation})$ $p(.)$	5	8680.33	437.59	0.00	1.00

Table S4. Apparent survival (ϕ) and detection probabilities (p) were estimated using program MARK through the RMark package in R. Geolocator was included as a covariate to estimate the influence of geolocators on apparent survival of Ovenbirds breeding at Hubbard Brook Experimental Forest, NH. The most parsimonious model indicated that geolocators influence both apparent survival and detection probability of male Ovenbirds. However, apparent survival and detection probability was higher for individuals with geolocators than males without.

Table 8

Model	K	AIC _c	Δ AIC _c	Model Weight	Cumulative Model Weight
ϕ (Geolocator) p (Geolocator)	4	342.09	0.00	0.45	0.45
ϕ (Time) p (Geolocator)	5	342.19	0.09	0.43	0.88
ϕ (Geolocator) p (.)	3	344.59	2.50	0.13	0.99
ϕ (.) p (.)	2	354.63	12.54	0.01	1.00
ϕ (Time) p (Time)	6	361.16	19.07	0.00	1.00

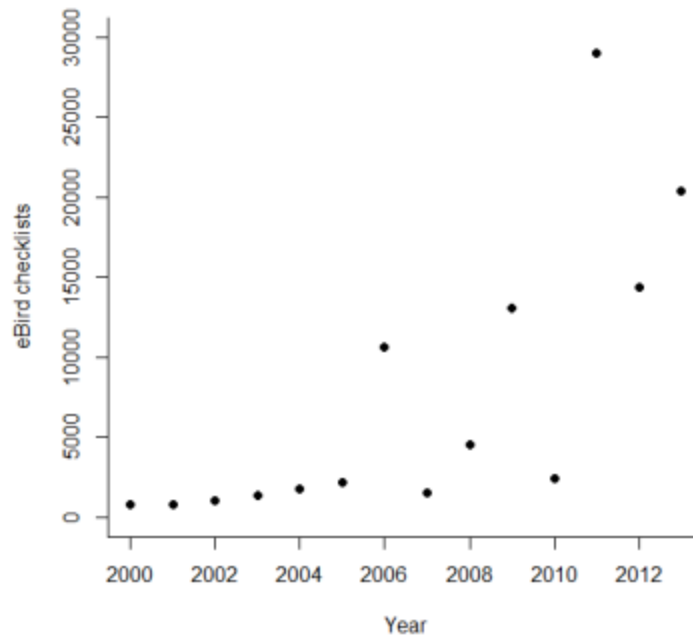


Figure 9

Figure S1. Number of eBird checklists submitted that reported effort, and every species detected that occurred within the non-breeding distribution of Ovenbirds between 1 November and 31 March. The number of checklists has increased exponentially since 2008.

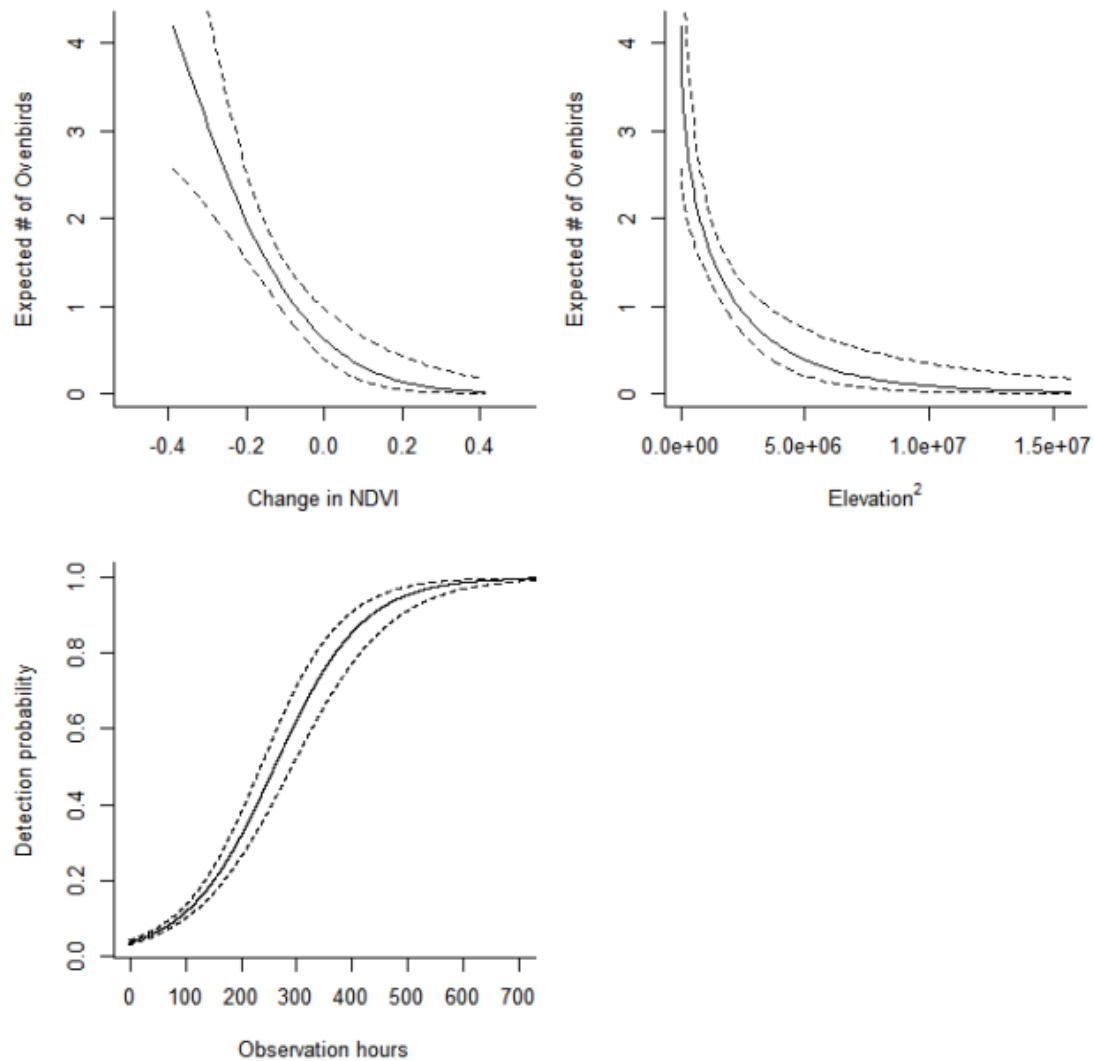


Figure 10

Figure S2. The influence of change in Normalized Difference Vegetation Index (NDVI) from November to March and elevation² (m) on Ovenbird abundance during the non-breeding season obtained via eBird checklists between 1 November and 31 March during 2010 - 2013. NDVI values < 0 indicate browning, values = 0 indicate no change, while values > 0 indicate greening from November to March. The estimated number of Ovenbirds (solid line) and 95% CI of the estimates (dotted lines) as a function of difference in NDVI values (A) and elevation² (B). Detection probability (solid line) and 95% CI of detection probability as a function of the number of count minutes (depicted in hours).

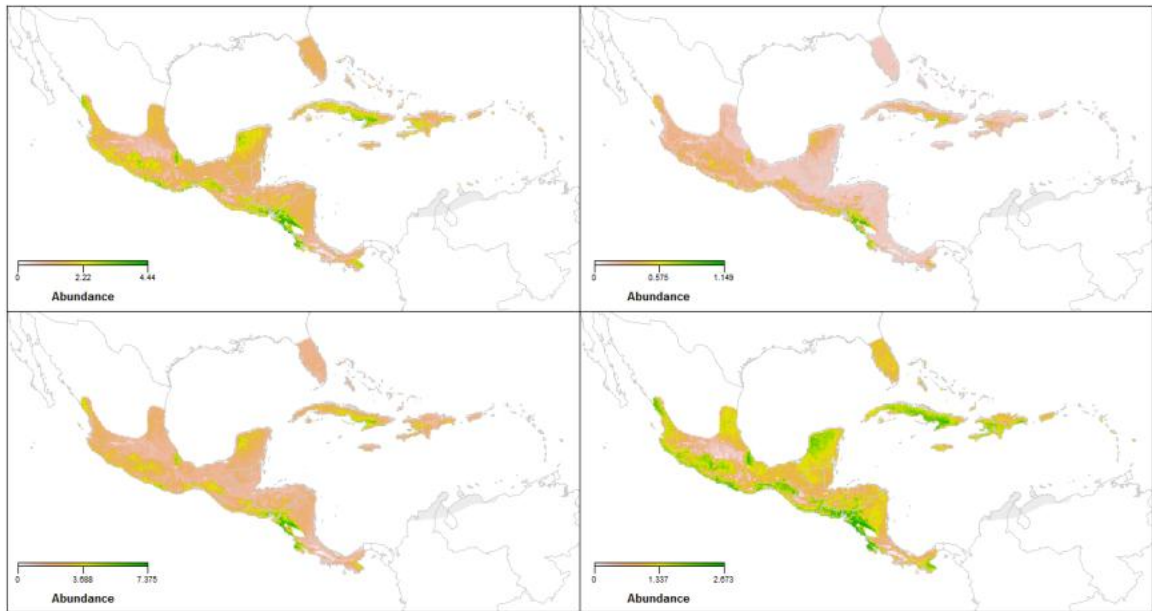


Figure 11

Figure S3. Predicted Ovenbird abundance (top left), and the SE (top right), upper (bottom left) and lower (bottom right) estimates of most parsimonious model ($\lambda(\text{Elevation}^2 + \text{NDVI})$ p(Mins)) derived via eBird checklists during the non-breeding season with N-mixture models in the 'unmarked' R package.

LITERATURE CITED

- Åkesson, S., R. Klaassen, J. Holmgren, J. W. Fox, and A. Hedenström. 2012. Migration routes and strategies in a highly aerial migrant, the Common Swift *Apus apus*, revealed by light-level geolocators. PLoS ONE 7:e41195.
- Ambrosini, R., A. P. Møller, and N. Saino. 2009. A quantitative measure of migratory connectivity. Journal of Theoretical Biology 257:203–211.
- Andrew Royle, J., and D. R. Rubenstein. 2004. The role of species abundance in determining breeding origins of migratory birds with stable isotopes. Ecology 14:1780–1788.
- Arlt, D., M. Low, and T. Pärt. 2013. Effect of geolocators on migration and subsequent breeding performance of a long-distance passerine migrant. PLoS ONE 8:e82316.
- Barg, J. J., J. Jones, and R. J. Robertson. 2005. Describing breeding territories of migratory passerines: suggestions for sampling, choice of estimator, and delineation of core areas. Journal of Animal Ecology 74:139–149.
- Bridge, E. S., J. F. Kelly, A. Contina, R. M. Gabrielson, R. B. MacCurdy, and D. W. Winkler. 2013. Advances in tracking small migratory birds: a technical review of light-level geolocation. Journal of Field Ornithology 84:121–137.
- Boulet, M., L. H. Gibbs, and K. A. Hobson. 2006. Integrated analysis of genetic, stable isotope and banding data reveal migratory connectivity and flyways in the northern yellow warbler (*Dendroica petechia*; *aestiva* group). Ornithological Monographs 61: 29-78.
- Clegg, S. M., J. F. Kelly, M. Kimura, and T. B. Smith. 2003. Combining genetic markers and stable isotopes to reveal population connectivity and migration patterns in a Neotropical migrant, Wilson's warbler (*Wilsonia pusilla*). Molecular Ecology 12: 819-830.
- Contina, A., E. S. Bridge, N. E. Seavy, J. M. Duckles, and J. F. Kelly. 2013. Using geologgers to investigate bimodal isotope patterns in Painted Buntings (*Passerina ciris*). The Auk 130:265–272.

- Cormier, R. L., D. L. Humple, T. Gardali, and N. E. Seavy. 2013. Light-level geolocators reveal strong migratory connectivity and within-winter movements for a coastal California Swainson's Thrush (*Catharus ustulatus*) population. *The Auk* 130:283–290.
- Costantini, D., and A. P. Møller. 2013. A meta-analysis of the effects of geolocator application on birds. *Current Zoology* 59:607–706.
- Delmore, K. E., J. W. Fox, and D. E. Irwin. 2012. Dramatic intraspecific differences in migratory routes, stopover sites and wintering areas, revealed using light-level geolocators. *Proceedings of the Royal Society B: Biological Sciences* 279:4582–4589.
- Faaborg, J., and W. J. Arendt. 1984. Population sizes and philopatry of winter resident warblers in Puerto Rico. *Journal of Field Ornithology* 55:376–378.
- Fiske, I. and R. Chandler. 2011. unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*. 43: 1-23.
- Flockhart, T., L.I. Wassenaar, T. Martin, K.A. Hobson, M. Wunder, and D.R. Norris. 2013. Tracking multi-generational colonization of the breeding grounds by monarch butterflies in eastern North America. *Proceeding of the Royal Society of London B* 280, 20131087
- Fraser, K. C., B. J. M. Stutchbury, C. Silverio, P. M. Kramer, J. Barrow, D. Newstead, N. Mickle, B. F. Cousens, J. C. Lee, D. M. Morrison, T. Shaheen, P. Mammenga, K. Applegate, and J. Tautin. 2012. Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. *Proceedings of the Royal Society B: Biological Sciences*. 279:4901–4906.
- Gómez, J., C. I. Michelson, D. W. Bradley, D. R. Norris, L. L. Berzins, R. D. Dawson, and R. G. Clark. 2013. Effects of geolocators on reproductive performance and annual return rates of a migratory songbird. *Journal of Ornithology*:1–8.
- González-Prieto, A.M., K.A. Hobson, N. J. Bayly and C. Gomez. 2011. Geographic origins and timing of fall migration of veery in northern Colombia. *Condor* 113:860–868.
- Hallworth, M. T., C. E. Studds, T. S. Sillett, and P. P. Marra. 2013. Do archival light-level geolocators and stable hydrogen isotopes provide comparable estimates of breeding-ground origin?. *The Auk* 130:273–282.
- Heckscher, C. M., S. M. Taylor, J. W. Fox, and V. Afanasyev. 2011. Veery (*Catharus fuscescens*) wintering locations, migratory connectivity, and a revision of its winter range using geolocator technology. *The Auk* 128:531–542.

- Hill, R.D. 1994. Theory of geolocation by light levels. *Elephant Seals: Population Ecology, Behavior, and Physiology* (eds J. Burney, B.J. Boeuf & R.M. Laws), pp. 227–236. University of California Press, Berkley.
- Hijmans R. J., and J. van Etten. 2012. raster: Geographic data analysis and modeling. R package version 2.0-41.
- Hobson, K. A. 2005. Stable isotopes and the determination of avian migratory connectivity and seasonal interactions. *The Auk* 122:1037–1048.
- Iwamura, T., H. P. Possingham, I. Chadès, C. Minton, N. J. Murray, D. I. Rogers, E. A. Treml, and R. A. Fuller. 2013. Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations. *Proceedings of the Royal Society B: Biological Sciences* 280:20130325.
- Irwin, D. E., J. H. Irwin and T. B. Smith. 2011. Genetic variation and seasonal migratory connectivity in Wilson's warblers (*Wilsonia pusilla*): species-level differences in nuclear DNA between western and eastern populations. *Molecular Ecology* 15: 3102–3115.
- Langin, K. M., P. P. Marra, Z. Németh, F. R. Moore, T. K. Kyser, and L. M. Ratcliffe. 2009. Breeding latitude and timing of spring migration in songbirds crossing the Gulf of Mexico. *Journal of Avian Biology* 40:309–316.
- Laughlin, A. J., C. M. Taylor, D. W. Bradley, D. LeClair, R. G. Clark, R. D. Dawson, P. O. Dunn, A. Horn, M. Leonard, D. R. Sheldon, D. Shutler, L. A. Whittingham, D. W. Winkler, and D. R. Norris. 2013. Integrating information from geolocators, weather radar, and citizen science to uncover a key stopover area of an aerial insectivore. *The Auk* 130:230–239.
- Lisovski, S., C. M. Hewson, R. H. G. Klaassen, F. Korner-Nievergelt, M. W. Kristensen, and S. Hahn. 2012. Geolocation by light: accuracy and precision affected by environmental factors. *Methods in Ecology and Evolution* 3:603–612.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking Winter and Summer Events in a Migratory Bird by Using Stable-Carbon Isotopes. Pages 1884–1886. American Association for the Advancement of Science, 282.
- Marra, P. P., D. Hunter, and A. M. Perrault. 2011. Migratory connectivity and the conservation of migratory animals. *Envtl. L.* 41:317.

