POPULATION DYNAMICS OF SPECIES RECOVERY: MULTISCALE DEMOGRAPHY IN RESTORED HABITATS

A Dissertation

Presented to the Faculty of the Graduate School

of Cornell University

In Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

by

Darin James McNeil, Jr.

August 2019

ABSTRACT

Darin James McNeil, Jr., Ph.D.

Cornell University 2019

With habitat loss remaining one of the greatest global threats to biodiversity, habitat restoration has become an important tool for species recovery and conservation. Yet despite the conceptually-appealing lens of "if you build it, they will come" (*i.e.*, the 'Field of Dreams' Hypothesis), restoration outcomes are highly variable and generally lack rigorous monitoring and evaluation. Species responses to habitat restoration can vary with a wide range of factors, including life history of the focal species, multi-scale habitat attributes and local or regional demography, which highlights the need to assess species response to habitat restoration through multiple ecological frameworks.

This dissertation assessed behavioral, ecological, and demographic factors affecting restoration outcomes for a Nearctic-Neotropical migratory songbird, the Golden-winged Warbler (*Vermivora chrysoptera*). Over the past half-century, Golden-winged Warbler populations have declined, in part, due to the loss of early-successional breeding habitat. One strategy to address declines has been to restore breeding habitat according to established and evidence-based "best management practices". Restoration through initiatives like the Natural Resource Conservation Service's 'Working Lands For Wildlife' and 'Regional Conservation Partnership

Program' have already created > 6,000 hectares of breeding habitat since 2012, with more hectares anticipated over the coming decade. However, the response of Golden-winged Warblers to restoration remains poorly understood. In this study, we evaluated the degree to which variation in restoration outcomes were explained by habitat and landscape features, local population trends, breeding productivity, and behavioral and ecological needs at contrasting life stages (*e.g.*, nesting, post-fledging).

From 2015-2018, we surveyed male Golden-winged Warblers and measured vegetation attributes in 672 restored habitats in the Great Lakes (n = 215) and Appalachian Mountains (n = 457) regions of the breeding range. In addition to estimating occupancy, we quantified full-season reproductive productivity and survival based on the survival of 341 nests and 258 fledglings in two regions in Pennsylvania along with previously published data. Occupancy data were analyzed in program R (package *unmarked*) using static and dynamic occupancy models including multi-scale habitat features as model covariates, whereas nest/fledgling survival data were analyzed in program MARK to assess how components of breeding productivity varied with habitat features within focal landscapes.

Our results suggest that, although Golden-winged Warblers commonly used restored habitats, occupancy probability was related to micro-habitat attributes and landscape context. Warblers were most likely to occupy structurally complex sites that were eight years post-treatment and located in landscapes with no mixed coniferous-deciduous forest within 1 km. However, even after controlling for micro-habitat and landscape attributes, occupancy rates varied widely, demonstrating that even "if you build it…" they *may not* come. Local breeding output (# juveniles /pair

/year), was positively associated with occupancy rates, but only between focal landscapes in the Appalachian Mountains where the species was rare and declining; occupancy in Great Lakes focal landscapes were uniformly high despite intermediate levels of breeding output.

In addition to regional and landscape-level variability, we found evidence that restoration outcomes differed among life stages – a pattern consistent with a growing body of literature indicating that the needs of many forest bird species differ between nesting and post-fledging periods. For Golden-winged Warblers, nest success (the probability of fledging at least one young) did not vary with micro-habitat conditions in restored habitats, but survival rates varied across life stages in ways that scaled up to yield landscape-specific differences in productivity. For example, the threefold difference in breeding output between two Appalachian landscapes (*i.e.*, Pocono Mountains and Pennsylvania Wilds) were driven by differential nestling/fledgling (< 10 days post-fledging) survival but not egg or older fledgling (> 11 days post-fledging) survival.

The greater vulnerability of nestlings and young fledglings may stem partly from developmental processes related to shifting energetic requirements and foraging development. Fledgling energetic needs are likely intense given that they replace almost all body plumage during the post-fledging period via a rapid pre-formative molt, most pronounced from 13-17 days post-fledging. Difficulty in meeting nutritional demands might also be reflected by the fact that Golden-winged Warblers began foraging almost immediately after fledging and rapidly specialized on probe-and-gape foraging (> 7 days post-fledging). Although adult Golden-winged Warblers provided extensive parental care over the post-fledging period, parental feeding may not offset the physiological and behavioral challenges faced by young fledglings during this dangerous life stage.

Overall, this research provides grounds to reject the Field of Dreams Hypothesis and thereby highlights the importance of considering multi-scale habitat and demographic factors that drive restoration outcomes. Our results also emphasize the need to anticipate how stage-specific survival and life history constraints, like those we documented during the post-fledging period, may shape population-level responses to habitat restoration. This is especially important given that species conservation plans may disregard understudied life stages, including the post-fledging period. Ultimately, our analyses provide one of the most comprehensive assessments of breeding habitat restoration for an imperiled migratory songbird, while also offering new insights into the breeding biology of Golden-winged Warblers and other passerines.

BIOGRAPHICAL SKETCH

Darin J. McNeil arrived at Cornell University after completing a B.Sc. degree in Fisheries and Wildlife from Michigan State University and an M.S. degree in Biology from Indiana University of Pennsylvania. Throughout his academic career, Darin participated in or directed a variety of field-based ecological and conservation studies across the eastern United States, mostly focused on birds (*e.g.*, House Wrens, American Robins, Gray Catbirds, and Golden-winged Warblers), amphibians (*e.g.*, gray treefrogs, American toads, and red-backed salamanders), and other native wildlife (*e.g.*, bumble bees). These experiences cultivated a passion for ornithological research that ultimately led Darin to pursue a graduate work focused on birds.

Initially, Darin's passion for birds and background with Golden-winged Warblers brought him to the Lab of Jeff Larkin at Indiana University of Pennsylvania (IUP). At IUP, Darin studied early-successional forests and natural shrub wetlands in northeastern Pennsylvania to understand how conservation efforts might yield high-quality habitat for Golden-winged Warblers, a species in need of habitat conservation. He also honed his leadership skills by leading crews of field technicians while also expanding his writing abilities and developing a publication record. In addition to his thesis research, Darin also published several side-projects on topics including rare snake habitat conservation and fisher reintroduction ecology. As his time at IUP drew to a finish, Darin was accepted into the Lab of Amanda Rodewald at Cornell University to develop a project on Golden-winged Warbler conservation.

While at Cornell, Darin developed a much deeper understanding of the scientific process while working across new taxa (*e.g.*, insects), new topics (*e.g.*, behavioral ecology), and with a new network of professionals. During his time as a doctoral student, he worked with both federal and state agencies, such as Natural Resource Conservation Service and Pennsylvania Game Commission, to develop research questions that simultaneously investigated new or understudied ecological principles or natural history, while also providing conservation guidance for land managers and practitioners. Darin's broad interests that span basic and applied dimensions of ecology are reflected in both his doctoral research as well as the wide variety of side-projects he developed, including those on polygamous behavior in wood-warblers, detection probability in bumble bees, and even aberrant coloration in salamanders.

Though his interests are grounded in science, Darin also is deeply committed to teaching, mentoring, and outreach. For example, he regularly engages with diverse stakeholders, representing communities of practitioners, landowners, nature enthusiasts, and the public. On campus, Darin was an engaged teacher and was awarded the Spencer Prize for designing and instructing a freshman writing seminar. Moreover, as part of his field research, Darin mentored a total of 45 field technicians, many of whom were undergraduate students, working across five states: Minnesota, Wisconsin, Maryland, Pennsylvania, and New Jersey. After graduating from Cornell, Darin will work as a post-doctoral fellow at the Pennsylvania State University, where he will study demography and conservation of honey bees. Over the long term, Darin plans to study animal ecology and conservation across a variety of taxa.

ACKNOWLEDGEMENTS

The work presented here was made possible by the dedication and passion of a diverse group of researchers, field technicians, volunteers, conservation practitioners, land managers, birders, and forest landowners across the eastern United States. I am unable to name them all here due to space limitations so please recognize that the following is not a comprehensive list of everyone deserving of thanks. For their instrumental support in all aspects of this work, I am grateful to my doctoral committee and the Cornell Lab of Ornithology Conservation Science Program. André Dhondt mentored me from day one at Cornell, broadening my horizons across a diverse suite of scientific topics. André's office door was always open (quite literally) wherein I consistently found excellent guidance and conversation. I am very thankful for Rich Stedman's input on this project – Rich challenged me to think about critical topics outside my comfort zone and this made me a better ecologist. I am deeply indebted to the efforts of Viviana Ruiz-Gutierrez for her dedication to science and her excellent mentoring skills. Without Viviana's patience for explaining detailed analytical questions – often repeatedly – I would have never been successful in this endeavor. Another mentor of deep patience was Ken Rosenberg. Ken, thank you for always entertaining my pestering questions/thoughts/musings, even when you were already swamped with other work. I am also grateful for the insights of Pat Sullivan, Sara Barker, and Ron Rohrbaugh who offered guidance, ideas, and many excellent conversations about science and wildlife conservation.