- Marra, P. P., D. R. Norris, S. M. Haig, M. S. Webster, and J. A. Royle. 2006. Migratory connectivity. Pages 157–183 in K. R. Crooks and M. A. Sanjayan, editors. Connectivity conservation. Cambridge University Press.
- McKellar, A. E., P. P. Marra, S. J. Hannon, C. E. Studds, and L. M. Ratcliffe. 2013. Winter rainfall predicts phenology in widely separated populations of a migrant songbird. *Oecologia* 172:595–605.
- McKinnon, E. A., C. Q. Stanley, K. C. Fraser, M. M. MacPherson, G. Casbourn, P. P. Marra, C. E. Studds, N. Diggs, and B. J. Stutchbury. 2013. Estimating geolocator accuracy for a migratory songbird using live ground-truthing in tropical forest. *Animal Migration* 1:31–38.
- Miller, N. G., L. I. Wassenaar, K. A. Hobson, and D. R. Norris. 2012. Migratory connectivity of the Monarch Butterfly (*Danaus plexippus*): Patterns of spring recolonization in eastern North America. *PLoS ONE* 7:e31891.
- Naef-Daenzer, B. 2007. An allometric function to fit leg-loop harnesses to terrestrial birds. *Journal of Avian Biology* 38:404–407.
- Norris, D. R., P. P. Marra, G. J. Bowen, L. M. Ratcliffe, J. A. Royle, and T. K. Kyser. 2006. Migratory connectivity of a widely distributed songbird, the American redstart (*Setophaga ruticilla*). *Ornithological Monographs*:14–28.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Renfrew, R. B., D. Kim, N. Perlut, J. Smith, J. Fox, and P. P. Marra. 2013. Phenological matching across hemispheres in a long-distance migratory bird. *Diversity and Distributions*. 19:1008-1019.
- Ridgely, R.S., T.F. Allnutt, T. Brooks, D.K. McNicol, D.W. Mehlman, B.E. Young, and J.R. Zook. 2003. Digital Distribution Maps of the Birds of the Western Hemisphere, version 1.0. NatureServe, Arlington, Virginia, USA.
- Rockwell, S. M., C. I. Bocetti, and P. P. Marra. 2012. Carry-over effects of winter climate on spring arrival date and reproductive success in an endangered migratory bird, Kirtland's warbler (*Setophaga kirtlandii*). *The Auk* 129:744–752.
- Royle, J. A. and D. R. Rubenstein. 2004. The role of species abundance in determining breeding origins of migratory birds with stable isotopes. *Ecological Applications* 14: 1780–1788.

- Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Academic Press.
- Rundel, C. W., M. B. Wunder, A. H. Alvarado, K. C. Ruegg, R. Harrigan, A. Schuh, J. F. Kelly, R. B. Siegel, D. F. Desante, T. B. Smith, and J. Novembre. 2013. Novel statistical methods for integrating genetic and stable isotope data to infer individual-level migratory connectivity. *Molecular Ecology* 22: 4163-4176.
- Ryder, T. B., J. W. Fox, and P. P. Marra. 2011. Estimating migratory connectivity of gray catbirds (*Dumetella carolinensis*) using geolocator and mark-recapture Data. *The Auk* 128:448-453.
- Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2012. The North American breeding bird survey, results and analysis 1966-2011. Version 07.03.2013 USGS Patuxent Wildlife Research Center, Laurel, MD.
- Sibert, J. R., A. Nielsen, J. Ancheta, B. Galuardi and C. H. Lam. 2012. kfttrack. R package version 0.70.
- Small-Lorenz, S. L., L. A. Culp, T. B. Ryder, T. C. Will, and P. P. Marra. 2013. A blind spot in climate change vulnerability assessments. *Nature Climate Change* 3:91-93.
- Snäll, T., O. Kindvall, J. Nilsson, and T. Pärt. 2011. Evaluating citizen-based presence data for bird monitoring. *Biological Conservation* 144:804-810.
- Stanley, C. Q., M. MacPherson, K. C. Fraser, E. A. McKinnon, and B. J. M. Stutchbury. 2012. Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. *PLoS ONE* 7:e40688.
- Studds, C. E., T. K. Kyser, and P. P. Marra. 2008. Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory songbird. *Proceedings of the National Academy of Sciences* 105:2929-2933.
- Studds, C. E., K. P. McFarland, Y. Aubry, C. C. Rimmer, K. A. Hobson, P. P. Marra, and L. I. Wassenaar. 2012. Stable-hydrogen isotope measures of natal dispersal reflect observed population declines in a threatened migratory songbird. *Diversity and Distributions* 18:919-930.
- Stutchbury, B. J., S. A. Tarof, T. Done, E. Gow, P. M. Kramer, J. Tautin, J. W. Fox, and V. Afanasyev. 2009. Tracking long-distance songbird migration by using geolocators. *Science* 323:896.

- Tøttrup, A. P., R. H. G. Klaassen, R. Strandberg, K. Thorup, M. W. Kristensen, P. S. Jørgensen, J. Fox, V. Afanasyev, C. Rahbek, and T. Alerstam. 2012. The annual cycle of a trans-equatorial Eurasian–African passerine migrant: different spatio-temporal strategies for autumn and spring migration. *Proceedings of the Royal Society B: Biological Sciences* 279:1008–1016.
- Tøttrup, A. P., K. Thorup, K. Rainio, R. Yosef, E. Lehikoinen, and C. Rahbek. 2008. Avian migrants adjust migration in response to environmental conditions en route. *Biology Letters* 4:685–688.
- Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution* 17:76–83.
- Wilson, S., S. L. LaDeau, A. P. Tøttrup, and P. P. Marra. 2011. Range-wide effects of breeding-and nonbreeding-season climate on the abundance of a Neotropical migrant songbird. *Ecology* 92:1789–1798.
- Wunder, M.B. and D. R. Norris. 2008. Analysis and design for isotope-based studies of migratory animals. Pages 107-128 In K.A. Hobson and L.I. Wassenaar (eds) *Tracking Animal Migration with Stable Isotopes*. Academic Press, London.

SUPPLEMENTAL

- Laake, J.L. 2013. RMark: An R interface for analysis of capture-recapture data with MARK. Alaska Fisheries Science Center., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

CHAPTER 4: SEASONAL INTERACTIONS INFLUENCE INDIVIDUALS AND THE
POPULATION GROWTH RATE OF A LONG DISTANCE MIGRATORY
SONGBIRD

Michael T. Hallworth^{1,2,3}, T. Scott Sillett¹, Larry L. Rockwood², and Peter P.
Marra¹

¹Migratory Bird Center, Smithsonian Conservation Biology Institute, National
Zoological Park, MRC 5503, Washington DC 20013

²College of Science, George Mason University, 4400 Patriot Drive, Fairfax VA.
22030

³Email: mhallwor@masonlive.gmu.edu

Formatted for submission to Proceedings of the Royal Society B: biological sciences

ABSTRACT

Understanding how stages of the annual cycle interact to shape individual- and population-level dynamics is critical for effective management and conservation. Population dynamics are influenced by carry-over effects, a type of non-lethal seasonal interaction experienced by individuals that produce residual effects in subsequent seasons; thus conservation efforts need to consider the full annual-cycle. Here, we identify how seasonal interactions from non-breeding to breeding periods influence reproductive performance and population growth rate (λ) for the Ovenbird (*Seiurus aurocapilla*). Males that arrived early to breeding grounds paired earlier and at higher rates, and improved their body condition throughout the season compared to late arriving males. Using archival light-level geolocators we found that departure from the non-breeding grounds was directly linked to breeding season arrival, highlighting the importance of the non-breeding season in the annual cycle. Incorporating carry-over effects into λ estimates suggests that early arriving males contribute significantly to population growth while late arriving males do not. For each day of delayed arrival, λ decreased by 0.028 ± 0.003 . Reproductive performance had no effect on departure date from the breeding grounds identified using geolocators. Our findings show a strong carry-over effect in spring mediated by departure date from the non-breeding grounds but no carry-over effect in the fall arising from reproductive effort. This study highlights the importance of integrating seasonal interactions on both individuals and population dynamics.

Keywords: Bayesian, path-analysis, geolocator, carry-over effect, population dynamics, Geo-logger

INTRODUCTION

Carry-over effects are types of seasonal interactions that are non-lethal but have residual effects on fitness, reproductive performance and/or survival during subsequent phases of the annual cycle [1,2]. Since carry-over effects can affect many individuals in a population they likely have important demographic consequences. For example, [3] demonstrated that the summer and autumn diet of Elk (*Cervus elaphus*) influenced the probability of pregnancy, yearling growth and probability of survivorship during the subsequent winter. Similarly, [4] found calving success of the Gray Whale (*Eschrichtius robustus*) was reduced when foraging locations were restricted by ice during the previous summer impacting physical condition of adults prior to birth. In both examples, the population dynamics of migratory populations whose breeding and non-breeding seasons are separated by thousands of kilometers are influenced by events that occur during previous stages of the annual cycle, highlighting the importance of seasonal interactions on population dynamics. However, our ability to identify seasonal interactions is inhibited by the large spatial scales in which migratory organisms occur annually and for small organisms, our inability to track individuals throughout the year [5,6].

Many migratory bird populations in North America have shown population declines in recent decades [7,8]. The cause of these declines are largely unknown but may result from direct habitat loss [9,10]; and indirect factors such as climate change

impacting populations throughout the annual cycle via seasonal interactions that reduce reproductive success [11,12] or survival [13] or a combination of these factors. The role that season interactions play in population dynamics needs to be identified in order to determine where and when in the annual cycle conservation measures are to be implemented. To date, research demonstrating the importance of seasonal interactions has focused on individual-level effects of non-breeding season events on the subsequent breeding season's reproductive success. These studies, mainly indirectly through the use of stable-isotopes, have demonstrated that habitat quality during the non-breeding season is correlated with breeding ground arrival date [14–18], pairing success [19], clutch size [20], the number of young produced [11,19,21], natal dispersal [22] and annual survival [13,16]. An interaction from the breeding to non-breeding season is likely an important component of the annual cycle for migratory birds but remains largely unexplored [23], in part because of our inability to track individuals throughout the annual cycle. Breeding events are physiologically costly and as such may determine the timing of molt [24], departure schedules for fall migration [25], rate of migration, and arrival into the tropics [24].

Population-level dynamics are tied to reproductive performance, adult and juvenile survival [26]. All parameters likely influenced by seasonal interactions at the individual-level [2]. Thus, population dynamics may be influenced by seasonal interactions through the culmination of individual-level interactions when populations exhibit strong migratory connectivity [1,6]. For many species, the strength of migratory connectivity and the geographic link between breeding and non-breeding populations,

remain unknown [6,27] and has limited our ability to quantify the impacts of seasonal interactions on population dynamics.

Technology has existed for tracking large migratory animals, both terrestrial and aquatic, for a number of years using satellite telemetry or Global Positioning Systems (GPS), and this has dramatically improved our knowledge of migration routes [28,29], habitat use [30,31], and behavior [32]. Until recently, the small size of migratory songbirds has precluded the use of such tracking devices. Recent technological advances through the miniaturization of archival light-level geolocators have improved our ability to track small (< 20g) migratory individuals throughout the year [33–35]. Such advances have made it possible to directly link phases of the annual cycle while allowing breeding to non-breeding season carry-over effects to be determined [24].

Here, using archival light-level geolocators in combination with intensive monitoring of a marked breeding population of Ovenbirds (*Seiurus aurocapilla*), we examine how seasonal interactions throughout the year affected both individuals and the population growth rate. Importantly, the use of geolocators allowed us to track individuals throughout the year directly linking phases of the annual cycle which until recently, was only possible indirectly using stable-isotopes. To determine how carry-over effects influence individuals throughout the annual cycle, we constructed a path analysis to test hypotheses derived from previous findings involving migratory songbirds. Because individuals wintering in high quality habitats depart for breeding earlier [14] and arrive at the breeding grounds in better condition [14,36,37] than individuals from lower quality habitats, we predicted that individual condition would be positively related to

arrival date. In addition, early arrival to the breeding grounds improves clutch size, reproductive success and the number of young fledged [11,19–21,42, but see 43]. Therefore we included reproductive parameters such as nestling condition and the number of young fledged in our path model. Because reproductive success is directly tied to annual fecundity we predicted that factors influencing reproductive success would show the strongest carry-over effect.

Seasonal interaction research has been dominated by work searching for non-breeding to breeding interactions, while the interactions between breeding and the subsequent non-breeding season remain largely unexplored [23–25]. To look for breeding to non-breeding carry-over effects we determined how reproductive effort affected departure from the breeding grounds using geolocators. We predicted that the number of young fledged and fledge date would be positively related to departure from the breeding grounds indicating the presence of a breeding to non-breeding seasonal interaction.

METHODS

The Ovenbird is a small (~20g), ground nesting, Neotropical migratory songbird that breeds in deciduous and mixed deciduous forests throughout northern North America and winters in the Caribbean basin and Central America [40]. Ovenbirds are large enough to carry geolocators [41], and their reproductive success can be easily quantified allowing seasonal interactions to be determined throughout the annual cycle. Additionally, Ovenbirds exhibit relatively strong site fidelity to both breeding and non-breeding sites

[41], their population has remained stable [7], and the strength of migratory connectivity for our study population appears strong [Hallworth et al., *in review*].

Field work was conducted at Hubbard Brook Experimental Forest (HBEF) in central New Hampshire, U.S.A. (43.93° N, 71.93° W) during the 2010-2012 breeding seasons (1 May - 1 August). HBEF is a 3160 ha forest ranging in elevation from 222m to 1015m located within the larger White Mountain National Forest. The forest within HBEF is dominated by northern hardwood species such as sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*) at lower elevations, transitioning to red spruce (*Picea rubens*), balsam fir (*Abies balsamea*) and white birch (*B. papyrifera*) at higher elevations [42].

Demographic data were collected within study plots located at 300m, 500m, and 720m asl to maximize differences in Ovenbird demography because predator abundance and habitat structure vary [43]. Within the three study plots Ovenbirds were captured using simulated territorial intrusions. Once captured, birds were aged using molt limits [44] and tail morphology [45]. Because male and female Ovenbirds are indistinguishable in the field, individuals were sexed using the presence of a cloacal protuberance (males) or brood patch (females). Individuals were marked with a unique combination of one United States Geological Survey aluminum leg band and three color leg bands for identification during field observations. Standard morphometric data including mass, wing, tail, tarsus length, and bill measurements (length, depth and width) were collected on all individuals at time of capture. Individual condition was determined using size corrected body mass

[46] with morphometric data collected at the time of capture. We attempted to capture all un-banded males that bred within our study plots each year.

Study plots were surveyed for Ovenbirds every two days to determine arrival beginning prior to their return to the breeding grounds (2010: 1 May, 2011: 26 April, 2012: 26 April). Upon arrival, Ovenbirds sing to establish territories and solicit females enabling arrival dates to be determined accurately. After arrival, Ovenbird territories were visited at least once every three days to determine whether a male was paired, to search for nests, and to collect location data using a hand held Global Positioning System (GPS) unit. Males were considered paired if 1) a non-vocal conspecific was located within a male's territory without an aggressive interaction, 2) the female's distinctive call note was heard in response to a male's song [40], 3) copulation was observed, 4) an individual was seen carrying nest material within the territory or 5) an active nest was found. Once found, nests were monitored every two days until nest failure or nestlings reached day six. If nests reached day six they were visited every day until fledging to determine fledge date. A nest was determined to have failed if 1) no eggs were present after clutch completion, or 2) nestlings were absent prior to potential fledge day (day 8-9). Location data were collected for males until their nests fledged. Territory boundaries were constructed with minimum convex polygons in ArcMap 10.1 (Environmental Systems Research Institute, Redlands, California, USA). Minimum convex polygons were used instead of kernel density estimates because location data were not collected in a time-structured manner.

Predator Abundance -Five minute predator surveys were conducted at 15 locations within each study plot to quantify nest predator abundance [43]. During each survey, field technicians counted the number of eastern chipmunks (*Tamias striatus*) and red squirrels (*Tamiasciurus hudsonicus*), seen or heard. These rodents are the primary predators of ground nests at HBEF [47]. Each location was sampled four times during five, two-week sampling periods, resulting in 20 predator surveys per year (May - July). We modeled predator abundance with an N-mixture [48,49] model using elevation and the squared term of elevation as predictors. Survey date was included in the model to account for changes in detectability over the sampling period. Each predator species was modeled separately. Model predictions were mapped using the raster package [50] in R [51]. Ovenbird territories were overlaid and the estimated mean number of eastern chipmunks and red-squirrels within each territory were extracted. We assumed the effect of eastern chipmunks and red-squirrels on Ovenbird nest predation was additive and thus we used the combined mean eastern chipmunk and mean red-squirrel count per territory as a metric for predation pressure. The combined number of predators was rounded down to the nearest integer.