While most graduate students have a single adviser, I was very lucky to have two. Jeff Larkin advised me from 2013-19, beginning when I started in his lab as a Master's Student at Indiana University of Pennsylvania. Jeff's passion for wildlife conservation, which is truly contagious, spans broadly across taxonomic bounds and fostered my own love for the natural world and development as an ecologist. Jeff, thank you so much for providing me with both a sound scientific education and the sense of a 'second family' in Pennsylvania. Amanda Rodewald has advised me since I began in her lab as a PhD student in 2015. Amanda provided a truly flawless balance between the guidance necessary for success and the freedom to pursue a varied suite of research questions. I believe this advising style fosters strong intellectual growth which allowed me to write this dissertation covering a diversity of scientific topics. This is further made possible by Amanda's background and interest spanning a wide array of topics. Perhaps most of all, I am so grateful for the personal growth Amanda has cultivated in me. Amanda, thank you so much for helping me grow as a scientist and as a person – I couldn't have done this without you.

I am thankful for assistance from many people who were instrumental in facilitating logistics, field work, and contacts over the course of this research: T. Ladner, T. Dugan, D. Heggenstaller, W. Ford, P. Dieser, K. Shepperd, R. Veasley, E. Bellush, C. Bertsch, and S. Petzinger. Special thanks to several folks I harassed particularly often: C. Sayer, O. Robinson, M. Strimas-Mackey, and K. Aldinger. Finally, I am deeply indebted to my field crew(s) who often worked in tick, mosquito, bear, and rattlesnake-filled forests, listed alphabetically: M. Andersen, T. Barbee, K. Barton, L. Benjou, A. Berten, G. Cammarata, C. Campbell-Schall, N. Christensen, H. Conley, R. Conner, M. Cowell, P. Dougherty, H. A. Faulkner, H. M. Faulkner, C.

Fiss, M. Florkowski, J. Geisel, K. Glanville, L. Gray, V. Gray, M. Hack, D. Hiles, E. Johnston, K. Johnson, M. Kunerth, J. T. Larkin, C. Loucks, J. Mibroda, D. Morris, E. Moser, T. Nielsen, H. Parker, B. Ramer, K. Rogers, F. Rodriguez, J. Saborse, C. Sayers, E. Sertyl, C. Snell, S. Toner, R. Veasley, P. Walker, T. Warren, W. Westerkamp, and R. Wlodek.

I am so grateful for the support of my closest friends: John Rusan, Cody Porter, Cam Fiss, and Kyle Aldinger. I have also been so lucky to have the support of my family: Peggy McNeil, George McNeil, Carissa McNeil, Rebekah Jones, and Alex Jones. I also remain grateful to my earliest mentors: Mike Boyce, Clint Otto, and Gary Roloff – you taught me so much. I am so lucky to have such a fantastic group of friends in Cornell, Conservation Science: Ruth Bennett, Rose Swift, Bryant Dossman, Gerardo Soto, Steven Sevillano, and Anna Lello-Smith: you guys have been fantastic and I wish you all the best in the coming years. My partner, Mona Kazour, has always been there for me. Thank you for being my stable point through two graduate degrees.

This project was funded by the U.S. Department of Agriculture (USDA) - Natural Resource Conservation Service (NRCS) Conservation Effects Assessment Project (CEAP), the Pennsylvania Game Commission, the Cornell Laboratory of Ornithology and its Athena Fund, and the American Bird Conservancy. Additional thanks to support from the Golden-winged Warbler Working Group, New Jersey Department of Fish and Game, and the Maryland Department of Natural Resources.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

INTRODUCTION

Background

With habitat loss and degradation as one of the greatest threats to global biodiversity today (Andrén 1994, Jantz et al. 2015), restoration has become an indispensable tool to conserve species and ecosystems alike (Scott et al. 2001, Suding 2011). Among the best known success stories are efforts of the North American Waterfowl Management Plan, which has led to the recovery of many previously-imperiled duck species (Nichols et al. 1995, Williams et al. 1999, Sauer et al. 2017, USFWS 2017). Other high-profile restoration efforts have included those relying upon natural colonization as for Golden-cheeked Warblers (*Setophaga chrysoparia;* Anders and Dearborn 2004) as well as initiatives supplemented by translocation as done for black-footed ferrets (*Mustela nigripes*; Jachowski and Lockhart 2009). While a handful of habitat restorations are demonstrated to yield successful outcomes, surprisingly few studies have carefully assessed ecological responses of focal species to restoration at meaningful spatial scales (Menz et al. 2013).

Despite the obvious importance of monitoring restoration success, predictions about how animal populations might respond to habitat restoration remain largely theoretical (Huxel and Hastings 1999, Brudvig 2011). When restorations incorporate monitoring, practitioners can better adapt and improve subsequent implementation and avoid wasting limited resources on ineffective activities (Menz et al. 2013; McIntosh et al. 2018). Indeed, monitoring data have informed species recovery programs, such as for Kirtland's Warblers (*Setophaga kirtlandii*) where habitat restoration enabled populations to rebound from only a few hundred individuals to thousands of breeding pairs in only a few decades (Probst et al. 2003, Donner et al. 2008). Among the best monitored examples of species restorations involve New Zealand's endemic bird species (Robertson et al. 2011, Germano et al. 2018). Indeed, conservation efforts aimed at enhancing habitat through predator removal has allowed Little Spotted Kiwi (*Apteryx owenii*) and Rowi (*A. rowi*) populations to increase by 27% and 100%, respectively over the period of only 10 years (2008-18; Germano et al. 2018). While the success of restorations for species like black-footed ferrets, kiwis, and Kirtland's Warblers are clearly demonstrated by monitoring data (Jachowski and Lockhart 2009, Bocetti et al. 2014), most restoration efforts do not fit a binary view of success (*i.e*., yes/no) but are, instead, only partially successful (*i.e*., mixed measures of recovery; Scott et al. 2001, Jones and Schmitz 2009). Consequently, pairing restoration interventions with rigorous monitoring is imperative to successful conservation and continuous improvement through the adaptive management process.

While counts of focal species within restored habitats is a common metric of monitoring species response (Bibby et al. 2000, Bock and Jones 2004), considerations of relative vital rates (*e.g*., birth rates, death rates, etc.) provide more informative assessments of habitat quality as they more directly relate to population growth (Van Horne 1983, Pulliam 1988). Failure to explicitly consider vital rates (Heppell et al. 2000, Vonesh and De la Cruz 2002, Radchuk et al. 2013), undermine restoration outcomes, (Gilroy et al. 2011, Hollander et al. 2011). The role of breeding productivity (juvenile output and survival) in population regulation has been demonstrated across many taxa but is especially important in those with low adult survival and high-fecundity (*i.e*., R-selected species; Stahl and Oli 2006). Furthermore, conservation biologists are often challenged by contrasting patterns among *components* of individual vital rates (*e.g*., nest- and fledgling survival; Bridge et al. 2011, Cox et al. 2014, Kays et al. 2015) and understanding habitat quality requires assessments of multiple components of productivity.

The capacity of a species to find, occupy, and thrive within restored sites is partly a function of decisions made by dispersing individuals across a hierarchy of scales, from foraging substrates to landscapes (Hildén 1965, Hutto 1985). The key implication from hierarchical habitat selection is that, even when restored sites contain appropriate micro-structure for a focal species, the landscape context of restored habitats may ultimately determine colonization potential and thus restoration success (Hanski 1998, Scott et al. 2001). For example, landscapes with poor habitat connectivity may not be conducive to dispersal and settlement (Brederveld et al. 2011). Moreover, even connectivity among habitat patches may be non-binary with landscape matrices comprised of a mosaic of dispersal resistance impacts (Amaral et al. 2016). Even within landscapes that support dispersal, restored habitats in close proximity to population centers are more likely to be colonized than isolated sites or those in sparsely-occupied parts of a species' range (Skellam 1951, Adrén 1994, Paracuellos and Tellería 2006).

Among taxa of conservation concern, Nearctic-Neotropical migratory songbirds provide excellent opportunities to evaluate restoration outcomes. Because habitat loss has contributed to the steep declines in many species of migratory songbirds (Faaborg et al. 2010, Sauer et al. 2017), the several large-scale conservation efforts have focused on habitat management and restoration (*e.g.*, Black-capped Vireo [*Vireo atricapilla*, Noa et al. 2007], Cerulean Warbler [*Setophaga cerulea*, Ciuzio et al. 2013, Wood et al. 2013]). As with other taxa, systematic evaluations of restoration outcomes are limited. Among the most common has been nest survival and these measures have been very useful for designing and refining best management recommendations for various species (*e.g.*, Roth et al. 2012, Terhune et al. 2016). Though nest data are clearly valuable, a growing body of literature suggests that the period between fledging and independence (*i.e.*, the post-fledging period) may be a critical component of the avian lifecycle (Naef-Daenzer and Grüebler 2016).

Indeed, ornithologists have identified the post-fledging period to be as- or more important to avian population growth than the nesting period (Cox et al. 2014) suggesting that nest success is a poor proxy for breeding output (Streby et al. 2014). Although the likely importance of the post-fledging period has long been recognized, technological limitations have, until recently, precluded tracking the fledglings of small bird species once they leave the nest (Sykes et al. 1990, Faaborg et al. 2010). Over the past several decades, tracking technology has improved and transmitters small enough to be used on small passerines are commercially available (Bridge et al. 2011). The availability of miniature radio transmitters has given rise to a proliferation of post-fledging studies, many of which have been focused on habitat selection and survival (Cox et al. 2014). One major theme to emerge from recent post-fledging studies has been that many bird species shift broad habitat types between nesting and post-fledging (Pagan et al. 2000, Streby et al. 2016, Vitz and Rodewald 2011). These habitat shifts range from micro-habitat (Raybuck 2016, Fiss 2018) to broad cover type shifts (Anders et al. 1997, Vega Rivera et al. 1998) and, commonly include both (Anders et al. 1998, Vitz and Rodewald 2011). Additionally, most studies report high mortality during the post-fledging period, usually most pronounced in the first few days post-fledging (Cox et al. 2014, Naef-Daenzer and Grüebler 2016). Given the high rates of mortality associated with the post-fledging period, this period has been cited as a major limiting component of the avian lifecycle in some species (Faaborg et al. 2010, Robinson et al 2004).

While fledgling habitat needs and basic demography are important metrics for conservation, the behavioral ecology of fledgling migratory songbirds is largely unstudied. Fledgling behavior has been studied in non-migratory species and those with lengthy parental care (Langen1996, Russell et al. 2004), however, long-distance migratory species have important life history differences, such as truncated breeding seasons and post-fledging development periods constrained by fall migration (Ogden and Stutchbury 1996, Hecksecher et al. 2017, Mumme 2018). Obligatory fall migration necessitates a brief period of post-fledging care which, in turn, requires that behavioral development and molt must occur either a) within the brief window of parental care or b) between the onset of independence and fall migration (Streby et al. 2014, Naef-Daenzer and Grüebler 2016). This includes all parent-fledgling interaction (Trivers 1985, Royle et al. 2012), foraging development (Trivers 1974, Chandler et al. 2016), and pre-formative molt (Nolan 1978, Howell et al. 2003). Given these unique stressors, it seems unlikely that patterns of behavioral development and molt for long-distance migratory species would resemble those reported for species with lengthy parental care (*e.g.*, Langen1996, Russell et al. 2004).

Study System

My dissertation addresses restoration outcomes and breeding ecology for an imperiled migratory songbird, the Golden-winged Warbler (*Vermivora chrysoptera*). Golden-winged Warbler populations, like those of many songbird species, have declined since at least the 1960s (Sauer et al. 2017) or longer (Hill and Hagen 1991). In response to chronic population losses, the Golden-winged Warbler Status Review and Conservation Plan (hereafter, 'Conservation Plan'; Roth et al. 2012) produced a set of science-based best management practices and population goals for the species across its breeding- and non-breeding distributions. While threats facing Golden-winged Warbler populations are varied, one of the principle drivers of declines is the loss of early-successional breeding habitat (Buehler et al. 2007, Rohrbaugh et al. 2016). Likewise, other species reliant upon early-successional communities also are declining as habitats become unsuitable through the natural process of ecological succession coupled with altered disturbance regimes across eastern forest landscapes (Trani et al. 2001, King et al. 2011). The term "habitat restoration" holds a variety of meanings (Miller and Hobbs 2007). Throughout this dissertation, we use the term "habitat restoration" to refer to the process of restoring the early-successional component of a broader ecosystem (forest) through mimicking natural disturbance regimes via anthropogenic means (*e.g.*, timber harvest, shrub shearing, etc.).

Following the publication of the Conservation Plan in 2012, multiple agencies and NGOs initiated habitat restoration programs for Golden-winged Warblers. The most ambitious programs are USDA-NRCS Working Lands for Wildlife (WLFW) and Regional Conservation Partnership Program (RCPP; Ciuzio et al. 2013, WLFW 2016), which focus primarily on restoring private lands through a variety of management activities and partnerships (McNeil et al. 2017). For example, in West Virginia, shrub management is commonly implemented using prescribed fire and/or prescribed grazing to arrest ecological succession (Aldinger 2018) whereas sites in Minnesota and Wisconsin are treated using shearing of aspen (*Populus* spp.) or alder (*Alnus* spp.; C. Bertsch, Pers Comm.). While prescribed fire, shearing, and other habitat restoration methods provide high-quality nesting habitat for Golden-winged Warblers (McNeil et al. 2017), overstory removal by timber harvesting (*i.e.*, those leaving 2.2 – 8.9 m^2/ha residual basal area) is among the most efficient approach because sites are commercially viable and integrate easily into forest management plans. Although Golden-winged Warblers are known to use and successfully breed in restored habitats (Bakermans et al. 2015, McNeil et al. 2017, 2018), responses at regional scales remain poorly understood. Assessing the response of Golden-winged Warblers to habitat restoration across their breeding range is imperative given that > 6,000 ha of habitat has been restored since 2012 with thousands more hectares planned over the next several years (WLFW 2016).

Dissertation organization

This dissertation is comprised of six chapters, each written as a manuscript formatted for publication. In Chapter 2, we assess the extent to which state and federal habitat restoration programs improve breeding habitat for Golden-winged Warblers across the majority of its range and identify the key factors driving outcomes. In Chapter 3, we evaluate the degree to which reproductive capacity, especially juvenile output, and subpopulation trends influence responses to restorations. In Chapter 4, we review the literature on avian post-fledging ecology with a focus on eastern North America's forest-dependent bird species. In Chapter 5, we quantify the contributions of stage-specific demography (*e.g.*, egg, nestling, fledgling stages) to regional differences in restoration outcomes. In Chapter 6, we both examine a previously unacknowledged stressor (i.e., pre-formative molt of fledglings) and provide the first estimates of daily energetic expenditure for molting fledgling songbirds. Finally, in Chapter 7, we describe the ontogeny of behavioral development in a long-distance migratory songbird and consider constraints placed by and implications for parental care. Collectively, the research presented here highlights the challenges associated with restoring habitat for species like the Golden-winged Warbler, especially in regions where a species has already become rare, and underscores the importance of considering behavioral and demographic drivers of species responses.

Works Cited

Aldinger, K. R. (2018). Ecology and Management of Golden-Winged Warblers (*Vermivora chrysoptera*) and Associated Avian Species in the Allegheny Mountains of West Virginia (Unpublished doctoral dissertation). West Virginia University, Morgantown, West Virginia, USA.

Amaral, K. E., M. Palace, K. M. O'Brien, L. E. Fenderson and A. I. Kovach (2016). Anthropogenic habitats facilitate dispersal of an early successional obligate: Implications for restoration of an endangered ecosystem. PloS one 11:e0148842.

Anders, A. D., D. C. Dearborn, J. Faaborg and F. R. T. Iii (1997). Juvenile survival in a population of Neotropical migrant birds. Conservation Biology 11:698-707.

Anders, A. D., and D. C. Dearborn (2004). Population trends of the endangered golden-cheeked warbler at Fort Hood, Texas, from 1992–2001. The Southwestern Naturalist 49:39-48.

Andrén, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355-366.

Bakermans, M. H., J. L. Larkin, B. W. Smith, T. M. Fearer and B. C. Jones (2011). Golden-winged Warbler habitat best management practices in forestlands in Maryland and Pennsylvania. American Bird Conservancy, The Plains, Virginia, USA.

Bakermans, M., B. Smith, B. Jones and J. L. Larkin (2015). Stand and within-stand factors influencing Golden-winged Warbler use of regenerating stands in the central Appalachian Mountains. Avian Conservation and Ecology 10:1.

Bibby, C. J., N. D. Burgess, D. A. Hill and S. Mustoe (2000). Bird census techniques. Elsevier, Amsterdam, Netherlands

Bocetti, C. I., D. M. Donner and H. F. Mayfield (2014). Kirtland's Warbler (*Setophaga kirtlandii*), version 2.0. In The Birds of North America (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.19

Bock, C. E., and Z. F. Jones (2004). Avian habitat evaluation: should counting birds count?. Frontiers in Ecology and the Environment 2:403-410.