Food Availability- Food availability is an important determinant of Ovenbird habitat quality during both the breeding [52,53] and non-breeding seasons [54–57]. Ovenbird food availability is correlated with leaf litter depth, and is higher within territories than at randomly selected locations within forests [58]. We quantified food availability by collecting two leaf litter samples from 0.25m² quadrats placed at random locations 5m from active nests; samples were taken during three stages of the nesting

cycle (nest building and incubation, nestling days 5-7, and 7 days post-fledging). We placed the leaf litter samples into Berlese funnels under a 25watt light-bulb. After 48 hours, we collected the invertebrates that migrated into a killing jar and placed them in a drying oven at 60°C for 24 hours. We used the mean dry mass per nest as our measure for food availability on individual territories.

Nestling Condition- Nestlings were banded, weighed, and a tarsus measurement taken five days after hatching. Nestling condition was calculated as the residuals of a linear regression of mass and tarsus length while accounting for nestling age [46]. However, we were uncertain about nestling age for some nests because either weather conditions were not conducive to banding, or a nest was found after day 5. We thus included nestling age in statistical models. We used median nestling condition as our measure of condition because individuals within a nest are not independent samples.

Migratory Connectivity and Departure Dates

We deployed archival light-level geolocators on a subset of males (mass > 19.0g) at HBEF during 2010 (n = 17) and 2011 (n = 34) to determine 1) non-breeding locations [Hallworth et al., in review] and 2) departure dates from the breeding grounds. Departure dates were identified as the date preceding the first day when geocator estimates fell outside the longitudinal range of the breeding 95% kernel density estimate in a direction consistent with fall migration [see Hallworth et al. in review for details]. Longitudinal estimates were used to determine breeding season departure because: 1) error in latitude estimates increased in August, presumably due to feather molt, and 2) many Ovenbirds departed during the period around fall equinox (7 September – 8 October) when estimates

in latitude were unreliable. Departure dates from the non-breeding grounds were determined as the date preceding the first geolocator estimate that fell permanently outside of the non-breeding season 95% kernel density estimate, consistent with spring migration.

Statistical analyses

Survival estimates-

Annual survival probability was estimated with a Cormack-Jolly-Seber (CJS) model and included constant detection probability. We were interested in testing the hypothesis that arrival date influenced annual survival; thus our intention was not to model factors that influence annual survival. We assessed the correlation between breeding season arrival time and estimated annual survival. However, we were unable to determine other parameters related to seasonal interactions, such as departure date from the breeding season or migration distance, because we only had geolocator-acquired data from surviving individuals.

Nest survival- We used a known fate CJS model with detection probability equal to 1 to determine daily nest survival [59]. We included year as a random variable in the model. We again included arrival date as a covariate to elucidate how male arrival at the breeding grounds may affect daily nest survival.

Within season persistence- Territory persistence may be an indirect way to determine territory quality where high quality sites have higher rates of persistence throughout the season. We constructed capture histories for each male comprised of weekly intervals between 1 May and 1 August to quantify within season persistence. We

used the CJS model to account for imperfect detection in persistence measures and incorporated arrival date to determine how arrival may contribute to within-season persistence. Year was included as a random effect in the model.

Individual level-

Confirmatory Path Analysis- We tested how seasonal interactions influence reproductive parameters of Ovenbirds breeding at HBEF by constructing a directed acyclic graph (DAG) of our hypotheses (Figure 1). We used Shipley's d-sep test [60,61] to test if our path model was adequate because our data are hierarchical in nature with repeated measures of individuals in subsequent years (see supplemental materials for details). Once our path model was determined to be a plausible causal model given the observed data ($C = 112.80$, $2k = 134$, $P = 0.908$) we fit the hypothesized models using individual generalized linear mixed-models treating year as a random effect [60].

Parameters included in Path model:

Arrival date, pair date and condition upon arrival were included in the model because various studies have shown that early arriving males produce more young than late arriving males [14,19,38]. Change in body condition (Δ Condition) during the season was added as a proxy for habitat quality [62] which has been linked to fitness [15]. The duration between initial capture and subsequent captures was 37.39 ± 0.69 days (mean \pm 1 SE). We included the number of eggs clutch⁻¹ for the first complete clutch of the first nest attempt as a metric of reproductive effort. Nest attempts where clutch completion was later than the first known re-nest attempt (2010: 158, 2011: 159, 2012: 160) were excluded. The total number of eggs laid within a season was used as a measure of

reproductive stress as eggs are laid after each nest failure. Nestling condition and the number of young fledged were included as reproductive measures. We used predator abundance and food availability as a proxy for territory quality. We replaced incomplete reproductive histories with the mean [63]. Little is known about departure date dynamics from the breeding grounds but it may be related to reproductive effort or success and thus was included in our path analysis [24,25]. Explanatory variables were standardized to assist with model convergence (see below, [49]). Missing values in explanatory variables were replaced with the mean [63]. We did not standardize response variables and missing values were retained.

All analyses were conducted in a Bayesian framework using vague priors in JAGS 3.4.0 (Just Another Gibbs Sampler) [64] accessed through program R using the R2jags package [65]. We generated three Markov chains, each consisting of 15000 iterations after an initial burn in of 5000 iterations. We saved every 5th iteration resulting in 6000 samples from the posterior distribution retained for each parameter [66]. Model convergence was inspected visually using plots of the posterior distributions and the Brooks-Gelman-Rubin (\hat{R} statistic) diagnostic. Models were considered converged if \hat{R} was < 1.05 for all parameters [66]. If the model did not converge after 15000 iterations we increased the number of iterations to 50000 and re-assessed convergence. Model fit of univariate models contained within the path analysis were assessed using the Bayesian P value (mean = 0.579, SE = 0.031) by calculating the sum of squared Pearson residuals for the actual data and the data simulated given the model [67].

We modeled the number of eggs laid and the number of young fledged as bounded counts using a binomial distribution following:

$$y \sim \text{Binomial}(N_{\text{year}}, p)$$

$$\text{logit}(p) = \alpha + \beta * x$$

where N is the maximum count in a specific year and p is the probability of producing the maximum number of eggs per clutch or number of young fledged for that year. We modeled bounded counts because the use of a Poisson distribution resulted in a lack of fit producing overly-dispersed residuals determined by the Bayesian P value. Beta estimates for these models are reported on the logit scale.

Population level-

To determine the influence of seasonal interactions on population-level dynamics we calculated the population growth rate (λ) with and without seasonal interactions. A λ value = 1 signifies a stable population while values > 1 or < 1 indicate population growth and decline, respectively. We combined the models of [68] and [26] to determine the population growth rate. We then included arrival date into the model to determine how seasonal interactions influence λ for our population of Ovenbirds at HBEF. Arrival date to the breeding grounds is a commonly used metric to quantify seasonal interactions and is strongly correlated with departure from the non-breeding season (see Results). We used the following model to determine population growth rate:

$$\lambda = \frac{N_{t+1}}{N_t}$$

$$N_{t+1} = (N_t * \gamma * NS * (1 + Pr - NS * Pr + Pd) * Pp) * Pj + N_t * Pa)$$

We defined annual fecundity (\bar{Y}) as half the mean number of young fledged which assumes an equal sex ratio of nestlings within the nest [69]. We defined nest success (NS) as dns^n where dns is daily nest survival and n is the number of days from clutch initiation to fledging ($n=24$, [40]). We included the probability of re-nesting after an initial failure (P_s) and the probability of double-brooding (P_d). Radio telemetry was used to determine the probability of re-nesting and double brooding. During 2011 and 2012 we attached radio transmitters (0.75g, Model # A1035, ATS, Inc. Minnesota, USA.) to females ($n=25$, 2011: $n=13$, 2012: $n=12$) during the breeding season. Females were captured while incubating their first nest attempt using a butterfly net [68]. We assumed females with radio transmitters were representative of the entire female population within our study plots and used their re-nesting and double brooding rates to parameterize the model. The probability of re-nesting after an initial failure was 0.348, and the probability of double brooding was 0.130.

Female and juvenile survival influence the finite rate of increase for Ovenbird populations [26]. Our annual survival estimates for females was low (0.358, CI 0.121-0.863). Detection probability was also low within (0.702, CI 0.677-0.776) and between seasons (0.585, CI 0.149-0.981) for females. We felt our estimates of female survival were uncharacteristically low, likely caused by permanent emigration and not actual mortality. Because of these factors, we used published estimates of female survival (0.633, CI 0.545-0.721, [26,68]). We also used published estimates of fledgling survival (P_f) [70]. The study conducted by [70] took place within 30 km of HBEF and was also located within the White Mountain National Forest in central New Hampshire. We

assumed that fledgling survival at HBEF was the same as those reported by [70] (0.68). We used fledgling survival coupled with non-breeding period (migration and non-breeding) survival estimates to determine juvenile survival [26,70]. Non-breeding survival rates are not available for many migratory species including Ovenbirds. Here, we assumed a non-breeding period survival (including migratory periods) of 0.70 [70].

The finite rate of increase for Ovenbirds is influenced by pairing success [68]. Whether or not a male is paired may not preclude them from siring young. In Maryland, [71] found 28% of Ovenbird nestlings were sired by extra pair males and 46% of broods contained at least one extra pair young. Although Ovenbirds may exhibit moderate rates of cuckoldry, we assumed only males that successfully paired fledged young. We modeled the effect of arrival date on pairing success using logistic regression.

We computed λ with and without the influence of seasonal interactions. To include seasonal interactions into the calculation of λ , we used the following models to determine fecundity (γ) and the probability of pairing (Pp):

$$\gamma = \frac{\exp(\alpha + \beta * x)}{(1 + \exp(\alpha + \beta * x))} * C * 0.5$$

$$Pp = \frac{\exp(\alpha + \beta * x)}{(1 + \exp(\alpha + \beta * x))}$$

where C is the maximum clutch size (5), x is standardized arrival date, α and β are the intercept and beta estimates from the respective analyzes. We assumed that all females in the population paired. We quantified the uncertainty for λ estimates by running 1000 iterations of the model while allowing female survival to be drawn randomly from a uniform distribution bounded between 0.545 and 0.721, the 95% confidence interval

reported by [26]. N_t was arbitrarily set at 1000 individuals for each scenario and iteration [26]. In addition to determining λ with and without the effect of seasonal interactions, we simulated how λ would be affected if males arrived to the breeding grounds 10 days later than observed.

RESULTS

Our results indicate that seasonal interactions strongly influence events at the individual level through carry-over effects and this, in turn, has important effects at the population level for breeding Ovenbirds (Figure 1 and Figure 3, respectively). We also found that carry-over effects influenced individuals in the spring but not the fall.

Departure date from the non-breeding areas determined arrival date at the breeding grounds. Arrival date was tied to reproductive parameters such as pairing success, timing of pairing and clutch completion. However, neither the number of young fledged or fledge date influenced departure date from the breeding location. Incorporating seasonal interactions into calculations of population growth rate (λ) confirmed that seasonal interactions do have an effect on population-level dynamics.

Individual-level-

Departure date from the non-breeding grounds was directly related to arrival on the breeding grounds (Figure 2, see Figure 1 for beta estimates and CIs). Males that arrived early paired sooner, had earlier clutch completion dates and had improved body condition when re-captured later in the season. Condition upon arrival, the number of eggs laid per clutch and nestling condition were not related to arrival date. Earlier clutch

completion dates led to more young fledged and nestling condition was negatively related to the change in male body condition over the season (see Figure 1 for beta estimates and CIs). The number of eggs laid per clutch did not influence the number of young fledged; however, the total number of eggs laid during the season did. The total number of eggs laid was related to later fledging dates. Neither the number of young fledged nor fledging date influenced departure date from the breeding season.

Our measures of territory quality, predator abundance and food availability, did not influence overall reproductive success. However, predator abundance was correlated with the total number of eggs laid but not fledging date. Although food availability has been indicated as a measure of habitat quality important for Ovenbirds [52,53], it was not significantly related to a change in body condition during the season, the number of eggs laid per clutch or nestling condition.

We found no evidence that carry-over effects mediated by arrival to the breeding grounds were correlated with survival metrics. Arrival date to the breeding grounds was not associated with annual survival ($\beta = 0.042$, CI -0.013-0.086), within breeding-season persistence ($\beta = -0.016$, CI -0.039:0.005) or daily nest survival ($\beta = 0.072$, CI -0.077-0.217).

Population Modeling

Population growth rates are closely tied to the number of young produced, as well as survivorship of juveniles and females. The model was parameterized with 198 Ovenbird nests from 2010-2012 (2010: $n = 55$, 2011: $n = 47$, 2012: $n = 96$). Over the course of the study daily nest survival (*dns*) was 0.998 (CI 0.991 – 1.00), the number of

young fledged was 2.35 ± 0.21 (mean \pm SE) and the mean pairing success rate (Pr) was 0.52 (CI 0.49 – 0.55) ($n = 224$). The population growth rate (λ) for Ovenbirds breeding at HBEF is 0.99 (CI 1.07-0.90) indicating that the population is approximately stable.

Due to variation in individual performance, individuals within a population do not contribute equally to the overall population growth rate [72]. As such, population growth rates are likely influenced by seasonal interactions because pairing success and reproductive parameters are affected by events during the preceding non-breeding season. Arrival date significantly influenced pairing probability ($\beta = -0.550$, CI -0.951:-0.180), with early arriving males pairing at a higher proportion than later arriving males. When the influence of arrival date was incorporated into λ via pairing success, early arriving males added significantly to the population while later arriving males did not (Figure 3a). Although the number of young produced increased with arrival date ($\beta = 0.33$, CI 0.06:0.61), when incorporating seasonal interactions into λ calculations via fecundity, estimates for early arriving males were significantly higher than λ estimates when not including seasonal interactions (Figure 3b). The population growth rate estimates that incorporated seasonal interactions into both pairing success and fecundity indicate that early arriving males add significantly to the population while the estimates decrease significantly for late arriving males (Figure 3c). This was further supported by simulations that assumed males arrived 10 days later than observed. The simulated arrival data significantly reduced λ estimates for all but the latest arriving individuals (Figure 3d).

DISCUSSION

We demonstrated that seasonal interactions via carry-over effects influence individual and then population-level dynamics of a long distance migratory songbird. Using geolocators, we found that departure date from the non-breeding season determines arrival at the breeding grounds, directly linking non-breeding and breeding events. Furthermore, arrival date, mediated by non-breeding departure, can have cascading effects on breeding season demography. To our knowledge, this is the first study that ties non-breeding departure to breeding season arrival, individual reproductive performance and population growth rate.

Seasonal interactions from non-breeding to breeding seasons influenced individual reproductive performance via arrival to the breeding grounds. Earlier arriving males paired earlier and at higher proportions, initiated nests earlier, and improved their body condition throughout the season compared to late arriving males. The presence of a spring seasonal interaction suggests that non-breeding events play an important role in the annual cycle of migratory bird populations and that factors determining departure schedules from the non-breeding season are inexplicably linked to reproductive success. The ecological and/or environmental factors responsible for driving variation in departure dates for our population are unknown. Day length [73] and endogenous cues [74,75] have been shown in captivity to determine departure date when simulating day length changes experienced during the non-breeding season. Breeding latitude has also been shown to determine departure schedules in one species of shorebird [76]. Departure schedules for new world songbirds from the non-breeding season is determined by habitat [14,77]

where individuals in high quality habitat depart for spring migration earlier than individuals in low quality habitat. In addition, using a longitudinal analysis of individuals, rainfall has been linked to departure schedules [78] and subsequent arrival to the breeding season [11,12,37], where both departure and arrival are earlier in wet years. Rainfall may provide increased food availability [78] and improve individual condition which has been shown to influence departure in American redstarts (*Setophaga ruticilla*) [79] but not greater snow geese (*Chen caerulescens atlantica*) [80]. The non-breeding environmental or ecological factors that determine departure date for linked populations must be considered to better understand individual dynamics as these have implications during the breeding season.

We found no relationship between reproductive effort and departure dates from the breeding grounds. Arrival to the non-breeding grounds may not be critical for securing high quality habitat, especially for older dominant individuals [82 but see 80]. In American redstarts, older, dominant individuals have been shown to displace females and subordinate males from high quality habitat upon arrival [82]. In addition, Ovenbirds appear to exhibit variability in patterns of space use during the non-breeding season where some individuals defend home-ranges while others float between areas of high food availability [55]. Young and experienced individuals of both sexes employed floating strategies which was maintained across multiple seasons. Floaters were able to maintain body condition despite diminishing food resources as the season progressed suggesting that acquiring a territory early may not be beneficial especially in habitats with unpredictable food resources [55]. These studies, together with our findings suggest

that departure from the breeding and subsequent arrival at the non-breeding grounds is likely not under strong selection.