Brederveld, R. J., S. C. Jähnig, A. W. Lorenz, S. Brunzel and M. B. Soons (2011). Dispersal as a limiting factor in the colonization of restored mountain streams by plants and macroinvertebrates. Journal of Applied Ecology 48:1241-1250.

Bridge, E. S., K. Thorup, M. S. Bowlin, P. B. Chilson, R. H. Diehl, R. Fléron, … and M. Wikelski (2011). Technology on the move: recent and forthcoming innovations for tracking migratory birds. BioScience 61:689-698.

Brudvig, L. A. (2011). The restoration of biodiversity: where has research been and where does it need to go?. American Journal of Botany, 98(3), 549-558.

Buehler, D. A., A. M. Roth, R. Vallender, T. C. Will, J. L. Confer, R. A. Canterbury, ... and L. P. Bulluck (2007). Status and conservation priorities of Golden-winged Warbler (*Vermivora chrysoptera*) in North America. The Auk 124:1439-1445.

Ciuzio, E., W. L. Hohman, B. Martin, M. D. Smith, S. Stephens, A. M. Strong and T. Vercauteren (2013). Opportunities and challenges to implementing bird conservation on private lands. Wildlife Society Bulletin 37:267-277.

Cox, W. A., F. R. Thompson III, A. S. Cox and J. Faaborg (2014). Post-fledging survival in passerine birds and the value of post-fledging studies to conservation. The Journal of Wildlife Management 78:83-193.

Donner, D. M., J. R. Probst and C. A. Ribic (2008). Influence of habitat amount, arrangement, and use on population trend estimates of male Kirtland's warblers. Landscape Ecology 23:467-480.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux ... and S. C. Latta (2010). Conserving migratory land birds in the New World: Do we know enough?. Ecological applications 20:398-418.

Fiss, C. J. (2018). Multiscale Habitat Selection and Movement of Fledgling Golden-Winged Warblers (*Vermivora chrysoptera*) in Two Managed Mixed-Oak Forest Communities of Northern Pennsylvania (Unpublished masters thesis). Indiana University of Pennsylvania, Indiana, Pennsylvania, USA.

Germano, J., S. Barlow, I. Castro, R. Colbourne, M. Cox, C. Gillies, K. Hackwell, J. Harawira, M. Impey, A. Reuben, H. Robertson, J. Scrimgeour, W. Sporle and S. Yong (2018). Kiwi Recovery Plan 2018–2028. New Zealand Department of Conservation.

Gilroy, J. J., G. Q. A. Anderson, J. A. Vickery, P. V. Grice and W. J. Sutherland (2011). Identifying mismatches between habitat selection and habitat quality in a ground-nesting farmland bird. Animal Conservation 14: 620-629.

Hanski, I. (1998). Metapopulation dynamics. Nature 396:41.

Heppell, S. S., H. Caswell and L. B. Crowder (2000). Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology 81:654-665.

Hildén, O. (1965). Habitat selection in birds: a review. Annales Zoologici Fennici 2:53-75.

Hill, N. P. and J. M. Hagan III (1991). Population trends of some northeastern North American landbirds: a half-century of data. The Wilson Bulletin 103:165-182.

Hutto, R. L. (1985). Habitat selection by nonbreeding, migratory land birds. Pages 455–473 in M. L. Cody (Ed.). Habitat Selection in Birds. Academic Press, New York, USA.

Huxel, G. R. and A. Hastings (1999). Habitat loss, fragmentation, and restoration. Restoration Ecology 7:309-315.

Jachowski, D. S., R. A. Gitzen, M. B. Grenier, B. Holmes and J. J. Millspaugh (2011). The importance of thinking big: large-scale prey conservation drives black-footed ferret reintroduction success. Biological Conservation 144:1560-1566.

Jantz, S. M., B. Barker, T. M. Brooks, L. P. Chini, Q. Huang, R. M. Moore ... and G. C. Hurtt (2015). Future habitat loss and extinctions driven by land-use change in biodiversity hotspots under four scenarios of climate-change mitigation. Conservation Biology 29:1122-1131.

Kays, R., M. C. Crofoot, W. Jetz and M. Wikelski (2015). Terrestrial animal tracking as an eye on life and planet. Science 348:aaa2478.

King, D. I., K. H. Nislow, R. T. Brooks, R. M. DeGraaf and M. Yamasaki (2011). Early-successional forest ecosystems: far from “forgotten”. Frontiers in Ecology and the Environment 9:319-320.

McIntosh, E. J., S. Chapman, S. G. Kearney, B. Williams, G. Althor, J. P. Thorn, ... and R. Grenyer (2018). Absence of evidence for the conservation outcomes of systematic conservation planning around the globe: a systematic map. Environmental Evidence 7:22.

McNeil, D. J., K. R. Aldinger, M. H. Bakermans, J. A. Lehman, A. C. Tisdale, J. A. Jones, ... and J. L. Larkin (2017). An evaluation and comparison of conservation guidelines for an at-risk migratory songbird. Global Ecology and Conservation 9:90-103.

McNeil, D. J., C. J. Fiss, E. Wood, J. Duchamp, M. H. Bakermans and J. L. Larkin (2018). Using a natural reference system to evaluate songbird habitat restoration. Avian Conservation and Ecology 13:1.

Menz, M. H., K. W. Dixon and R. J. Hobbs (2013). Hurdles and opportunities for landscape-scale restoration. Science 339:526-527.

Miller, J. R., & Hobbs, R. J. (2007). Habitat restoration—Do we know what we’re doing?. Restoration Ecology 15:382-390.

Naef-Daenzer, B. and M. U. Grüebler (2016). Post-fledging survival of altricial birds: ecological determinants and adaptation. Journal of Field Ornithology 87:227-

250.

Nichols, J. D., F. A. Johnson and B. K. Williams (1995). Managing North American waterfowl in the face of uncertainty. Annual Review of Ecology and Systematics 26:177-199.

Noa, L. A., D. H. Hirth, T. M. Donovan and D. Cimprich (2007). Demographic differences of Black-capped Vireos in two habitat types in central Texas. The Journal of wildlife management 71:1042-1049.

Pagen, R. W., F. R. Thompson III, and D. E. Burhans (2000). Breeding and post-breeding habitat use by forest migrant songbirds in the Missouri Ozarks. The Condor 102:738-747.

Paracuellos, M. and J. L. Tellería (2004). Factors affecting the distribution of a waterbird community: the role of habitat configuration and bird abundance. Waterbirds 27:446-453.

Probst, J. R., D. M. Donner, C. I. Bocetti, and S. Sjogren (2003). Population increase in Kirtland's warbler and summer range expansion to Wisconsin and Michigan's Upper Peninsula, USA. Oryx 37:365-373.

Probst, J. R. and J. P. Hayes (1987). Pairing success of Kirtland's Warblers in marginal vs. suitable habitat. The Auk 104:234-241.

Pulliam, H. R. (1988). Sources, sinks, and population regulation. The American Naturalist 132:652-661.

Radchuk, V., C. Turlure and N. Schtickzelle (2013). Each life stage matters: the importance of assessing the response to climate change over the complete life cycle in butterflies. Journal of Animal Ecology 82:275-285.

Raybuck, D. W. (2016). Migration and the post-fledging period: Examining two critical stages of the Cerulean Warbler life cycle. (Unpublished Master's Thesis). Arkansas State University, Jonesboro, Arkansas, USA.

Robertson, H. A., Colbourne, R. M., Graham, P. J., Miller, P. J., & Pierce, R. J. (2011). Experimental management of brown kiwi *Apteryx mantelli* in central Northland, New Zealand. Bird Conservation International 21:207-220.

Robinson, R. A., R. E. Green, S. R. Baillie, W. J. Peach, and D. L. Thomson (2004). Demographic mechanisms of the population decline of the Song Thrush *Turdus philomelos* in Britian. Journal of Animal Ecology 73:670–682.

Rohrbaugh, R. W., D. A. Buehler, S. B. Swarthout, D. I. King, J. L. Larkin, K. V. Rosenberg, A. M. Roth, R. Vallender, and T. Will. (2016). Conservation perspectives: Review of new science and primary threats to Golden-winged Warblers. Pp. 207–215 in H. M. Streby, D. E. Andersen, and D. A. Buehler (Eds). Golden-winged Warbler ecology, conservation, and habitat management. Studies in Avian Biology (no. 49), CRC Press, Boca Raton, Florida, USA.

Roth, A. M., R. W. Rohrbaugh, T. Will, and D. A. Buehler, Eds. (2012). Golden-winged Warbler Status Review and Conservation Plan. www.gwwa.org/

Roth, A. M., D. J. Flaspohler and C. R. Webster (2014). Legacy tree retention in young aspen forest improves nesting habitat quality for Golden-winged

Warbler (*Vermivora chrysoptera*). Forest Ecology and Management 321:61-70.