The time period between the termination of breeding and departure for fall migration may allow individuals to overcome condition deficiencies derived from reproductive effort. The mean interval between fledge date and departure for fall migration was 82.33 ± 5.22 days. Given that fledglings become independent within 25 days [26], this would allow individuals approximately 55 days to molt and potentially recuperate from reproductive stressors. This seems likely given that individuals can significantly improve their condition within approximately 37 days while simultaneously attempting to breed. For example, reproductive timing and success influences feather molt patterns in albatross. In years when they breed successfully feather molt is delayed, resulting in failure to breed the subsequent season [83,84]. The timing and geographic location of feather molt appears to be important for breeding ground departure for *Tyrannus* flycatchers [85]. In addition, molt schedules and energetic condition have been shown to influence arrival in the tropics for Wood Thrush (*Hylocichla mustelina*) [24] and reproductive timing influenced the onset of fall migration for Savannah Sparrows (*Passerculus sandwichensis*) [25]. In the above examples, albatross are long-lived species whereas *Tyrannus* flycatchers, Wood Thrush and the Savannah sparrow are long and short distance migrants that are relatively short lived. Seasonal interactions between breeding and non-breeding seasons likely differ among species because of different fundamental life history strategies. Here, it appears that selective forces may not be as strong for breeding season departure as they are for arrival to the breeding grounds.

However, more research is clearly needed to understand the role that reproductive performance and molt play in determining breeding season departure schedules, as well as subsequent arrival and habitat occupancy on the non-breeding grounds.

The use of archival light-level geolocators was essential for incorporating departure information from both the non-breeding and breeding seasons into our path analysis. With geolocators, we were able to track individuals through the different phases of the annual cycle, directly linking non-breeding season departure, arrival to the breeding season and reproductive success. Previous research demonstrating carry-over effects have used stable-isotopes to infer information about the previous life history phase indirectly. Here, with the use of geolocators, we provide the first empirical evidence that non-breeding season events mediated via departure date have profound effects on both individuals and populations during the breeding season.

Our path analysis demonstrated that carry-over effects from the non-breeding to the breeding season have potential to influence population dynamics. Indeed, early arriving males contributed significantly to the population growth rate. The contribution was especially pronounced when including carry-over effects on pairing success and the number of young fledged into the model simultaneously. The population growth rate decreased by 0.012 ± 0.0009 for each day arrival to the breeding grounds was delayed. Although the number of young fledged was positively correlated with arrival date, the effect of pairing success on the population growth rate (-0.011 day^{-1}) was nearly three times larger than the number of young fledged (0.0038 day^{-1}). While carry-over effects from the non-breeding period have been shown to influence parameters involved in

population growth rates such as pairing success [19, this study], and apparent [21] as well as realized reproductive success [19], this is one of the first studies to empirically demonstrate that carry-over effects influence population growth rates [86], and the first to do so with a migratory organism. By comparison, experimental manipulation of *Drosophila* density resulted in lower per capita growth rate for individuals that experienced high densities during the previous non-breeding period [86]. Our results do not explicitly include density-dependent influences, as the density on our study plots remained constant throughout the study period during the breeding season. A long term study would likely detect differences in density and help elucidate the role that density-dependent mechanisms play during the breeding season. The role of density-dependent mechanisms during the non-breeding season remains unknown for most bird species.

For migratory species, processes that limit or regulate populations likely operate within both breeding and non-breeding seasons. However, like the phases of the annual cycle these processes also interact to influence both individual- and population-level dynamics. Our findings emphasize that it is essential to incorporate events from the full annual cycle when trying to uncover the factors that limit or regulate such populations. Furthermore, the degree to which regulatory processes interact between phases of the annual cycle may depend on the strength of migratory connectivity [5,6]. Future research should identify how mechanisms limiting or regulating migratory organisms differ for populations that exhibit varying strengths of migratory connectivity in order to elucidate how these mechanisms interact across phases of the annual cycle to shape population dynamics.

ACKNOWLEDGEMENTS

We thank A. Bloomfield, L. Bryant, A. Costa, V. Dwiggins, M. Grant, B. Lang, K. Long, D. Narango and J. Welklin and the 2010-2012 Black-throated blue warbler field technicians at Hubbard Brook Experimental Forest for their assistance in the field. We thank R. Greenberg and M. Webster for providing telemetry equipment. Funding was provided by Smithsonian Institution's Endowment Bond (MTH and PPM), Cosmos Scholars (MTH), American Ornithologists' Union (MTH) and the National Science Foundation's Long-term Research in Environmental Biology Program (PPM and TSS).

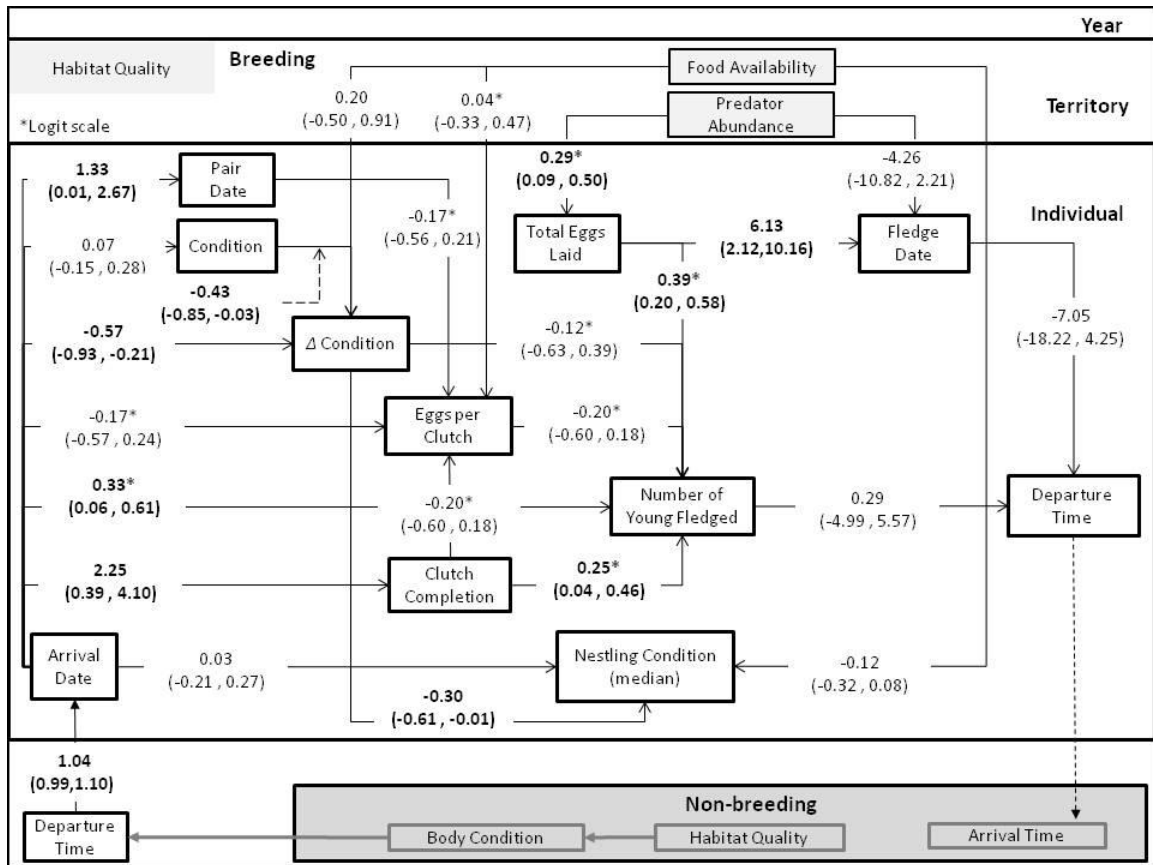


Figure 12

Figure 1: Confirmatory path analysis demonstrating the influence of seasonal interactions on individual-level dynamics of the Ovenbird breeding at Hubbard Brook Experimental Forest in central New Hampshire. The figure illustrates the hypothesized causal relationships between breeding parameters measured during the 2010-2012 breeding seasons. The relationship (beta estimate and 95% credible interval) between the hypothesized connections are shown along the line. Beta estimates where the 95% credible interval did not include zero are shown in bold font. Beta estimates accompanied by an asterisk are presented on the logit scale. We were not able to determine how departure date from the breeding grounds was related to non-breeding season arrival (dotted line, see text). The non-breeding season is grayed out because we did not measure any metrics associated with the non-breeding season but instead was included to put breeding season events into the context of the full annual cycle.

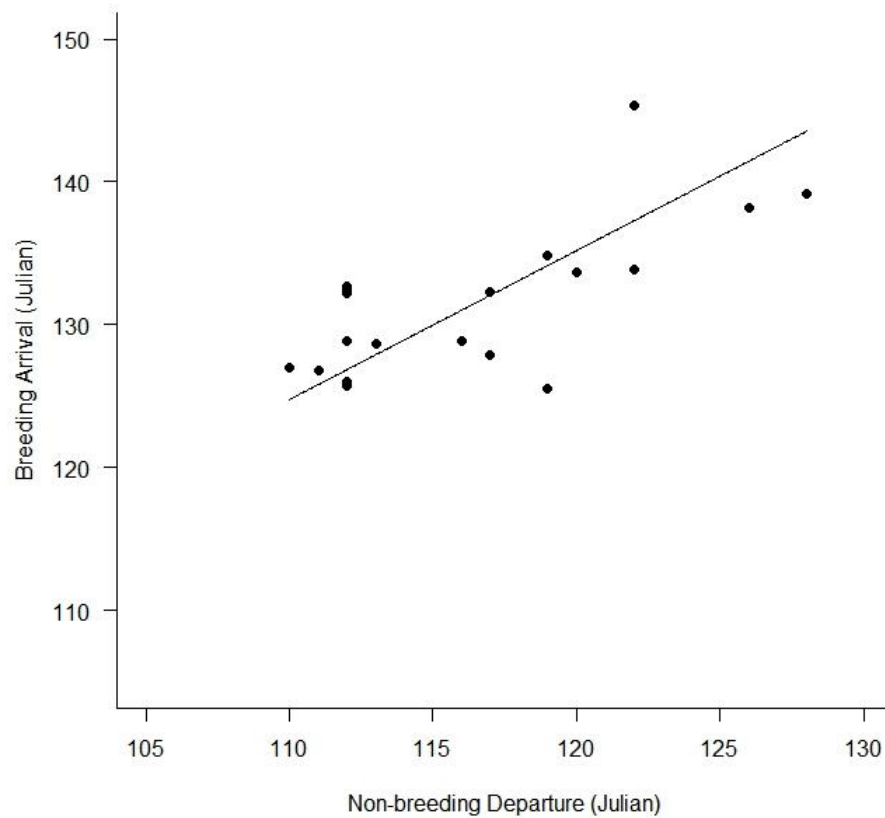


Figure 13

Figure 2: The relationship between non-breeding season departure date and subsequent arrival the breeding season for Ovenbirds breeding at Hubbard Brook Experimental Forest, NH as determined by archival light-level geolocators. Arrival date was determined by departure from the non-breeding season.

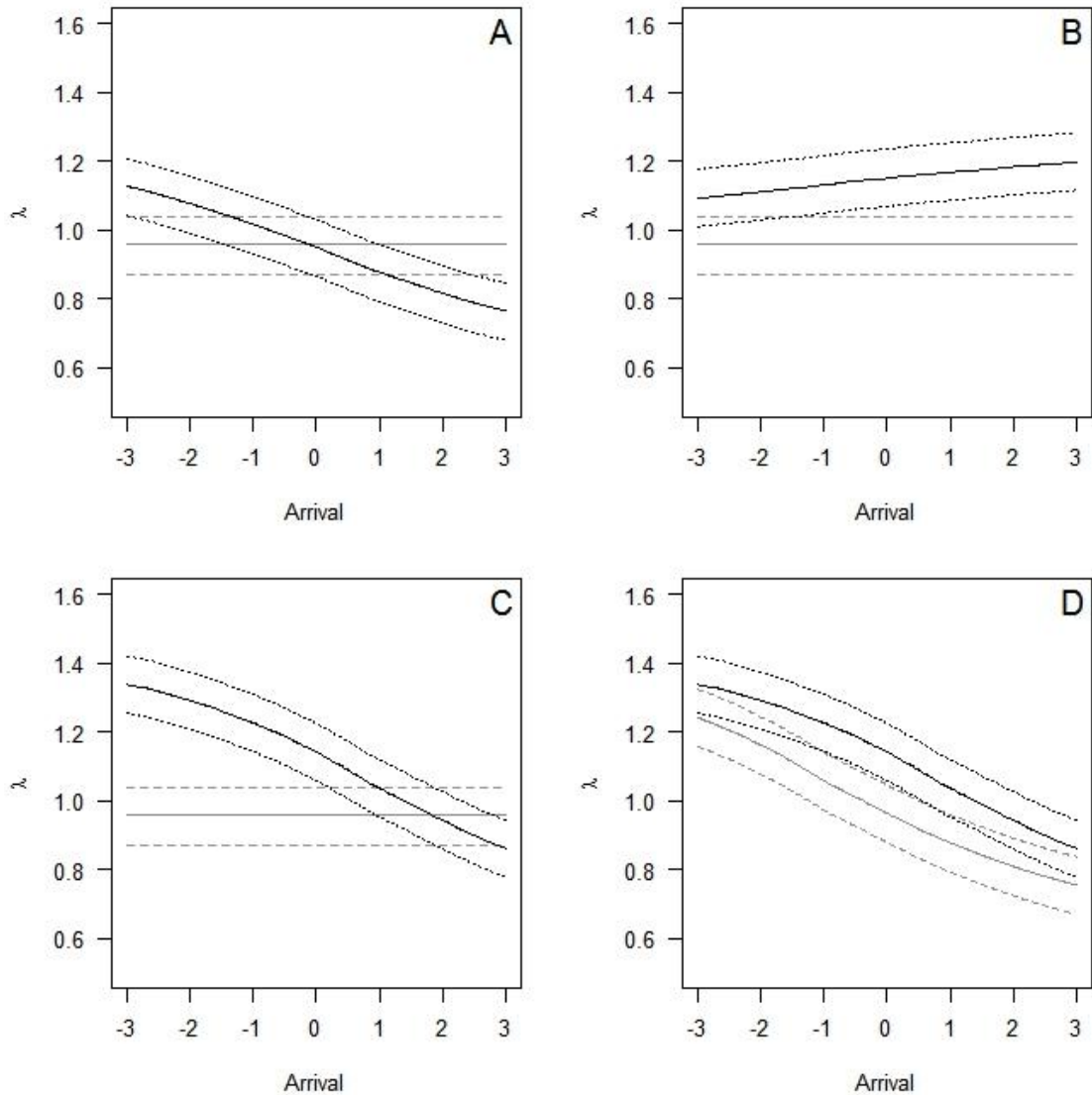


Figure 14

Figure 3: The influence of seasonal interactions on population level dynamics. The finite rate of increase (λ) (solid line) and 95% confidence interval (dotted line) without incorporating seasonal interactions for Ovenbirds breeding at Hubbard Brook Experimental Forest, NH is shown in gray (a,b,c). The finite rate of increase (λ) after incorporating seasonal interactions into pairing success (a), fledging success (b) and both pairing and fledging success (c) are shown in black. Simulations incorporating seasonal interactions into λ estimates (d) assuming individuals arrived 10 days later than observed (gray) and observed arrive dates (black).

Supplemental information:

Path analysis -

We first identified all variable pairs within our model that did not have an arrow between them. A conditioning set of variables for each pair were identified as variables that are direct causes (in our model) of the variables in the pair. The pair of variables along with the conditioning set constitute an independence claim. The full list of independence claims within a path model defines the basis set (Supplemental Table 1). For each independence claim we regressed one of the variables in the pair as the response variable and the other along with the conditioning set of variables as explanatory variables. We assessed the probability that the pair of variables within an independence claim were statistically independent conditional on the conditioning set by obtaining the posterior distribution of the slope for the variable in the pair used as an explanatory variable. The posterior probability of the slope (p) were then combined in the following equation

$$C = -2 \sum_{i=1}^k \log (p_i)$$

to calculate the test statistic C , where k = number of independence claims tested. The test statistic was then compared to a χ^2 distribution with $2k$ degrees of freedom. The path model is not supported if the P-value is less than 0.05 [60,61].