Sauer, J. R., D. K. Niven, J. E. Hines, D. J. Ziolkowski, Jr, K. L. Pardieck, J. E. Fallon, and W. A. Link. (2017). The North American Breeding Bird Survey, Results and Analysis 1966 - 2015. Version 2.07.2017 USGS Patuxent Wildlife Research Center, Laurel, MD

Scott, T. A., W. Wehtje and M. Wehtje (2001). The need for strategic planning in passive restoration of wildlife populations. Restoration ecology 9:262-271.

Skellam, J. G. (1951). Gene dispersion in heterogeneous populations. Heredity 5:433-435.

Stahl, J. T., and M. K. Oli (2006). Relative importance of avian life-history variables to population growth rate. Ecological modelling 198:23-39.

Streby, H. M., J. M. Refsnider and D. E. Andersen (2014). Redefining reproductive success in songbirds: moving beyond the nest success paradigm. The Auk 131:718-726.

Streby, H. M., S. M. Peterson, and D. E. Andersen. (2016). Survival and habitat use of fledgling Golden-winged Warblers in the western Great Lakes region. Pp. 127–140 in H. M. Streby, D. E. Andersen, and D. A. Buehler (Eds). Golden-winged Warbler ecology, conservation, and habitat management. Studies in Avian Biology (no. 49), CRC Press, Boca Raton, Florida, USA.

Suding, K. N. (2011). Toward an era of restoration in ecology: successes, failures, and opportunities ahead. Annual Review of Ecology, Evolution, and Systematics 42:465-487.

Sykes, P. W., J. W. Carpenter, S. Holzman, and P. H. Geissler. (1990). Evaluation of three miniature radio transmitter attachment methods for small passerines. Wildlife Society Bulletin 18:41-48.

Trani, M. K., R. T. Brooks, T. L. Schmidt, V. A. Rudis and C. M. Gabbard (2001). Patterns and trends of early successional forests in the eastern United States. Wildlife Society Bulletin 29:413-424. [Editor's note: Victor A. Rudis, Southern Research Station scientist, co-authored this publication.].

United States Fish and Wildlife Service (2017) Waterfowl population status, 2017. U.S. Department of the Interior, Washington, D.C. USA.

Van Horne, B. (1983). Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Vega Rivera, J. H., J. H. Rappole, W. J. McShea and C. A. Haas (1998). Wood Thrush postfledging movements and habitat use in northern Virginia. The Condor 100:69-78.

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

Vonesh, J. R. and O. De la Cruz (2002). Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. Oecologia 133:325-333.

Williams, B. K., M. D. Koneff and D. A. Smith (1999). Evaluation of waterfowl conservation under the North American waterfowl management plan. The Journal of Wildlife Management 63:417-440.

Working Lands for Wildlife. 2016. Healthy Forests for Golden-winged Warbler. FY 17-21 Conservation Strategy. 20pp. nrcs.usda.gov/wildlife.

Wood, P.B., J. Sheehan, P. Keyser, D. Buehler, J. Larkin, A. Rodewald, S. Stoleson, T.B., Wigley, J. Mizel, T. Boves, G. George, M. Bakermans, T. Beachy, A. Evans, M. McDermott, F. Newell, K. Perkins, and M. White (2013). Management guidelines for enhancing Cerulean Warbler breeding habitat in Appalachian hardwood forests. American Bird Conservancy. The Plains, Virginia, USA.

CHAPTER 2

MULTI-SCALE DRIVERS OF RESTORATION OUTCOMES FOR AN IMPERILED SONGBIRD

Abstract

Habitat restoration is a cornerstone of conservation biology, particularly for habitat-limited species. At best, restoration efforts are evidence-based and guided by species-specific best management practices, however, outcomes are seldom monitored or rigorously evaluated. Wildlife dependent upon early-successional habitats have become the focus of concerted habitat restoration efforts aimed at stemming habitat-related population declines in species like the Golden-winged Warbler (*Vermivora chrysoptera*, GWWA). Herein, we provide one of the first rigorous assessments of a national conservation program aimed at restoring habitat for the GWWA across its breeding range: USDA-NRCS Working Lands for Wildlife and Regional Conservation Partnership Program. More specifically, we studied GWWA response (occupancy and abundance) to implementation of habitat restoration across two broad regions with opposing population trajectories and assessed factors driving species use of restored habitats across regional, landscape, and micro-habitat scales. From 2015-17, we conducted 1,145 (n = 457 locations) and 519 point counts (n=215 locations) across the Appalachian Mountain and Great Lakes GWWA Conservation Regions (respectively) within early-successional habitats treated with overstory-removal timber harvests. Warbler abundance within restored habitats across the Great Lakes varied with latitude, longitude, elevation, forest type (mixed), and # growing seasons. Similarly, GWWA occupancy of restored habitats within the Appalachian Mountains varied with longitude, elevation, forest type (deciduous and mixed), and number of growing seasons. Detections were restricted to areas within close proximity to population centers (usually < 24 km) in the Appalachian Mountains, where GWWAs are rare, but not in the Great Lakes, where GWWAs remain common. Our study demonstrates that even when best management practices are carefully implemented, restoration outcomes vary across regions and with multi-scale habitat attributes. Further, the extent of restoration success may be conditional upon regional abundance. Finally, our results demonstrate that programs aimed at early-successional habitat restoration, when implemented in the framework of adaptive forest management, have the potential to benefit to habitat limited species while remaining within the realm of standard forestry.

Introduction

Habitat restoration is a cornerstone of conservation, particularly for habitat-limited species (Dobson et al. 1997, Perring et al. 2015). At best, restoration efforts are evidence-based, grounded in science, and guided by best management practices (BMPs, Brudvig 2017). However, even when restoration efforts are based on rigorous BMPs, outcomes are seldom monitored or rigorously evaluated (Török and Helm 2017). While restoring habitat can be a critical first step toward ensuring the survival of certain species, so too is evaluation and refinement to achieve intended outcomes (Suding et al. 2011). Most studies of habitat restoration report mixed outcomes (Scott et al. 2001, Jones and Schmitz 2009), yet few empirical assessments of species response to restoration at meaningful scales exist (Menz et al. 2013, McIntosh et al. 2018). Understanding best practices in restoration is further complicated by the likely bias toward reporting positive outcomes (Suding et al. 2011).

A wide variety of behavioral, ecological, and biological factors mediate the success of restoration programs (Palmer et al. 1997, Sudduth et al. 2011). For example, species capacity to colonize restored habitats is limited by the availability of dispersing individuals that may settle within restored sites (Snäll et al. 2003, Piqueray et al. 2013). Additionally, a species may behave differently across its range, especially if abundance varies widely (*e.g.*, density-dependent factors; Einum et al. 2008). Landscape composition may contribute to variation in restoration outcomes by influencing the likelihood that new habitats will be discovered and colonized, given that landscape attributes can profoundly affect dispersal (Bond and Lake 2003, Crouzeilles et al. 2016, Wood et al. 2016). At local scales, factors including microhabitat structure (Triska et al. 2016, Corrêa et al. 2018) and plant species composition (Boves et al. 2013, Leuenberger et al. 2017) are important predictors of species response to restoration.

One group of species that may benefit from restoration are those reliant upon early-successional habitats in eastern North America (Amaral et al. 2016, Hazard-Daniel et al. 2017). Early-successional habitats are classic disturbance-dependent communities characterized by young and short-stature vegetation, like shrubs and saplings (Litvaitis 2001, DeGraaf and Yamasaki 2003). Changes to disturbance regimes (*e.g.*, fire suppression, beaver [*Castor canadensis*] activity reduction) over the last several decades have reduced the availability of ephemeral habitats to the point that many associated wildlife species have declined (Askins et al. 2001, Trani et al. 2001, Swanson et al. 2011). In response to these declines, early-successional species, such as the Golden-winged Warbler (*Vermivora chrysoptera*), have been widely studied to understand how best to create- and maintain nesting habitat (*i.e*., best management practices, BMPs; Bakermans et al. 2011, Roth et al. 2012). Moreover, a variety of programs have been initiated to implement BMPs for species like the Golden-winged Warbler (Ciuzio et al. 2013, WLFW 2016). To this end, we provide one of the first rigorous assessments of a national conservation program aimed at restoring habitat for an imperiled species across its range. More specifically, we studied species response (occupancy and abundance) to implementation of habitat restoration across two broad regions with opposing population trajectories and assessed factors driving species use of sites treated with BMPs (*i.e*., restoration success) across regional, landscape, and micro-habitat scales.

Methods

Focal species

Golden-winged Warblers (hereafter, “GWWA”) are Nearctic-Neotropical migratory songbirds that nest within early-successional communities in eastern North America (Confer et al. 2011). Like many early-successional specialists, GWWA populations have declined steadily since the 1960s (Sauer et al. 2017) or longer (Hill and Hagen 1991) due in part to loss of breeding habitat (Roth et al. 2012, Rosenberg et al. 2016). Today, GWWAs have become rare and/or patchily-distributed across landscapes where they were once abundant (*e.g*., the Appalachian Mountains; Gill 2004, King and Schlossberg 2014) though populations in the Great Lakes are more secure (Sauer et al.

2017).

Habitat Guidelines and Restoration Implementation

In 2012, conservationists published a set of science-based best management practices detailing conservation strategies for GWWAs across its entire lifecycle (hereafter, the “Conservation Plan”; Bakermans et al. 2011, Roth et al. 2012, Bennett et al. 2018). The Conservation Plan has been readily adopted by multiple agencies and NGOs to help stem GWWA population declines (WLFW 2016, McNeil et al. 2017). Two of the most ambitious programs, Working Lands for Wildlife (WLFW) and Regional Conservation Partnership Program (RCPP), were initiated by USDA-NRCS in 2012 (WLFW) and 2016 (RCPP) to manage private lands for GWWA across the Appalachians and Great Lakes (Ciuzio et al. 2013, WLFW 2016). Since their inception, WLFW and RCPP have managed > 6,000 ha of breeding habitat for GWWAs and hope to double this from 2017-21 (WLFW 2016).

Among the most efficient habitat restoration tools recommended by the Conservation Plan are overstory removal timber harvests (Bakermans et al. 2015, McNeil et al. 2018). Overstory removal harvests (2.2 – 8.9 m^2/ha residual basal area; Bakermans et al. 2011) are rigorously demonstrated to provide quality habitat for GWWA territorial establishment (Bakermans et al. 2015), pairing (Roth et al. 2014), and nesting (McNeil et al. 2017), created from mature forest otherwise unsuitable for nesting. When implemented such that adequate regeneration occurs, overstory removal harvests are a convenient management type because they are often commercially viable and incorporate easily into forest management plans (Johnson et al. 2009, McCaskill et al. 2009). Although WLFW/RCPP use a variety of implementation tools for restoring/enhancing GWWA habitat across the breeding range (*e.g.*, shrubland management; WLFW 2016), overstory removals are the most common method and we thus sampled only habitats restored using overstory removal.

Study Area and Site Selection

We studied restored habitats across both the Great Lakes (high latitude) and Appalachian Mountains (high elevation) Conservation Regions (*sensu* Roth et al. 2012). The Great Lakes Conservation Region is estimated to host ~ 95% of the global breeding GWWA population (Roth et al. 2012). In the Western Great Lakes, we surveyed 17 counties in Minnesota and five counties in Wisconsin, ranging from 249 - 540 m above sea level. Upland deciduous forests dominate the region, intermixed with natural wetlands (Dyer 2006, Fry et al. 2011, Omernik and Griffith 2014). Red maple (*Acer rubrum*), birches (*Betula* spp.), aspens (*Populus* spp.), and oaks (*Quercus* spp.) are among the most common tree species in the region. Understory species are similarly varied but commonly include alder (*Alnus* spp.), willow (*Salix* spp.), and dogwood (*Cornus* spp.). We monitored all available locations that had been restored through WLFW/RCPP in Minnesota and Wisconsin between 2015-17 (*i.e.*, 0-2 growing seasons, post-treatment).

The 10 states within the Appalachian Mountains Conservation Region support ~5% of the global breeding population of GWWAs (Roth et al. 2012). Across the Appalachian Mountains, we sampled counties in Maryland (2), Pennsylvania (26), and New Jersey (2) that were located 416 - 677 m above sea level. Restored habitats in the Appalachian Mountains were dominated by Appalachian oak and northern hardwood forest communities (Dyer 2006; Fry et al. 2011) with maples (*Acer* spp.) birches, hickories (*Carya* spp.), and oaks the most common genera. A variety of understory plants occurred across the study area, including mountain laurel (*Kalmia latifolia*), witch-hazel (*Hamamelis virginiana*), black huckleberry (*Gaylussacia baccata*), and blueberry (*Vaccinium* spp.). We monitored all available locations that had been restored through WLFW/RCPP in Pennsylvania, Maryland and New Jersey between 2012-17 (*i.e*., 0-5 growing seasons, post-treatment). Additionally, we included a comparable sample of restored habitats on nearby public lands in the Appalachian Mountains, managed using the same prescription (Bakermans et al 2011, 2015, McNeil et al. 2017; overstory removal, 0-9 growing seasons, post-treatment).

Point Count Surveys

Following methods of McNeil et al. (2018), we recorded all GWWA males seen or heard at 1-2 random points located >80 m from a habitat edge and spaced >250 m apart. We sampled Golden-winged Warblers twice/breeding season by a single observer using a combined passive + playback method (Kubel and Yahner 2007, McNeil et al. 2014). Our point count protocol was identical to those of McNeil et al. (2018) except that we added conspecific playback immediately after our 10-minute point count surveys. Playback consisted of one minute of GWWA type 2 song, one minute of Eastern Screech-owl (*Megascops asio*)/Black-capped Chickadee (*Poecile atricapillus*) mobbing, and one minute of silence. We visually identified the plumage phenotype for each *Vermivora* spp. to avoid false positive identifications based on song mismatch (Ficken and Ficken 1969, Highsmith 1989) and excluded birds detected outside the boundaries of restoration sites. Prior to field sampling, we extensively trained all technicians to consistently and accurately estimate distances to birds to the nearest 5 m interval (McNeil et al. 2018). This allowed us to record the distance from point count center to each GWWA (when first observed) for distance sampling analyses (see “Statistical Analyses” section, below). Data from the playback component of our point count (minutes 10-13) were not included in our distance analysis (Buckland et al. 2015, McNeil et al. 2014).

Surveys of Micro-habitat

We surveyed microhabitats at each point from 15 June – 15 July each year following the methods of McNeil et al. (2018). Briefly, vegetation was measured at 10-m intervals along three 100-m radial transects oriented 0°, 120°, and 240° from point count centers (James and Shugart 1970). Vegetation strata recorded at each stop consisted of the presence/absence of sapling, shrub, *Rubus* spp., forb, and sedge/grass (hereafter, “grass”). Trees were quantified using a basal area prism at the 0m, 50m, and 100m locations along each transect (n=7 total readings/point).

Remote-Sensed Landscape Data

We incorporated remotely-sensed data from two primary sources: National Land Cover Database (NLCD; Fry et al. 2011) and U.S. Forest Service Forest Inventory and Analysis data (FIA; Chojnacky 2000). We summarized land cover at an ecologically-meaningful scale to GWWAs (1 km radius; Bakermans et al. 2015) for the following land cover classes: 1. deciduous forest, 2. mixed forest, 3. coniferous forest, 4. shrubland, 5. forested wetland, 6. emergent wetland, 7. pasture, 8. row-crops, and 9.

human development. From the FIA dataset, we summarized data for the following ‘forest type groups’ : 1. aspen-birch, 2. maple-beech (*Fagus* spp.), 3. oak-hickory, and 4. spruce (*Picea* spp.) - fir (*Abies* spp.). Each covariate was modeled as percent cover within a 1 km radius buffer.

Statistical Analyses

i. Occupancy modeling. We modeled GWWA observations from the Appalachian Mountains using static occupancy models in the R package *unmarked* (Fiske & Chandler, 2011, R Core Team, 2018). We used only records of GWWA ≤ 100 m of the observer in all analyses. Package *unmarked* allows the user to fit linear models within a maximum likelihood framework that can be combined with an Information Theoretic approach (Andersen 2007) for model selection (*e.g*., using Akaike’s Information Criterion adjusted for small sample size; AIC_c; Burnham and Andersen 2002). We formatted data using a stacked structure to allow multiple years of data to be modeled together (McClure and Hill 2012, Fogg et al. 2014). We used a four-step approach (Figure 2.1A – D) to creating our final candidate occupancy model set (Fig. 2.1E). We first modeled factors that impact detection probability using four survey covariates: i. minutes since sunrise (mssr), ii. Julian date, iii. Beaufort wind index and iv. cloud cover [%]). To reduce the number of categories within the Beaufort wind index, we simplified values of ≤ 2 to ‘calm’ and those >2 to ‘windy’. We created all possible combinations of 0 – 4 survey covariates on detection using the dredge function in the R package *MuMIn* (Barton 2018, R Core Team, 2018; Fig. 2.1A) and included informative detection covariates in all following occupancy models. We first tested broad geographic patterns: latitude, longitude, and elevation using all possible combinations of additive covariates including quadratic relationships for latitude and longitude (*i.e.*, $x + x^2$; Fig. 2.1B). We incorporated all the top model from this candidate set (detection + lat./long./elev. covariates) into all following model sets, as well as all additive combinations of additional covariates and null (intercept-only) models. We treated all competing models (*e.g.*, $\Delta AIC_c < 2.0$; Burnham and Andersen 2002) as plausible and included them in consecutive model sets. We next modeled all possible combinations of previous models + additive combinations with micro-habitat (Fig. 2.1C) and landscape covariates (Fig. 2.1D). Within our micro-habitat model set, we also included # growing seasons and habitat area (hectares) as covariates. Finally, using the supported models from both our micro-habitat and landscape habitat models (Fig. 2.1C-D), we created a global model that combined all supported covariates together and dredged this top model to create our final candidate set (Fig. 2.1E). Prior to each analysis, we calculated Pearson's Correlation Coefficient among all pairwise combinations of covariates and removed variables at the $R = 0.7$ threshold (Sokal and Rohlf 1969). To assess the extent to which detections in the Appalachians might be clumped, we also calculated Ripley's K for points with GWWA detections as compared to all sampling locations.