Supplemental Table 1. Basis set for the confirmatory path analysis identifying the influence of seasonal interactions on individual-level dynamics. The probability (P_i) of the beta estimate for explanatory variable including zero while conditioned on by all variables in the independence claim (See methods for details).

Table 9

Independence Claim	P_i
(Arrival, TotalEggs) { Condition, Pair, NestCond, Clutch, Eggs, D.Condition, Fledged, FledgeDate }	0.990
(Arrival, FledgeDate) { Condition, Pair, NestCond, Clutch, Eggs, D.Condition, Fledged, Depart.2 }	0.974
(Arrival, Depart.2) { Condition, Pair, NestCond, Clutch, Eggs, D.Condition, Fledged }	0.904
(Arrival, Food) { Condition, Pair, NestCond, Clutch, Eggs, D.Condition, Fledged }	0.985
(Arrival, Preds) { Condition, Pair, NestCond, Clutch, Eggs, D.Condition, Fledged, TotalEggs, FledgeDate }	0.004
(Clutch, Depart.1) { Eggs, Fledged, Arrival }	0.976
(Clutch, Condition) { Eggs, Fledged, D.Condition }	0.984
(Clutch, Pair) { Eggs, Fledged }	0.976
(Clutch, D.Condition) { Eggs, Fledged, NestCond }	0.996
(Clutch, TotalEggs) { Eggs, Fledged, FledgeDate }	0.000
(Clutch, NestCond) { Eggs, Fledged }	0.995
(Clutch, FledgeDate) { Eggs, Fledged, Depart.2 }	0.589
(Clutch, Depart.2) { Eggs, Fledged }	0.856
(Clutch, Preds) { Eggs, Fledged, TotalEggs, FledgeDate }	0.503
(Condition, Depart.1) { D.Condition, Arrival }	0.979
(Condition, Pair) { D.Condition, Eggs }	0.995
(Condition, Eggs) { D.Condition, Fledged }	0.884
(Condition, TotalEggs) { D.Condition, Fledged, FledgeDate }	0.362
(Condition, NestCond) { D.Condition }	0.978
(Condition, Fledged) { D.Condition, Depart.2 }	0.085
(Condition, FledgeDate) { D.Condition, Depart.2 }	0.813
(Condition, Depart.2) { D.Condition }	0.904
(Condition, Food) { D.Condition, Eggs, NestCond }	0.988
(Condition, Preds) { D.Condition, TotalEggs, FledgeDate }	0.069
(D.Condition, Depart.1) { Fledged, NestCond, Arrival }	0.886
(D.Condition, Pair) { Fledged, NestCond, Eggs }	0.970
(D.Condition, Eggs) { Fledged, NestCond }	0.689
(D.Condition, TotalEggs) { Fledged, NestCond, FledgeDate }	0.083
(D.Condition, FledgeDate) { Fledged, NestCond, Depart.2 }	0.937
(D.Condition, Depart.2) { Fledged, NestCond }	0.975
(D.Condition, Food) { Fledged, NestCond, Eggs }	0.994
(D.Condition, Preds) { Fledged, NestCond, TotalEggs, FledgeDate }	0.664
(Depart.1, Pair) { Arrival, Eggs }	0.927
(Depart.1, Eggs) { Arrival, Fledged }	0.975
(Depart.1, TotalEggs) { Arrival, Fledged, FledgeDate }	0.825

(Depart.1,NestCond) { Arrival }	0.999
(Depart.1,Fledged) { Arrival,Depart.2 }	0.027
(Depart.1,FledgeDate) { Arrival,Depart.2 }	0.936
(Depart.1,Depart.2) { Arrival }	0.942
(Depart.1,Food) { Arrival,D.Condition,Eggs,NestCond }	0.991
(Depart.1,Preds) { Arrival,TotalEggs,FledgeDate }	0.655
(Depart.2,Pair) { Eggs }	0.999
(Depart.2,Eggs) { Fledged }	0.913
(Depart.2,TotalEggs) { Fledged,FledgeDate }	0.884
(Depart.2,NestCond) { Ø }	0.995
(Depart.2,Food) { D.Condition,Eggs,NestCond }	0.999
(Depart.2,Preds) { TotalEggs,FledgeDate }	0.533
(Eggs,TotalEggs) { Fledged,FledgeDate }	0.056
(Eggs,NestCond) { Fledged }	0.983
(Eggs,FledgeDate) { Fledged,Depart.2 }	0.890
(Eggs,Preds) { Fledged,TotalEggs,FledgeDate }	0.665
(Fledged,Pair) { Depart.2,Eggs }	0.967
(Fledged,NestCond) { Depart.2 }	0.985
(Fledged,FledgeDate) { Depart.2 }	0.933
(Fledged,Food) { Depart.2,D.Condition,Eggs,NestCond }	0.998
(Fledged,Preds) { Depart.2,TotalEggs,FledgeDate }	0.017
(FledgeDate,Pair) { Depart.2,Eggs }	0.993
(FledgeDate,NestCond) { Depart.2 }	0.992
(FledgeDate,Food) { Depart.2,D.Condition,Eggs,NestCond }	0.983
(Food,Pair) { D.Condition,Eggs,NestCond }	0.977
(Food,TotalEggs) { D.Condition,Eggs,NestCond,Fledged,FledgeDate }	0.542
(Food,Preds) { D.Condition,Eggs,NestCond,TotalEggs,FledgeDate }	0.193
(NestCond,Pair) { Eggs }	0.987
(NestCond,TotalEggs) { Fledged,FledgeDate }	0.443
(NestCond,Preds) { TotalEggs,FledgeDate }	0.624
(Pair,TotalEggs) { Eggs,Fledged,FledgeDate }	0.400
(Pair,Preds) { Eggs,TotalEggs,FledgeDate }	0.400

LITERATURE CITED

1. Norris, D. R. & Marra, P. P. 2007 Seasonal interactions, habitat quality, and population dynamics in migratory birds. *The Condor* **109**, 535–547.
2. Runge, M. C. & Marra, P. P. 2005 Modeling seasonal interactions in the population dynamics of migratory birds. *Birds Two Worlds Ecol. Evol. Migr. Johns Hopkins Univ. Press Baltim. Md. USA* , 375–389.
3. Cook, J. G., Johnson, B. K., Cook, R. C., Riggs, R. A., Delcurto, T., Bryant, L. D. & Irwin, L. L. 2004 Effects of summer-autumn nutrition and parturition date on reproduction and survival of Elk. *Wildl. Monogr.* **155**, 1–61.
4. Perryman, W. L., Donahue, M. A., Perkins, P. C. & Reilly, S. B. 2002 Gray whale calf production 1994–2000: are observed fluctuations related to changes in seasonal ice cover? *Mar. Mammal Sci.* **18**, 121–144.
5. Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S. & Holmes, R. T. 2002 Links between worlds: unraveling migratory connectivity. *Trends Ecol. Evol.* **17**, 76–83.
6. Marra, P. P., Norris, D. R., Haig, S. M., Webster, M. S. & Royle, J. A. 2006 Migratory connectivity. In *Connectivity conservation* (eds K. R. Crooks & M. A. Sanjayan), pp. 157–183. Cambridge University Press.
7. Sauer, J. R., Hines, J. E., Fallon, J. E., Pardieck, K. L., Ziolkowski, D. J. & Link, W. A. 2014 The North American breeding bird survey, results and analysis 1966–2012. Version 02.19.2014.
8. Faaborg, J., Arendt, W. J., Toms, J. D., Dugger, K. M., Cox, W. A. & Mora, M. C. 2013 Long-term decline of a winter-resident bird community in Puerto Rico. *Biodivers. Conserv.* **22**, 63–75.
9. Robbins, C. S., Sauer, J. R., Greenberg, R. S. & Droege, S. 1989 Population declines in North American birds that migrate to the neotropics. *Proc. Natl. Acad. Sci. U. S. A.* **86**, 7658–7662.
10. Rappole, J. H. 1996 The importance of forest for the world’s migratory bird species. In *Conservation of faunal diversity in forested landscapes*, pp. 389–406. Springer..

11. Rockwell, S. M., Bocetti, C. I. & Marra, P. P. 2012 Carry-over effects of winter climate on spring arrival date and reproductive success in an endangered migratory bird, Kirtland's Warbler (*Setophaga kirtlandii*). *The Auk* **129**, 744–752.
12. McKellar, A. E., Marra, P. P., Hannon, S. J., Studds, C. E. & Ratcliffe, L. M. 2013 Winter rainfall predicts phenology in widely separated populations of a migrant songbird. *Oecologia* **172**, 595–605.
13. Sillett, T. S., Holmes, R. T. & Sherry, T. W. 2000 Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science* **288**, 2040.
14. Marra, P. P., Hobson, K. A. & Holmes, R. T. 1998 Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* **282**, 1884.
15. Gunnarsson, T. G., Gill, J. A., Newton, J., Potts, P. M. & Sutherland, W. J. 2005 Seasonal matching of habitat quality and fitness in a migratory bird. *Proc. R. Soc. B Biol. Sci.* **272**, 2319–2323.
16. Gill, J. A., Norris, K., Potts, P. M., Gunnarsson, T. G., Atkinson, P. W. & Sutherland, W. J. 2001 The buffer effect and large-scale population regulation in migratory birds. *Nature* **412**, 436–8.
17. Gordo, O. & Sanz, J. J. 2008 The relative importance of conditions in wintering and passage areas on spring arrival dates: the case of long-distance Iberian migrants. *J. Ornithol.* **149**, 199–210.
18. Both, C. et al. 2006 Pied flycatchers *Ficedula hypoleuca* travelling from Africa to breed in Europe: differential effects of winter and migration conditions on breeding date. *ARDEA-Wagening.* **94**, 511.
19. Reudink, M. W., Marra, P. P., Kyser, T. K., Boag, P. T., Langin, K. M. & Ratcliffe, L. M. 2009 Non-breeding season events influence sexual selection in a long-distance migratory bird. *Proc. R. Soc. B Biol. Sci.* **276**, 1619–1626.
20. Saino, N., Szép, T., Ambrosini, R., Romano, M. & Moller, A. P. 2004 Ecological conditions during winter affect sexual selection and breeding in a migratory bird. *Proc.-R. Soc. Lond. B* **271**, 681–686.
21. Norris, D. R., Marra, P. P., Kyser, T. K., Sherry, T. W. & Ratcliffe, L. M. 2004 Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proc. R. Soc. B Biol. Sci.* **271**, 59–64.
22. Studds, C. E., Kyser, T. K. & Marra, P. P. 2008 Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory songbird. *Proc. Natl. Acad. Sci.* **105**, 2929.

23. Bogdanova, M. I., Daunt, F., Newell, M., Phillips, R. A., Harris, M. P. & Wanless, S. 2011 Seasonal interactions in the Black-Legged Kittiwake, *Rissa Tridactyla*: links between breeding performance and winter distribution. *Proc. R. Soc. B Biol. Sci.* **278**, 2412–2418.
24. Stutchbury, B. J. ., Gow, E. A., Done, T., MacPherson, M., Fox, J. W. & Afanasyev, V. 2011 Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. *Proc. R. Soc. B Biol. Sci.* **278**, 131.
25. Mitchell, G. W., Newman, A. E., Wikelski, M. & Ryan Norris, D. 2012 Timing of breeding carries over to influence migratory departure in a songbird: an automated radiotracking study. *J. Anim. Ecol.* **81**, 1024–1033.
26. Streby, H. M. & Andersen, D. E. 2011 Seasonal productivity in a population of migratory songbirds: why nest data are not enough. *Ecosphere* **2**, art78.
27. Webster, M. S. & Marra, P. P. 2005 The importance of understanding migratory connectivity and seasonal interactions. *Birds Two Worlds Ecol. Evol. Migr.* , 199–209.
28. Luschi, P., Hays, G. C., Del Seppia, C., Marsh, R. & Papi, F. 1998 The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. *Proc. R. Soc. Lond. B Biol. Sci.* **265**, 2279–2284.
29. Martell, M. S., Henny, C. J., Nye, P. E. & Solensky, M. J. 2001 Fall migration routes, timing, and wintering sites of North American Ospreys as determined by satellite telemetry. *The Condor* **103**, 715–724.
30. James, M. C., Andrea Ottensmeyer, C. & Myers, R. A. 2005 Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. *Ecol. Lett.* **8**, 195–201.
31. Baumgartner, M. F. & Mate, B. R. 2005 Summer and fall habitat of North Atlantic right whales (*Eubalaena glacialis*) inferred from satellite telemetry. *Can. J. Fish. Aquat. Sci.* **62**, 527–543.
32. Eckert, S. A., Dolar, L. L., Kooyman, G. L., Perrin, W. & Rahman, R. A. 2002 Movements of whale sharks (*Rhincodon typus*) in South-east Asian waters as determined by satellite telemetry. *J. Zool.* **257**, 111–115.
33. Stutchbury, B. J. ., Tarof, S. A., Done, T., Gow, E., Kramer, P. M., Tautin, J., Fox, J. W. & Afanasyev, V. 2009 Tracking long-distance songbird migration by using geolocators. *Science* **323**, 896.

34. Bridge, E. S., Kelly, J. F., Contina, A., Gabrielson, R. M., MacCurdy, R. B. & Winkler, D. W. 2013 Advances in tracking small migratory birds: a technical review of light-level geolocation. *J. Field Ornithol.* **84**, 121–137.
35. Renfrew, R. B., Kim, D., Perlut, N., Smith, J., Fox, J. & Marra, P. P. 2013 Phenological matching across hemispheres in a long-distance migratory bird. *Divers. Distrib.* **19**, 1008–1019.
36. Bearhop, S., Hilton, G. M., Votier, S. C. & Waldron, S. 2004 Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. , S215–S218.
37. Saino, N., Szep, T., Romano, M., Rubolini, D., Spina, F. & Møller, A. P. 2004 Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecol. Lett.* **7**, 21–25.
38. McKellar, A. E., Marra, P. P. & Ratcliffe, L. M. 2013 Starting over: experimental effects of breeding delay on reproductive success in early-arriving male American redstarts. *J. Avian Biol.* **44**, 495–503.
39. Drake, A., Martin, M. & Green, D. J. 2014 Winter habitat use does not influence spring arrival dates or the reproductive success of Yellow Warblers breeding in the arctic. *Polar Biol.* **37**, 181–191.
40. Porneluzi, P., Van Horn, M. A. & Donovan, T. M. 2011 Ovenbird (*Seiurus aurocapilla*). *Birds N. Am. Online*
41. Hallworth, M. T., Studds, C. E., Sillett, T. S. & Marra, P. P. 2013 Do archival light-level geolocators and stable hydrogen isotopes provide comparable estimates of breeding-ground origin?. *The Auk* **130**, 273–282.
42. Holmes, R. T. 2011 Avian population and community processes in forest ecosystems: long-term research in the Hubbard Brook experimental forest. *For. Ecol. Manag.* **262**, 20–32.
43. Rodenhouse, N. L., Sillett, T. S., Doran, P. J. & Holmes, R. T. 2003 Multiple density-dependence mechanisms regulate a migratory bird population during the breeding season. *Proc. Biol. Sci.* **270**, 2105–2110.
44. Pyle, P. 1997 Identification guide to North American birds. Part I. Columbidae to Ploceidae. Braun-Brumfield. *Ann Arbor Mich. USA*
45. Donovan, T. M. & Stanley, C. M. 1995 A new method of determining ovenbird age on the basis of rectrix shape. *J. Field Ornithol.* **66**, 247–252.

46. Jakob, E. M., Marshall, S. D. & Uetz, G. W. 1996 Estimating fitness: a comparison of body condition indices. *Oikos* **77**, 61–67.
47. Sloan, S. S., Holmes, R. T. & Sherry, T. W. 1998 Depredation rates and predators at artificial bird nests in an unfragmented northern hardwoods forest. *J. Wildl. Manag.* **62**, 529–539.
48. Royle, J. A. 2004 N-Mixture models for estimating population size from spatially replicated counts. *Biometrics* **60**, 108–115.
49. Kéry, M. 2010 *Introduction to WinBUGS for ecologists: A Bayesian approach to regression, ANOVA and related analyses*. Academic Press. [cited 2014 Mar. 17].
50. Hijmans, R. J. & van Etten, J. 2010 raster: Geographic analysis and modeling with raster data. *R Package Version* **1**, r948.
51. R Core Team 2013 *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
52. Smith, T. M. & Shugart, H. H. 1987 Territory size variation in the ovenbird: the role of habitat structure. *Ecology* **68**, 695–704.
53. Haché, S., Villard, M.-A. & Bayne, E. M. 2012 Experimental evidence for an ideal free distribution in a breeding population of a territorial songbird. *Ecology* **94**, 861–869.
54. Brown, D. R. & Sherry, T. W. 2006 Food supply controls the body condition of a migrant bird wintering in the tropics. *Oecologia* **149**, 22–32.
55. Brown, D. R. & Sherry, T. W. 2008 Alternative strategies of space use and response to resource change in a wintering migrant songbird. *Behav Ecol* **19**, 1314–1325.
56. Johnson, M. D., Sherry, T. W. 2006 Assessing habitat quality for a migratory songbird wintering in natural and agricultural habitats. *Conserv. Biol.* **20**, 1433–1444.
57. Strong, A. M. & Sherry, T. W. 2000 Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. *J. Anim. Ecol.* **69**, 883–895.
58. Burke, D. M. & Nol, E. 1998 Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. *The Auk* **115**, 96–104.
59. Royle, J. A. & Dorazio, R. M. 2008 *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities*. Academic Press.

60. Shipley, B. 2009 Confirmatory path analysis in a generalized multilevel context. *Ecology* **90**, 363–368.
61. Clough, Y. 2012 A generalized approach to modeling and estimating indirect effects in ecology. *Ecology* **93**, 1809–1815.
62. Johnson, M. D. 2007 Measuring habitat quality: a review. *The Condor* **109**, 489–504.
63. Zuur, A. F., Ieno, E. N. & Smith, G. M. 2007 *Analysing ecological data*. Springer New York.
64. Plummer, M. 2003 *JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling*.
65. Su, Y.-S. & Yajima, Masanao 2012 R2jags: A package for running jags from R. *R Package Version 003-08*
66. Zipkin, E. F., Sillett, T. S., Grant, E. H. C., Chandler, R. B. & Royle, J. A. 2014 Inferences about population dynamics from count data using multistate models: a comparison to capture–recapture approaches. *Ecol. Evol.* **4**, 417–426.
67. Gelman, A., Meng, X.-L. & Stern, H. 1996 Posterior predictive assessment of model fitness via realized discrepancies. *Stat. Sin.* **6**, 733–760.
68. Podolsky, A. L., Simons, T. R., Collazo, J. A. & Lank, D. B. 2007 Modeling population growth of the ovenbird (*Seiurus aurocapilla*) in the southern Appalachians. *The Auk* **124**, 1359–1372.
69. Porneluzi, P. A. & Faaborg, J. 1999 Season-long fecundity, survival, and viability of ovenbirds in fragmented and unfragmented landscapes. *Conserv. Biol.* **13**, 1151–1161.
70. King, D. I., Degraaf, R. M., Smith, M.-L. & Buonaccorsi, J. P. 2006 Habitat selection and habitat-specific survival of fledgling ovenbirds (*Seiurus aurocapilla*). *J. Zool.* **269**, 414–421.
71. Roberts, P. K. 2009 Determinants of reproductive success in a Neotropical migratory songbird: timing, site-selection and mating strategies. Ph.D. dissertation, Dartmouth College, Hanover, New Hampshire.
72. Coulson, T., Benton, T. G., Lundberg, P., Dall, S. R. X., Kendall, B. E. & Gaillard, J.-M. 2006 Estimating individual contributions to population growth: evolutionary fitness in ecological time. *Proc. R. Soc. B Biol. Sci.* **273**, 547–555.

73. Kok, O. B., Van EE, C. A. & NEL, D. G. 1991 Daylength determines departure date of the spotted flycatcher *Muscicapa striata* from its winter quarters. *Ardea* **79**, 63–66.
74. Helm, B., Schwabl, I. & Gwinner, E. 2009 Circannual basis of geographically distinct bird schedules. *J. Exp. Biol.* **212**, 1259–1269.
75. Helm, B. & Gwinner, E. 2005 Carry-over effects of day length during spring migration. *J. Ornithol.* **146**, 348–354.
76. Conklin, J. R., Battley, P. F., Potter, M. A. & Fox, J. W. 2010 Breeding latitude drives individual schedules in a trans-hemispheric migrant bird. *Nat. Commun.* **1**, 67.
77. Studds, C. E. & Marra, P. P. 2005 Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. *Ecology* **86**, 2380–2385.
78. Studds, C. E. & Marra, P. P. 2011 Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. *Proc. R. Soc. B Biol. Sci.* **278**, 3437–3443.
79. Marra, P. P. & Holmes, R. T. 2001 Consequences of dominance-mediated habitat segregation in American Redstarts during the nonbreeding season. *The Auk* **118**, 92–104.
80. Bêty, J., Gauthier, G. & Giroux, J. 2003 Body condition, migration, and timing of reproduction in Snow Geese: a test of the condition-dependent model of optimal clutch size. *Am. Nat.* **162**, 110–121.
81. Stutchbury, B. J. 1994 Competition for winter territories in a Neotropical migrant: the role of age, sex and color. *The Auk* **111**, 63–69.
82. Marra, P. P. 2000 The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. *Behav. Ecol.* **11**, 299–308.
83. Rohwer, S., Viggiano, A. & Marzluff, J. M. 2011 Reciprocal tradeoffs between molt and breeding in albatrosses. *The Condor* **113**, 61–70.
84. Langston, N. E. & Rohwer, S. 1996 Molt-breeding tradeoffs in albatrosses: life history implications for big birds. *Oikos* **76**, 498–510.
85. Jahn, A. E. et al. 2013 Migration timing and wintering areas of three species of flycatchers (*Tyrannus*) breeding in the Great Plains of North America. *The Auk* **130**, 247–257.

86. Betini, G. S., Griswold, C. K. & Norris, D. R. 2013 Carry-over effects, sequential density dependence and the dynamics of populations in a seasonal environment. *Proc. R. Soc. B Biol. Sci.* **280**, 20130110.

CHAPTER 5: FITNESS RELATED CONSEQUENCES OF MACRO AND MICRO
NEST SITE SELECTION OF A NEOTROPICAL MIGRATORY BIRD

Michael T. Hallworth^{1,2,3}, T. Scott Sillett¹ and Peter P. Marra¹

¹ Migratory Bird Center, Smithsonian Conservation Biology Institute, National
Zoological Park, Washington, D.C. 20008

² George Mason University, College of Science, Fairfax, VA. 22030

³ mhallwor@masonlive.gmu.edu

Formatted for submission to the Condor

ABSTRACT

Identifying the habitat features that influence nest site selection and reproductive success is essential to elucidating the role that habitat selection plays in driving individual fitness. We examined which habitat features appeared to be driving nest site selection at two spatial scales and quantified reproductive consequences of that site selection. From 2010-2012, we monitored 189 Ovenbird (*Seiurus aurocapilla*) nests in a contiguous northern mixed-hardwood forest within Hubbard Brook Experimental Forest in central New Hampshire. We quantified the vegetation characteristics of nest sites along with four randomly selected control sites located within male territories at micro (1m radius) and macro (5m radius) scales. Habitat features that enhanced nest concealment were associated with nest sites at both spatial scales. We found no change in nest site selection for subsequent re-nest attempts following initial failure. Micro-topography of the forest floor was a primary determinant of nest site selection at the micro scale and increased daily nest survival. Habitat features at the macro scale had little influence on daily nest survival. Our results suggest that Ovenbird nest site selection, at least at the micro scale, may be adaptive and Ovenbirds select nest sites that improve reproductive success.

KEYWORDS

Ovenbird (*Seiurus aurocapilla*), Nest Survival, Adaptive selection, Nest predation, re-nest attempt

INTRODUCTION

Habitat selection by birds can range from broad spatial scales such as landscapes (Saab 1999, Rodewald and Yahner 2000, Rodewald et al. 2001, Driscoll et al. 2005) to fine spatial scales such as territories (Jones and Robertson 2001, Hallworth et al. 2008) and nest sites (Jones and Robertson 2001, Kolbe and Janzen 2002, Citta and Lindberg 2007, Goodnow and Reitsma 2011). Multiple strategies may exist for how individuals select habitat (Doligez et al. 2003). Experienced individuals may use previous knowledge of success to make habitat decisions (Switzer 1997). In contrast, young or inexperienced individuals that do not have previous knowledge may select habitat randomly (Dale and Slagsvold 1990) or make decisions on cues indirectly associated with reproductive success. For example, conspecific social cues (Doligez et al. 2002, Hahn and Silverman 2006) and information about conspecific reproductive success (Betts et al. 2008) have been shown to play a role in habitat selection. Environmental cues such as vegetation structure (Hallworth et al. 2008), predator abundance (Emmering and Schmidt 2011) or food availability (Burke and Nol 1998) are likely also used in habitat selection and may be assessed directly. The cues used in habitat selection may also differ depending on the spatial scale of selection (Saab 1999, Chalfoun and Martin 2007). Choices made at each spatial scale likely have fitness-related consequences (Chalfoun and Martin 2007), thus an individual's ability to assess the impacts of particular habitat features is paramount for habitat selection. Importantly, habitat cues used for selection may not be honest indicators of fitness and have either no fitness consequences (Davis 2005) or negative fitness consequences leading to maladaptive habitat selection (Donovan and Thompson

III 2001) such as is the case with ecological traps. Ecological traps arise when low quality habitats with reduced reproductive success and/or survival are preferred over available high quality habitats (Donovan and Thompson III 2001).

The importance of habitat structure to nest site selection may differ depending on spatial scales. For example, at fine spatial scales, features that increase concealment to avoid predation or create a suitable microclimate for efficient thermoregulation of eggs and young (With and Webb 1993) may be important, while features related to food availability or provide cover for newly fledged young may be important at broader spatial scales (King et al. 2006, Vitz and Rodewald 2011). Understanding what habitat variables influence nest site selection and the consequences of that selection, at various spatial scales, is important to better understand factors that influence reproductive performance.

Nest site selection is likely under strong selection and closely tied to fitness since annual fecundity is directly related to nest success. Nest success can be influenced by factors other than habitat structure such as clutch size (Slagsvold 1982, 1984) parental visitation rates (Martin et al. 2000, Fontaine and Martin 2006, Fontaine et al. 2007), conspecific density (Sillett et al. 2004, McKellar et al. 2013) and predator abundance (Morton 2005, Emmering and Schmidt 2011). Depredation on nests, in some systems is the major driver of nest failure (Lima 2009); thus nest sites are often selected that are located in areas that reduce predation risk (Morton 2005, Emmering and Schmidt 2011). . Therefore, nest sites that increase nest concealment, especially in ground nesting birds, should be favored. In addition, concealment of re-nest attempts after initial failure should increase within a single season (Latif et al. 2012). Here, we identify factors influencing

nest site selection at two spatial scales, 1) micro- (1m radius) and 2) macro-site (5m radius) and its consequences on reproductive success of a long distance migratory songbird, the Ovenbird (*Seiurus aurocapilla*) that nests on the forest floor.

The Ovenbird forages primarily on arthropods found in the leaf litter (Stenger 1958, Porneluzi et al. 2011) and is widely distributed throughout North America during the breeding season. Ovenbirds are well suited for the current study because they 1) construct a cryptic nest on the ground making them quite vulnerable to nest predators, primarily Eastern Chipmunks (*Tamias striatus*) and Red-squirrels (*Tamiasciurus hudsonicus*) (Reitsma et al. 1990, Sloan et al. 1998), 2) they exhibit short nestling period and, 3) they attempt to re-nest after initial nest failure, allowing fitness related consequences of nest site placement to be measured. We predicted that habitat cues associated with food availability would be selected for at the macro-site scale (5m radius) while habitat features related to concealment would be selected at the micro-site (1m radius). Because eggs and nestlings are not the primary food source for Eastern Chipmunks or Red-squirrels, they likely find Ovenbird nests opportunistically which has been found in other systems (Vickery et al. 1992). However, once found they may actively seek out nests (Pelech et al. 2010). Because of this we predicted that concealment measures directly around the nest would be higher than at randomly selected sites. Further, we predicted that nests would become more concealed after initial failure.

METHODS

Field work was conducted at the Hubbard Brook Experimental Forest (HBEF), N.H. (43.93° N, 71.93° W) during the 2010-2012 breeding seasons (1 May - 1 August). HBEF is a 3160 ha forest ranging in elevation from 222m to 1015m above sea level located within the larger White Mountain National Forest in central New Hampshire. The vegetation within HBEF is dominated by northern hardwood species such as sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*) at lower elevations transitioning to boreal forest consisting of red spruce (*Picea rubens*), balsam fir (*Abies balsamea*) and white birch (*Betula papyrifera*) at higher elevations (Holmes 2011).

Ovenbirds were monitored within three study plots located along an elevation gradient to maximize differences in Ovenbird demography (Rodenhouse et al. 2003). Male Ovenbirds were monitored every 2-3 days from arrival on the breeding grounds until 1 August during the 2010-2012 seasons to delineate male territories, to search for nests, and to determine reproductive success. While visiting male territories, location data were obtained opportunistically as males moved about their territories using a handheld global position system (GPS). Nests were found by observing parental behavior throughout the season, systematic territory searching or simply found randomly. Sites were visited by multiple observers to avoid bias in nest searching ability (Rodewald 2004). A subset of nests was found using radio telemetry. Radio transmitters (0.7g, Lotek Wireless Inc) were attached to 25 females (2010 n = 0; 2011 n =13; 2012 n = 12) captured using a butterfly net (Podolsky et al. 2007) while incubating their first nest attempt. Once nests were found they were monitored every two days until either nest

failure or they successfully fledged young. A nest was determined to be depredated if 1) no eggs were present after clutch completion, or 2) nestlings were absent prior to potential fledge date (day 8-9). Nests were considered abandoned if 1) construction of the nest was never completed or 2) eggs were present with no sign of predation but the nest failed to advance to nestlings. Upon nest failure, nest searching resumed within a male's territory to find subsequent re-nest attempts.

Micro-site-- Vegetation characteristics were quantified within 1m (micro-site) and 5m (macro-site: see below) radii around the nest site. In addition, four randomly selected 1m radius subplots located within the 5m radius plot centered on the nest were also sampled to determine micro-site nest site selection (Figure 1). Within each plot we estimated the percent cover of vegetation characteristics thought to be important for nest concealment, food resources or both. We standardized estimates between 10 observers (2010: n = 3, 2011: n = 4, 2012: n = 4) before collecting data. Specifically, we estimated the percent cover of the non-woody herbaceous layer (Herbs), stiff club moss (*Lycopodium annotinum*; *Lycopodium*), ferns, leaf litter (LL), bare ground (ground), mosses, grasses, water, rock, and coarse woody debris (CWD). We estimated the percentage coverage of the plot surface and up to 1m of low shrub stems and foliage (LowShrubs). We also counted the number of tall shrubs (>50cm tall) and trees (>8cm diameter breast height) located within the plots. Leaf litter depth (mm) was measured at 1m intervals along 5m transects in each cardinal direction originating from the nest. We used the mean of the leaf litter measurements as our measure of leaf litter depth. We also characterized micro-topography within each of the 1m radius plots by measuring the

vertical distance (cm) to the center of the subplot from the surrounding ground surface at 1m. Nests that were placed below the horizontal plane were given a negative value while nests placed above the horizontal plane were given a positive value. Slope was measured using a clinometer and was recorded as a positive number. Nest elevation was extracted from a digital elevation model of HBEF using Spatial Analyst for ArcMap 10.0 (Environmental Systems Research Institute, Redlands, CA.).

Macro-site—Four 5m radius plots were randomly generated within territories with a minimum distance of 10m between plot centroids to avoid overlap. Random points were constructed using the “create random points” tool in ArcMap 10.0. When territories were too small to accommodate four non-overlapping vegetation points, the maximum number of non-overlapping points were used (minimum of 3). The same vegetation characteristics that were enumerated within nest plots were also quantified within territory plots. The territory plots were used as control locations to compare to nest sites. All vegetation measurements were conducted between 10 July and 1 August during 2010-2012 after nests had either failed or fledged young.

Red-squirrels and Eastern Chipmunks account for 58% and 21 % of ground nesting predation at HBEF, respectively (Sloan et al. 1998) and Ovenbirds have been shown to respond to perceived predation pressure by Eastern Chipmunks (Emmering and Schmidt 2011). To assess how a non habitat structure feature, such as predation pressure influences macro-site selection we conducted five minute surveys at 15 locations within each study plot to determine the abundance of mammalian nest predators (see Rodenhouse et al. 2003). Each location was sampled four times during five two-week

sampling periods resulting in 20 predator surveys per year (May - July). During each survey the number of Eastern Chipmunks and Red-squirrels were quantified. Predator abundance was modeled with the N-mixture (Royle 2004, Kéry 2010) model using elevation and the squared term of elevation as covariates. To account for imperfect detection we used survey date as a covariate to account for changes in detection over the sampling period. Each predator species was modeled separately. Model predictions were mapped using the raster package (Hijmans and van Etten 2010) in R version 3.0 (R Development Core Team www.R-project.org). For more details see Hallworth et al. (in manuscript, Chapter 3). We overlaid nest locations and non-nest control sites on the modeled predator abundance maps and extracted the number of Eastern Chipmunks and Red-squirrels of each location.