ii. Hierarchical distance modeling. We modeled Great Lakes GWWA detections with hierarchical distance models (HDM) using *gdistsamp* in the R package *unmarked* (Fiske & Chandler, 2011, R Core Team, 2018). We binned detections in 20m wide bins such that we had 5 distance bins to model observations (Buckland et al. 2015) and stacked data as with our occupancy analyses. We used a five-step approach (Fig. 2.1F – J) to creating our final candidate HDM model set (Fig. 2.1K). We assessed all available detection functions (hazard rate, half-normal, exponential, and uniform; Kéry and Royle 2015; Fig. 2.1F) prior to assessing factors that impact detection using four survey covariates: i. mssr, ii. Julian date, iii. Beaufort wind index and iv. cloud cover (binary). To avoid overfitting our HDMs and ensure model convergence, we created all possible combinations of 0 – 1 survey covariates on detection (while holding occupancy constant; Fig. 2.1G). We then took the top-ranked detection model and incorporated it into all following HDM models. As with occupancy above, we tested broad geographic patterns: latitude, longitude, and elevation using all possible combinations of additive covariates including quadratic relationships for latitude and longitude (*i.e.*, $x + x^2$; Fig. 2.1H). We incorporated all the top model from this candidate set (detection + lat./long./elev. covariates) into all following model sets, as well as all additive combinations of additional covariates and null (intercept-only) models. We next modeled all possible combinations of previous models + additive combinations with micro-habitat (Fig. 2.1I) and landscape covariates (Fig. 2.1J). Finally, using the supported models from both our micro-habitat and landscape habitat models (Fig. 2.1I-J), we created all possible combinations of our top models from each set and compared them together using AIC_c (Fig. 2.1K).

Results

Appalachian Mountains Conservation Region

From 2015-17, we conducted 1145 point counts at 457 locations (each location surveyed twice per year) in the Appalachian Mountains Conservation Region. After accounting for detection probability (Table 2A), mean occupancy probability of restored habitats across this region was $\hat{\Psi} = 0.22$ (95% CI: 0.20 – 0.25). Occupancy probability was positively associated with longitude, and negatively associated with elevation (Table 2B, Fig. 2.3). The best-ranked micro-habitat model included a positive association with # growing seasons with no competing models (Table 1; Fig. 2.3). Likewise, GWWA occupancy across the Appalachian Mountains was negatively associated with percent mixed forest and positively associated with percent deciduous forest within 1 km (Table 2; Fig. 2.3). Our best-ranked occupancy model included longitude (positive), elevation (negative), mixed forest cover (negative), deciduous forest cover (positive) and growing seasons (positive; Table 2C). Our best-ranked model was found to fit our data reasonably well with only minor overdispersion ($\hat{c}$ = 1.14; Kéry and Royle 2015). When we projected these model results across the sampled portion Appalachian Conservation Region, occupancy was predicted highest in eastern Pennsylvania (*i.e.*, Pocono Mountains) and northwestern New Jersey ($\hat{\Psi}$ = 0.40 – 0.80) and intermediate in the Pennsylvania Wilds and southcentral Pennsylvania ($\hat{\Psi}$ = 0.10 – 0.40). The species was rare elsewhere ($\hat{\Psi}$ < 0.10; Fig. 2.4). Aside from GWWA, other *Vermivora* spp. were consistently rare across all years: Blue-winged Warbler (*V. cyanoptera*) naïve occupancy range: 6 – 7%, “Brewster’s” + “Lawrence’s” Warbler hybrids naïve occupancy range: 2 – 3%. Ripley’s K for point locations with GWWA detections as compared to all survey points revealed detections to be clustered at the 70 km scale, however, the magnitude of difference between detections and all points indicated that clustering was most pronounced at the 24 km radius scale (Fig. 2.5).

Great Lakes Conservation Region

From 2015-17, we conducted 519 point counts at 215 locations in the Great Lakes

Conservation Region. A half-normal detection function fit our distance data best with no competing models (second-ranked: hazard-rate, $\Delta AIC_c = 5.89$). After accounting for detection (Table 2A), mean density within restored habitats across this region was $\hat{\lambda} = 0.80$ males/ha (95% CI: 0.71 - 0.88) which equates to 2.50 males (95% CI: 2.23 - 2.76)/point count. Density was negatively associated with longitude, quadratically associated with latitude, and negatively associated with elevation, though a similar model with quadratic longitude was also supported (Table 2B, Fig. 2.5). The best-ranked micro-habitat model included a positive association with # growing seasons with no competing models (Table 1; Fig. 2.6). Likewise, GWWA density within Great Lakes restored habitats was negatively associated with percent mixed forest within 1 km (Table 2; Fig. 2.6). Our best-ranked density model included latitude^2, longitude^2, elevation (negative), mixed forest cover (negative) and # growing seasons (positive; Table 2C). Our best-ranked model was not overdispersed ($\hat{c} = 0.94$). When we projected these model results across the sampled portion Great Lakes Conservation Region, density was lowest in eastern Wisconsin and along the northern shore of Lake Superior ($\hat{\lambda} = 0 – 0.5$ males/ha) and highest in central Minnesota ($\hat{\lambda} = > 1.25$ males/ha; Fig. 2.7). Like the Appalachian Mountains Conservation Region, non-GWWA *Vermivora* spp. were consistently rare across all years: Blue-winged Warbler naïve occupancy range: 0 – 1%; neither Brewster’s nor Lawrence’s Warblers phenotypes were detected in the Great Lakes region.

Discussion

Best management practices have been developed for a wide array of species but are seldom implemented or systematically monitored at meaningful spatial scales (McIntosh et al. 2018). Our study demonstrates that even when BMPs are carefully implemented, restoration outcomes vary across regions and with multi-scale attributes. Additionally, the extent of restoration success was conditional upon regional abundance with most sites occupied in the Great Lakes (though abundance varied) while fewer sites were occupied in the Appalachians. With this in mind, the WLFW and RCPP had mixed success in achieving stated goals, like many habitat restoration efforts before (Scott et al. 2001, Jones and Schmitz 2009). Our results thus provide both a rare case-study of a national conservation program aimed at avian habitat restoration as well as a critical step in adaptive management for GWWAs (Rohrbaugh et al. 2016).

Across both regions, older sites were most beneficial to GWWAs, likely due to regeneration of understory vegetation over time (Fig. 2.8). While stand conditions like basal area and habitat area remain relatively constant over the timescales we studied here (< 10 years post-treatment), non-herbaceous stem cover increased markedly over growing seasons as herbaceous cover likewise declined (Fig. 2.8). Number of growing seasons, therefore, serves as a reasonable proxy for a suit of structural vegetation characteristics (Klaus & Buehler 2001, Confer et al 2003, Patton et al 2010). Importantly, the relationship between GWWA abundance and number of growing seasons is expected to be strongly non-linear (Otto and Roloff 2012), with suitability of sites initially improving with age but then deteriorating after 15-20 years of succession (Bakermans et al. 2011, Otto and Roloff 2012). Forest stands in the sapling stage, though not suitable nesting habitat for GWWAs, provides habitat to post-fledging GWWAs and other species (Streby et al. 2013, 2016, Fiss 2018), highlighting the need for a mosaic of forest successional stages. A major challenge for programs like WLFW and RCPP that focus on private lands will be to maintain adequate young forest cover for nesting GWWA populations in the face of extreme land parcelization (Haines et al. 2011).