Statistical Analyses—All nests were included in the nest site selection analysis including nests of unknown fate (i.e. nests found empty late in the season). Only nests with known fate were included in analyses that involved fitness parameters. We constructed models that fell into three categories based on our hypotheses. First, we constructed models with habitat variables involved with nest concealment to test whether concealment was important for micro and macro nest site selection. Second, models were constructed with variables that have been shown to be correlated with food availability (Burke and Nol 1998, Haché et al. 2012) along with variables important for Ovenbird foraging (M.T.H. personal observation). Lastly, we constructed models that characterized forest structure. We ran 17 *a priori* models for micro nest site selection: four univariate models, one null model, 11 additive models with ecologically meaningful variables and

one interaction model with slope and leaf litter depth. A fourth category was included for the macro nest site selection. We created models that included the number of Eastern Chipmunks, and Red-squirrels to test if nest sites were selected based on predator abundance. We did not test the predator hypothesis with the micro nest site selection because of the proximity of control locations and nest sites. We ran 15 *a priori* models for macro nest site selection: three univariate models, nine additive models and one interaction model with slope and leaf litter depth. We included variables in models with correlations < 0.7 (Newell and Rodewald 2011). Binary logistic regressions (nest site vs non nest site) with a logit link were analyzed in R. An information theoretic approach (Burnham and Anderson 2001) was used to compare models for both micro and macro nest site selection. Akaike's information criterion (AIC), corrected for small sample sizes (AICc; Burnham and Anderson 2001), was used to evaluate candidate models using the AICcmodavg package (Mazerolle 2011). Models with $\Delta AICc < 2.0$ receive substantial support balancing goodness-of-fit while minimizing the number of parameters (Burnham and Anderson 2001). We estimated the over dispersion parameter (\hat{c}) of the global model by dividing the model deviance by the degrees of freedom of the residuals (micro nest site $\hat{c} = 0.88$, macro nest site $\hat{c} = 0.86$).

To determine if habitat characteristics used to select nest sites impacted fitness, we ran the same models used for nest site selection to model daily nest survival. We included year and allowed daily nest survival (DNS) to vary through time in all models because DNS may depend on factors other than habitat or predators such as weather events. In addition, we included a model that included the proportion of nests that were

active at the time of clutch initiation (Density). If nest predators destroy Ovenbird nests encountered randomly, DNS should be lowest when the proportion of nests active is highest because there are more nests available to find. We used logistic exposure models to determine DNS using program MARK (White and Burnham 1999) accessed through the RMark package (Laake et al. 2011) in R.

RESULTS

The top model for both micro and macro nest site selection were models consistent with increased nest concealment. The top model for micro nest site selection included percent concealment ($\beta = -0.015 \pm 0.005$), micro-topography ($\beta = -0.41 \pm 0.097$), percent *Lycopodium* ($\beta = 0.032 \pm 0.006$), percent coarse woody debris (CWD $\beta = -0.036 \pm 0.011$) and percent herbaceous cover ($\beta = 0.016 \pm 0.007$). The model indicates that Ovenbirds selected micro sites that were in depressions on the forest floor, had higher percent *Lycopodium*, lower percent CWD and higher percentage of herbaceous plants than control sites. The top model for micro nest site selection was the only model with $\Delta AICc < 2.00$ and received substantial model weight (Table 1). Only one additional model received moderate support ($\Delta AICc < 2.90$) for micro nest site selection which included *Lycopodium*, micro-topography, ferns and herbs. Similarly, model selection indicated that macro nest site selection had a single top model that included percent *Lycopodium* ($\beta = 0.04 \pm 0.007$), percent ferns ($\beta = 0.004 \pm 0.008$) and percent herbaceous cover ($\beta = 0.03 \pm 0.007$; Table 2). The model for macro nest site selection indicates that Ovenbirds select nest sites with a higher percentage of *Lycopodium*, ferns and percent

herbaceous cover than control sites. No other models at the macro scale received moderate support $\Delta AICc < 7.0$. These results indicate that Ovenbirds select nest sites using features at both micro and macro scales that aid in nest concealment.

We found 189 Ovenbird nests in the period 2010-2012 (2010: $n = 44$; 2011: $n = 48$; 2012: $n = 97$) including 32 (17%) that were found using radio telemetry. Nests found using radio-telemetry had less bare ground (1.34%) than nests found without the aid of radio-telemetry (3.29%, $t = 3.05$, $df = 66$, $p = 0.0003$). However, the difference in bare ground is likely not biologically meaningful. There was no significant difference in any of the other habitat characteristics between the two groups of nests. The fate of 11 nests is unknown because they were found empty and were not used to determine DNS, but were included in nest site selection analyses. Sixty-eight percent ($n = 121$) of known fate nests contained at least one egg (2010: $n = 39$; 2011: $n = 34$; 2012: $n = 47$) and 70 nests (39%) successfully fledged at least one young (2010: $n = 22$; 2011: $n = 24$; 2012: $n = 24$).

Ovenbirds re-nest after initial nest failure and this allowed us to measure the change in nest site selection after initial failure. Predation (54%, 2010: $n = 19$; 2011: $n = 6$; 2012: $n = 33$) was the largest source of nest failure followed by abandonment (22%, 2010: $n = 2$; 2011: $n = 6$; 2012: $n = 16$) and undetermined causes (4%, 2010: $n = 2$; 2011: $n = 2$; 2012: $n = 0$). We observed as many as three nest attempts in a single season. The mean (mean \pm SE) clutch initiation date (Julian) of the first, second and third nest attempts were 148.88 ± 0.58 ($n = 72$), 168.59 ± 1.39 ($n = 41$), and 177.60 ± 2.89 ($n = 5$), respectively. We found no difference in vegetation characteristics of nest sites between initial and subsequent attempts except for percent herbaceous layer at the macro-site level

(Figure 2). Subsequent nests had lower percent herbaceous cover than initial nest attempts.

The most parsimonious model associated with DNS included micro-topography ($\beta = -0.198 \pm 0.16$), time of the season ($\beta = 0.012 \pm 0.01$) and year. These results are consistent with the nest-concealment hypothesis (Table 3). Nests placed in depressions had higher DNS rates than nests placed at or above the surrounding forest floor. However, 15 models had a $\Delta AIC < 2.00$ and all contained low model weights. Of the 15 models with $\Delta AIC < 2.00$, eight are consistent with the nest-concealment hypothesis including the top model, three are directly related to the abundance of nest predators (Eastern Chipmunks and/or Red-squirrels), and three are consistent with the food availability hypothesis. The remaining model contained the proportion of nests active at the time of clutch initiation. All but one of the models with $\Delta AIC < 2.00$ (Herbs_5m) excluding models of predator abundance were associated with micro nest site features and neither the top models for micro or macro nest site selection were among the models with $\Delta AIC < 2.00$.

DISCUSSION

Nest site selection is likely under strong selection since whether a nest succeeds or fails has important ramifications for annual fecundity and overall fitness. Ovenbirds are thought to be primarily single brooded (Podolsky et al. 2007, Porneluzi et al. 2011, Streby and Andersen 2011 but see Hallworth et al. in manuscript, Chapter 3), which increases the importance of initial nest site selection. Because of these factors we

hypothesized that features associated with nest concealment would influence nest site selection. We found that Ovenbirds selected nest sites with habitat features that enhanced nest concealment at both micro (1m) and macro (5m) spatial scales. However, DNS was mainly influenced by factors at the micro spatial scale.

The main nest predators within the HBEF are Eastern Chipmunks and Red-Squirrels (Reitsma et al. 1990, Sloan et al. 1998), which likely find Ovenbird nests opportunistically (Vickery et al. 1992) but may actively search for nests after a nest is found (Pelech et al. 2010). Therefore, habitat characteristics that increase concealment adjacent to nests may reduce predation risk. Indeed, nest concealment has been demonstrated to be important for various species (Flaspohler et al. 2000, Latif et al. 2011) including Ovenbirds at breeding sites in Minnesota (Mattsson et al. 2006). We predicted that Ovenbird nest site selection at the micro scale would increase nest concealment. Consistent with our predictions, micro nest site selection included habitat features that increased nest concealment. Ovenbirds selected micro nest sites that were located within depressions on the forest floor, contained a higher percentage of *Lycopodium* and herbaceous plants, and had a lower percentage of coarse woody debris than control sites. The increased percentage of *Lycopodium* and herbaceous plant cover at nest verses adjacent control sites improves nest concealment from Eastern Chipmunks and Red-squirrels, which both forage on the ground. Increased vegetative cover close to the ground likely provides visual obstruction from small ground-based predators. Although large amounts of coarse woody debris could provide concealment from predators,

mammalian predators such as Eastern Chipmunks may use coarse woody debris as travel pathways (Zollner and Crane 2003) potentially increasing the risk of predation.

The benefits of placing nests within depressions in the forest floor are three-fold. First, micro-topography may act to disguise nest provisioning by breaking the sight line of predators as adults attend nestlings. Secondly, nests placed in depressions may increase nest concealment without the use of vegetation. All of this reduces predation assuming predators use vegetation as cues to find nests (Fontaine and Martin 2006). Thirdly, micro-topography along the forest floor may provide climatic conditions which aid in thermoregulation (With and Webb 1993) during incubation and the nestling period, particularly during warm years.

We predicted that Ovenbird nest site selection at the macro scale would include habitat features that increased food availability. Contrary to our prediction, Ovenbirds selected macro nest sites with variables consistent with the concealment hypothesis and not food availability. Nest sites versus control sites had higher percent cover of ferns, *Lycopodium* and herbs. The food availability and concealment hypotheses may not be mutually exclusive at the macro-scale. For example, Ovenbirds were observed foraging on the underside of ferns and herbaceous plants as well as obtaining arthropods from *Lycopodium* (M.T.H. personal observation). In addition, a higher percentage of ferns and herbaceous plants could also increase food availability by creating microclimates that support increased arthropod populations within the leaf litter (Burke and Nol 1998). Leaf litter depth has been demonstrated to influence food availability and shown to be positively correlated with DNS (Mattsson et al. 2006) for Ovenbirds. However, leaf litter

depth was not associated with macro nest site selection in our study. Although reported as an indicator of food availability in other studies (Burke and Nol 1998), we found no relationship between arthropod dry weight and leaf litter depth (M.T.H. unpublished data). Therefore leaf litter depth within our study plots may not be a reliable indicator of food availability. Many of the studies that have found leaf litter depth to be an important factor influencing food availability and DNS have been conducted in fragmented landscapes. HBEF is a 3160 ha forest located with the larger White Mountain National Forest in central New Hampshire. Our findings are consistent with Mattsson et al. (2006) who found that leaf litter was not related to nest predation in landscapes with abundant core forest, such as HBEF.

Ovenbirds use cues such as predator communication to assess heterogeneous habitats and place nest sites accordingly (Emmering and Schmidt 2011). In contrast to the findings of Emmering and Schmidt (2011) we found no evidence that nest predators influenced nest site selection at the macro scale. However, our ability to detect heterogeneity in predator abundance within territories was likely low given that we modeled predator abundance using elevation (Hallworth et al. in manuscript) and the range in elevation within a territory was small (19.71 ± 0.85 m). The abundance of Eastern Chipmunks was among one of the top models influencing DNS. In addition, the combination of Eastern Chipmunks and Red-squirrels was among the top supported models. Indeed, the abundance of nest predators is an important variable influencing daily nest survival (Lima 2009), but the degree to which Ovenbirds select nest sites based on nest predator abundance at HBEF is unclear.

Ovenbirds will attempt to re-nest up to two additional times within a single breeding season if first nest attempts fail. We predicted that after initial nest failure, Ovenbirds would select subsequent nest sites that increase nest concealment. Contrary to our predictions, habitat characteristics at nest sites did not change after initial failure with the exception of a decrease in percent herbaceous layer at the macro scale. Similar results have been found with Hooded Warblers (*Setophaga citrina*) where nest concealment did not increase in subsequent nests after initial failure (Howlett and Stutchbury 1997). If Eastern Chipmunks and Red-squirrels find nests opportunistically, changes in nest site characteristics may not decrease predation rates (Clark and Shutler 1999). Additionally, DNS generally increased throughout the year. Because of this, concealment may be paramount for the first nest attempt when DNS tends to be lowest and nests are most vulnerable. Thus increasing concealment of nest sites in subsequent attempts may not be advantageous.

As long distance migrants, Ovenbirds have a short breeding season and as a consequence synchrony of initial nest attempts is usually high but become increasingly asynchronous as the season progresses due to nest failure. Such synchrony of the first nest attempts could result in a resource pulse (Yang et al. 2008) for predators. Indeed, DNS was lowest when the number of active nests was highest and the number of active nests at time of clutch initiation was among the models with $\Delta AIC < 2.00$ that explained DNS. Eastern Chipmunks and Red-squirrels may capitalize on Ovenbird nests while the abundance of nests is highest early in the season and potentially switch to other food

resources as the season progresses reducing the need for nest sites to increase concealment during subsequent attempts.

For nest site selection to be adaptive, fitness related consequences must result from selection. Clark and Shutler (1999) illustrated how the process of natural selection could result in adaptive nest site selection. First, habitat differences must exist between nest and control sites, which we found at both micro and macro spatial scales. Second, identifying the factors that determine successful versus unsuccessful nests is required (Clark and Shutler 1999) because these differences may be driving adaptive selection. We found that neither of the top models for micro- nor macro nest site selection was retained for DNS, instead micro-topography was the most parsimonious model influencing DNS. However, variables contained within the top models for nest site selection were among the variables with the largest model weights (micro-topography = 0.173, *Lycopodium* = 0.169, herbs = 0.149) suggesting that attributes used in nest site-selection increased daily nest survival. Our findings are consistent with Richmond et al. (2011) who found Ovenbird nest survival was positively associated with forb and seedling cover. Lastly, Clark and Shutler (1999) suggest that an increase in nest density should occur in habitats with high previous nest success. This last process may not apply here as it did to their study on ground nesting ducks because Ovenbirds are territorial and thus density of nest sites may not increase. Instead, site fidelity to territories with high reproductive success may occur. However, females within our study area exhibited low site fidelity. In fact, only three females (5%) over the course of our study paired with the

same male in subsequent years. Because of these factors we were unable to determine how previous nest success influenced nest site selection in subsequent years.

Here, we found Ovenbirds select nest sites that enhance concealment at micro and macro scales. In addition, we found that nest site selection has fitness related consequences at the micro scale suggesting that nest site selection may be adaptive. We focused on nest placement and how habitat features influenced nest site selection and daily nest survival. Future research should examine how daily nest survival in this system is influenced by clutch size, parental care, and conspecific density or a combination of these factors. Further research is needed to determine how predator abundance may shape nest site selection. In addition, understanding the role that seasonal interactions mediated via arrival time to the breeding grounds plays in nest site selection is needed to fully understand the factors influencing nest site selection.

ACKNOWLEDGEMENTS

We thank A. Bloomfield, L. Bryant, A. Costa, V. Dwiggins, M. Grant, B. Lang, K. Long, D. Narango and J. Welklin and the 2010-2012 Black-throated blue warbler field technicians at Hubbard Brook Experimental Forest for their assistance in the field. We thank R. Greenberg and M. Webster for providing telemetry equipment. Funding was provided by Smithsonian Institution's Bond Endowment (MTH and PPM), American Ornithologists' Union (MTH) and the National Science Foundation's Long-term Research in Environmental Biology Program (PPM and TSS).

Table 1. Akaike's information criterion (AIC) corrected for small sample sizes (AIC_c) was used to evaluate models describing micro nest site selection of Ovenbirds. The model with the lowest ΔAIC_c value indicates the model that best balances goodness of fit while minimizing the number of parameters (k). Nest sites were placed in depressions on the forest floor, had a higher percent *Lycopodium* and herbaceous cover and lower percent cover of coarse woody debris (CWD) than control sites. W_i are the ranked model weights. See text for a description of the variables included in models.

Table 10

Model	k	AIC_c	ΔAIC_c	W_i
MicroTopo+ <i>Lycopodium</i> +CWD+Herbs	5	865.85	0.00	0.79
<i>Lycopodium</i> +MicroTopo+Fern+Herbs	5	868.75	2.90	0.19
CWD+Fern+ <i>Lycopodium</i> +LowShrubs+Herbs+Rock	6	873.06	7.21	0.02
<i>Lycopodium</i> +MicroTopo	3	882.98	17.13	0
Fern+ <i>Lycopodium</i> +Herbs	4	885.57	19.72	0
<i>Lycopodium</i> +LowShrubs+LLdepth+Fern	5	892.78	24.55	0
LowShrubs+CWD+MicroTopo	4	898.76	32.91	0
<i>Lycopodium</i>	2	900.00	34.14	0
Herbs+MicroTopo	3	911.63	45.77	0
MicroTopo	2	915.19	49.34	0
LeafLitter+Lowshrubs+Ferns	4	915.20	49.35	0
Trees+TallShrubs+Slope	4	915.32	49.47	0
LeafLitter	2	921.74	55.89	0
LeafLitter+LLdepth	3	923.30	56.27	0
LLdepth	1	929.17	61.19	0
Null	2	930.94	63.31	0
LLdepth*Slope	4	934.39	64.15	0

Table 2. Akaikie's information criterion (AIC) was used to evaluate models describing micro nest site selection of Ovenbirds macro nest site selection. Nest sites had more percent *Lycopodium*, ferns and herbaceous cover than control sites located within the males territory.

Table 11

<i>Model</i>	k	AICc	Δ AICc	Wi
<i>Lycopodium</i> +Fern+Herbs	4	876.66	0.00	0.99
Mean.LL+ <i>Lycopodium</i> +Fern	4	887.59	10.93	0
LowShrubs+Mean.LL+ <i>Lycopodium</i>	4	889.58	12.92	0
Mean.LL+LL	3	893.48	16.82	0
CWD+LowShrubs+Mean.LL+Rock+Herbs	6	898.73	22.07	0
Herbs	2	903.48	26.82	0
LowShrubs+Moss+Herbs	4	903.92	27.25	0
LowShrubs+Mean.LL+Herbs+Fern	5	905.86	29.19	0
Chipmunks	2	918.96	42.30	0
Chipmunks+Squirrel	3	920.56	43.89	0
Squirrel	2	921.88	45.21	0
Null	1	924.37	47.71	0
Trees+CWD+LowShrubs+TallShrubs+Slope+Mean.LL	7	926.46	49.80	0
Slope+Mean.LL+(Slope*Mean.LL)	4	928.14	51.48	0

Table 3. Akaikie's information criterion (AIC) was used to evaluate models describing daily nest survival of Ovenbirds breeding at Hubbard Brook Experimental Forest, NH. We included the same models used for nest site selection with the added effect of time and year. In addition, we included the proportion of nests that were active at time of clutch completion (Density). The most parsimonious model included micro-topography, a characteristic also including in micro nest site selection. Daily nest survival was higher for nests placed in depressions than nests placed at or above the surrounding forest floor.

Table 12

Model	k	AICc	$\Delta AICc$	Wi
MicroTopography+Time+Year	5	433.90	0.00	0.088
Chipmunks+Time+Year	5	433.93	0.02	0.087
Herbs (5m) +Time+Year	5	434.71	0.81	0.059
Chipmunks+Squirrel+Time+Year	6	434.75	0.85	0.058
Fern+ <i>Lycopodium</i> +MicroTopography+Herbs+Time+Year	8	435.03	1.12	0.050
Density+Time+Year	5	435.03	1.13	0.050
MicroTopography+Herbs+Time+Year	6	435.04	1.14	0.050
Squirrel+Time+Year	5	435.18	1.28	0.047
LL+Time+Year	5	435.19	1.28	0.047
<i>Lycopodium</i> +Time+Year	5	435.32	1.41	0.044
LL Depth+Time+Year	5	435.42	1.51	0.042
Fern+ <i>Lycopodium</i> +Herbs+Time+Year	7	435.49	1.59	0.040
Fern+LL+LowShrubs+Time+Year	7	435.66	1.75	0.037
MicroTopography+ <i>Lycopodium</i> +Time+Year	6	435.73	1.83	0.035
Slope+Trees+TallShrubs+Time+Year	7	436.14	2.24	0.029
Time	2	436.27	2.36	0.027
Constant - Null	1	436.29	2.39	0.027

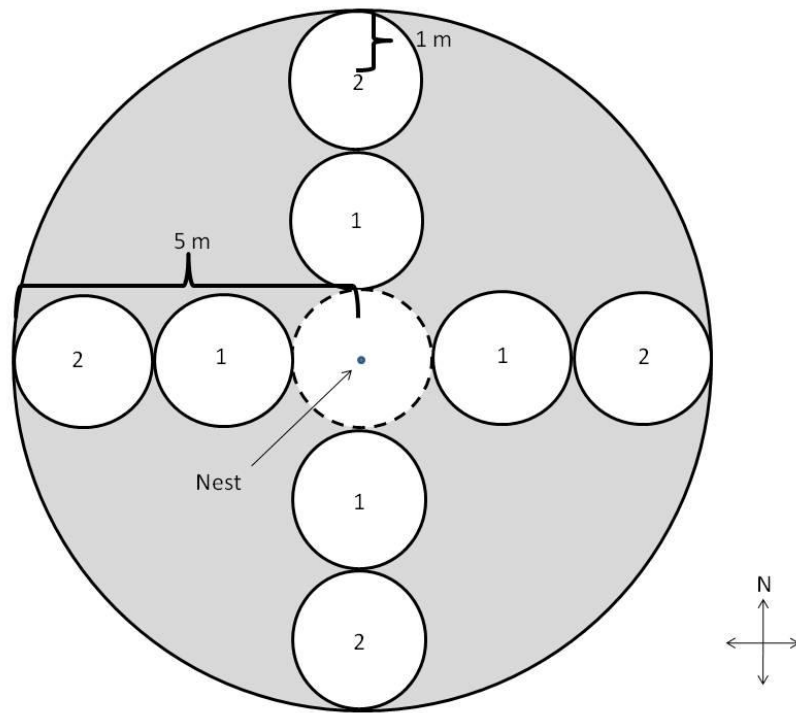


Figure 15

Figure 1. Schematic representation for sampling nest vegetation around nest sites to determine macro- (5m) and micro- (1m) nest site selection of Ovenbirds breeding at Hubbard Brook Experimental Forest, NH (see methods).

LITERATURE CITED

- Betts, M. G., A. S. Hadley, N. Rodenhouse, and J. J. Nocera. 2008. Social information trumps vegetation structure in breeding-site selection by a migrant songbird. *Proceedings of the Royal Society B: Biological Sciences* 275:2257–2263.
- Burke, D. M., and E. Nol. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. *The Auk*:96–104.
- Burnham, K. P., and D. R. Anderson. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* 28:111–120.
- Chalfoun, A. D., and T. E. Martin. 2007. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. *Journal of Applied Ecology* 44:983–992.
- Citta, J. J., and M. S. Lindberg. 2007. Nest-site selection of passerines: effects of geographic scale and public and personal information. *Ecology* 88:2034–2046.
- Clark, R. G., and D. Shutler. 1999. Avian habitat selection: pattern from process in nest-site use by ducks? *Ecology* 80:272–287.
- Dale, S., and T. Slagsvold. 1990. Random settlement of female pied flycatchers, *Ficedula hypoleuca*: significance of male territory size. *Animal Behaviour* 39:231–243.
- Davis, S. K. 2005. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. *The Condor* 107:605–616.
- Doligez, B., C. Cadet, E. Danchin, and T. Boulinier. 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Animal Behaviour* 66:973–988.
- Doligez, B., E. Danchin, and J. Clobert. 2002. Public information and breeding habitat selection in a wild bird population. *Science* 297:1168–1170.
- Donovan, T. M., and F. R. Thompson III. 2001. Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. *Ecological Applications* 11:871–882.
- Driscoll, M. J., T. Donovan, R. Mickey, A. Howard, and K. K. Fleming. 2005. Determinants of wood thrush nest success: a multi-scale, model selection approach. *Journal of Wildlife Management* 69:699–709.

- Emmering, Q. C., and K. A. Schmidt. 2011. Nesting songbirds assess spatial heterogeneity of predatory chipmunks by eavesdropping on their vocalizations. *Journal of Animal Ecology* 80:1305–1312.
- Flaspohler, D. J., S. A. Temple, and R. N. Rosenfield. 2000. Relationship between nest success and concealment in two ground-nesting passerines. *Journal of Field Ornithology* 71:736–747.
- Fontaine, J. J., M. Martel, H. M. Markland, A. M. Niklison, K. L. Decker, and T. E. Martin. 2007. Testing ecological and behavioral correlates of nest predation. *Oikos* 116:1887–1894.
- Fontaine, J. J., and T. E. Martin. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecology Letters* 9:428–434.
- Goodnow, M. L., and L. R. Reitsma. 2011. Nest-site selection in the Canada Warbler (*Wilsonia canadensis*) in central New Hampshire. *Canadian Journal of Zoology* 89:1172–1177.
- Haché, S., M.-A. Villard, and E. M. Bayne. 2012. Experimental evidence for an ideal free distribution in a breeding population of a territorial songbird. *Ecology* 94:861–869.
- Hahn, B. A., and E. D. Silverman. 2006. Social cues facilitate habitat selection: American redstarts establish breeding territories in response to song. *Biology Letters* 2:337–340.
- Hallworth, M., A. Ueland, E. Anderson, J. D. Lambert, and L. Reitsma. 2008. Habitat selection and site fidelity of Canada Warblers (*Wilsonia canadensis*) in central New Hampshire. *The Auk* 125:880–888.
- Hijmans, R. J., and J. van Etten. 2010. raster: Geographic analysis and modeling with raster data. R package version 1:r948.
- Holmes, R. T. 2011. Avian population and community processes in forest ecosystems: Long-term research in the Hubbard Brook Experimental Forest. *Forest Ecology and Management* 262:20–32.
- Howlett, J. S., and B. J. M. Stutchbury. 1997. Within-season dispersal, nest-site modification, and predation in renesting hooded warblers. *The Wilson Bulletin* 109:643–649.
- Jones, J., and R. J. Robertson. 2001. Territory and nest-site selection of Cerulean Warblers in eastern Ontario. *The Auk* 118:727–735.

- Kéry, M. 2010. Introduction to WinBUGS for ecologists: A Bayesian approach to regression, ANOVA and related analyses. Academic Press.
- King, D. I., R. M. Degraaf, M.-L. Smith, and J. P. Buonaccorsi. 2006. Habitat selection and habitat-specific survival of fledgling ovenbirds (*Seiurus aurocapilla*). *Journal of Zoology* 269:414–421.
- Kolbe, J. J., and F. J. Janzen. 2002. Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats. *Ecology* 83:269–281.
- Laake, J., E. Rakimberdiev, B. Collier, J. Rotella, and A. Paul. 2011. RMark: R Code for MARK Analysis. R package version 2.1. 0.
- Latif, Q. S., S. K. Heath, and J. T. Rotenberry. 2011. An “ecological trap” for yellow warbler nest microhabitat selection. *Oikos* 120:1139–1150.
- Latif, Q. S., S. K. Heath, and J. T. Rotenberry. 2012. How avian nest site selection responds to predation risk: testing an “adaptive peak hypothesis”. *Journal of Animal Ecology* 81:127–138.
- Lima, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biological Reviews* 84:485–513.
- Martin, T. E., J. Scott, and C. Menge. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 267:2287–2293.
- Mattsson, B. J., G. J. Niemi, and E. K. Bollinger. 2006. Factors influencing predation on ovenbird (*Seiurus aurocapilla*) nests in northern hardwoods: Interactions across spatial scales. *The Auk* 123:82–96.
- Mazerolle, M. J. 2011. AICcmodavg: model selection and multimodel inference based on (Q) AIC (c). R package version 1:16.
- McKellar, A. E., P. P. Marra, P. T. Boag, and L. M. Ratcliffe. 2013. Form, function and consequences of density dependence in a long-distance migratory bird. *Oikos* 123:356–364.
- Morton, E. S. 2005. Predation and variation in breeding habitat use in the Ovenbird, with special reference to breeding habitat selection in northwestern Pennsylvania. *The Wilson Bulletin* 117:327–335.
- Newell, F. L., and A. D. Rodewald. 2011. Role of topography, canopy structure, and floristics in nest-site selection and nesting success of canopy songbirds. *Forest Ecology and Management* 262:739–749.

- Pelech, S. A., J. N. M. Smith, and S. Boutin. 2010. A predator's perspective of nest predation: predation by red squirrels is learned, not incidental. *Oikos* 119:841–851.
- Podolsky, A. L., T. R. Simons, J. A. Collazo, and D. B. Lank. 2007. Modeling population growth of the ovenbird (*Seiurus aurocapilla*) in the southern Appalachians. *The Auk* 124:1359–1372.
- Porneluzi, P., M. A. Van Horn, and T. M. Donovan. 2011. Ovenbird (*Seiurus aurocapilla*). *The Birds of North America Online*.
- Reitsma, L. R., R. T. Holmes, and T. W. Sherry. 1990. Effects of removal of red squirrels, *Tamiasciurus hudsonicus*, and eastern chipmunks, *Tamias striatus*, on nest predation in a northern hardwood forest: an artificial nest experiment. *Oikos* 57:375–380.
- Richmond, S., E. Nol, and D. Burke. 2011. Avian nest success, mammalian nest predator abundance, and invertebrate prey availability in a fragmented landscape. *Canadian Journal of Zoology* 89:517–528.
- Rodenhouse, N. L., T. S. Sillett, P. J. Doran, and R. T. Holmes. 2003. Multiple density-dependence mechanisms regulate a migratory bird population during the breeding season. *Proceedings: Biological Sciences* 270:2105–2110.
- Rodewald, A. D. 2004. Nest-searching cues and studies of nest-site selection and nesting success. *Journal of Field Ornithology* 75:31–39.
- Rodewald, A. D., and R. H. Yahner. 2000. Influence of landscape and habitat characteristics on ovenbird pairing success. *The Wilson Bulletin* 112:238–242.
- Rodewald, A. D., R. H. Yahner, and J. Brawn. 2001. Avian nesting success in forested landscapes: influence of landscape composition, stand and nest-patch microhabitat, and biotic interactions. *The Auk* 118:1018–1028.
- Royle, J. A. 2004. N-Mixture models for estimating population size from spatially replicated counts. *Biometrics* 60:108–115.
- Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. *Ecological Applications* 9:135–151.
- Sillett, T. S., N. L. Rodenhouse, and R. T. Holmes. 2004. Experimentally reducing neighbor density affects reproduction and behavior of a migratory songbird. *Ecology* 85:2467–2477.

- Slagsvold, T. 1982. Clutch size, nest size, and hatching asynchrony in birds: experiments with the Fieldfare (*Turdus Pilaris*). *Ecology* 63:1389–1399.
- Slagsvold, T. 1984. Clutch size variation of birds in relation to nest predation: on the cost of reproduction. *Journal of Animal Ecology* 53:945–953.
- Sloan, S. S., R. T. Holmes, and T. W. Sherry. 1998. Depredation rates and predators at artificial bird nests in an unfragmented northern hardwoods forest. *The Journal of Wildlife Management* 62:529–539.
- Stenger, J. 1958. Food habits and available food of ovenbirds in relation to territory size. *The Auk* 75:335–346.
- Streby, H. M., and D. E. Andersen. 2011. Seasonal productivity in a population of migratory songbirds: why nest data are not enough. *Ecosphere* 2:78..
- Switzer, P. V. 1997. Past reproductive success affects future habitat selection. *Behavioral Ecology and Sociobiology* 40:307–312.
- Vickery, P. D., M. L. Hunter Jr., and J. V. Wells. 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. *Oikos* 63:281–288.
- Vitz, A. C., and A. D. Rodewald. 2011. Influence of condition and habitat use on survival of post-fledging songbirds. *The Condor* 113:400–411.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird study* 46:S120–S139.
- With, K. A., and D. R. Webb. 1993. Microclimate of ground nests: the relative importance of radiative cover and wind breaks for three grassland species. *The Condor* 95:401–413.
- Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What can we learn from resource pulses. *Ecology* 89:621–634.
- Zollner, P. A., and K. J. Crane. 2003. Influence of canopy closure and shrub coverage on travel along coarse woody debris by Eastern chipmunks (*Tamias striatus*) *American Midland Naturalist* 150:151–157.

CURRICULUM VITAE

Michael T. Hallworth graduated from Timberlane Regional High School, Plaistow, New Hampshire, in 2000. He received a Bachelor of Science and Master of Science from Plymouth State University in 2004 and 2007, respectively. He received his Doctor of Philosophy in Environmental Science and Public Policy from George Mason University in 2014.