Within both Conservation Regions, mixed forest cover was negatively associated with GWWA use of restored habitats. Although GWWAs are known to avoid coniferous-dominated landscapes (Buehler et al. 2007, Roth et al. 2012), our results demonstrate that even modest mixed forest cover (*e.g.*, 20% at a 1km radius; Figs. 2.3, 2.6) may stifle restoration success in this system. Like mixed forest cover, elevation was associated with negative GWWA response in both regions (Figs. 2.4, 2.7). This relationship was particularly interesting in the Appalachian Mountains Conservation Region wherein habitat management emphasizes montane habitats, in an effort to reduce sympatry with Blue-winged Warblers (Bakermans et al. 2011, 2015). (Wood et al. 2016). With this in mind, the patterns we report may be landscape-specific, and land managers wishing to conserve GWWAs should consider multiple factors (including local abundance) when selecting forests for restoration (≥ 75% deciduous cover, 200-500 m elevation; Figs. 2A-B).

Our finding that GWWAs failed to colonize restored habitats across portions of the Appalachian Mountains speaks to sparse distribution of populations in this region (Fig. 2.4). Historically, GWWAs were comparatively abundant across both regions of their breeding range (Gill 1980, 2004, Roth et al. 2012); however, populations have declined by an estimated 95% within the Appalachian Mountains (Wilson et al. 2012, Sauer et al. 2017). Chronic regional population declines were reflected by sparse occupancy in restored habitats across the Appalachian Mountains wherein restored habitats > 24 km from local population centers were least likely to be occupied (Fig. 2.5). Only one landscape in the Appalachians – the Pocono Mountains – had consistently high occupancy (Fig. 2.4). Across this landscape, GWWAs are known to occur in abundance in both managed forests like those studied here and natural wetlands that punctuate this landscape (McNeil et al. 2018). One interesting prediction from our map was that GWWA were expected to be common in northwestern New Jersey, although we never detected the species in the state. New Jersey's capacity to support GWWAs, unlike the Poconos, may be compromised by abundant Blue-winged Warblers (44 - 59% naïve occupancy), or other factors not assessed by our study (*e.g.*, invasive *Phragmites australis*; Roth et al. 2012).

Although our study is among the first to assess success of a national habitat restoration program aimed at recovering songbird populations, many parallels can be drawn between the efforts of WLFW/RCPP and habitat management for Kirtland's Warblers (*Setophaga kirtlandii*; Bocetti et al. 2014). Like the GWWA, Kirtland's Warbler is a Nearctic-Neotropical migratory songbird dependent upon early-successional forests in eastern North America. By the 1970s, fewer than 200 males were detected on annual population surveys and all detections were restricted to northern portions of Michigan's Lower Peninsula (Donner et al. 2008, Probst et al. 2003). In response to the critical state of the Kirtland's Warbler population, a multi-agency effort was initiated to manage thousands of hectares of habitat (Donner et al. 2008). By the early 1990s, the Kirtland's Warbler population began to grow in response to habitat management and, by 2003, 1,200 singing males were recorded (Donner et al. 2008). Although concerted habitat restoration intended to benefit GWWA is still early in the implementation stage, that similar approaches have been successful elsewhere is promising.

While the restored habitats we studied were not uniformly occupied by GWWAs, management of early-successional habitat remains essential to avoid regional extirpation of GWWA, especially in the Appalachian region (Rohrbaugh et al. 2016). Given that overstory removal harvests are already a commonplace method of managing hardwood forests (Johnson et al. 2009), our results demonstrate that habitat restoration for GWWAs is highly compatible with standard forestry practices (Nyland 2002). Although our study was focused on GWWA, we commonly observed other disturbance-dependent species (*e.g.*, Prairie Warblers *Setophaga discolor*) within restored GWWA habitats, suggesting the potential for GWWA BMP implementation to benefit a broad suite of animal species. Furthermore, a precursor to overstory removal treatment is frequently a series of shelterwood harvests (Johnson et al. 2009). Shelterwood harvests tend to have too much tree canopy to support GWWAs, but they often support imperiled species like Cerulean Warblers (*S. cerulea*) and, thus, further support the notion that standard forestry practices may benefit numerous bird species (Wood et al. 2013, Boves et al. 2015). Although our study is limited in scope, our results demonstrate that programs aimed at early-successional habitat restoration, when implemented in the framework of adaptive forest management, have the potential to benefit to habitat limited species while remaining within the realm of standard forestry.

Acknowledgments

This project was primarily funded by the United States Department of Agriculture - Natural Resource Conservation Service ‘Conservation Effects Assessment Project’ (CEAP) grant. Additionally, we are grateful for funding from the PA Game Commission (PGC), National Fish and Wildlife Foundation, and American Bird Conservancy. We also thank the PA Bureau of Forestry, the PGC, MD Dep’t of Natural Resources, Rice Lake National Wildlife Refuge (NWR), and Tamarack NWR for logistical assistance and access to their lands. We are grateful to Sharon Petzinger and the NJ Dep’t of Fish & Wildlife for their assistance with field work. Finally, this effort would not be possible without the efforts of many volunteers and paid field technicians. All work was conducted in accordance with USGS banding permit # 23277 and the guidelines of the Institutional Animal Care and Use Committees of both Cornell Univ. (#2013-029) and Indiana Univ. of PA (#14-1314).

Works Cited

Amaral K. E., M. Palace, K. M. O’Brien, L. E. Fenderson and A. I. Kovach (2016). Anthropogenic habitats facilitate dispersal of an early successional obligate: Implications for restoration of an endangered ecosystem. PLoS ONE 11:e0148842.

Askins, R. A. (2001). Sustaining biological diversity in early successional communities: the challenge of managing unpopular habitats. Wildlife Society Bulletin 20:407-412

Bakermans, M. H., J. L. Larkin, B. W. Smith, T. M. Fearer and B. C. Jones (2011). Golden-winged Warbler habitat best management practices in forestlands in Maryland and Pennsylvania. American Bird Conservancy, The Plains, Virginia, USA.

Bakermans, M., B. W. Smith, B. C. Jones and J. L. Larkin (2015). Stand and within-stand factors influencing Golden-winged Warbler use of regenerating stands in the central Appalachian Mountains. Avian Conservation and Ecology 10(1):10. http://dx.doi.org/10.5751/ACE-00747-100110

Barton, K. (2018). MuMIn: Multi-Model Inference. R package version 1.42.1. https://CRAN.R-project.org/package=MuMIn

Bennett, R.E., A. Rothman, K. V. Rosenberg, F. Rodriguez. (2016). Golden-winged Warbler non-breeding season conservation plan. In Roth, A.M., R.W. Rohrbaugh, T. Will, and D.A. Buehler, editors. Golden-winged Warbler Status Review and Conservation Plan. www.gwwa.org/

Bocetti, C. I., D. M. Donner, and H. F. Mayfield (2014). Kirtland's Warbler

(*Setophaga kirtlandii*), version 2.0. In The Birds of North America (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.19

Bond, N. R., and P. S. Lake (2003). Local habitat restoration in streams: constraints on the effectiveness of restoration for stream biota. Ecological Management and Restoration 4:193-198.

Boves, T. J., D. A. Buehler, J. Sheehan, P. B. Wood, A. D. Rodewald, J. L. Larkin, … and T. B. Wigley (2013). Spatial variation in breeding habitat selection by Cerulean Warblers (*Setophaga cerulea*) throughout the Appalachian Mountains. The Auk 130:46-59.

Boves, T. J., Rodewald, A. D., Wood, P. B., Buehler, D. A., Larkin, J. L., Wigley, T. B., & Keyser, P. D. (2015). Habitat quality from individual-and population-level perspectives and implications for management. Wildlife Society Bulletin 39:443-447.

Brudvig, L. A. (2017). Toward prediction in the restoration of biodiversity. Journal of Applied Ecology 54:1013-1017.

Buckland, S. T., E. A. Rexstad, T. A. Marques and C. S. Oedekoven (2015). Distance sampling: methods and applications. Springer, New York, New York, USA.

Buehler, D. A., A. M. Roth, R. Vallender, T. Will, J. L. Confer, R. A. Canterbury, … and L. P. Bulluck (2007). Status and conservation priorities of Golden-winged Warbler (*Vermivora chrysoptera*) in North America. The Auk 124:1439-1445.

Chojnacky, D. C. (2000). FIA forest inventory data for wildlife habitat assessment. Pp. 272-275 in: M. Hansen, T. Burk (Eds.) Integrated Tools for Natural Resources

Inventories in the 21st Century. Gen. Tech. Rep. NC-212. St. Paul, MN: US Dept. of Agriculture, Forest Service, North Central Forest Experiment Station.

Ciuzio, E., W. L. Hohman, B. Martin, M. D. Smith, S. Stephens, A. M. Strong, and T. Vercauteren, (2013). Opportunities and challenges to implementing bird conservation on private lands. Wildlife Society Bulletin 37:267–277.

Crouzeilles, R., M. Curran, M. S. Ferreira, D. B. Lindenmayer, C. E. Grelle, and J. M. R. Benayas (2016). A global meta-analysis on the ecological drivers of forest restoration success. Nature Communications 7:11666.

Confer, J. L., P. Hartman, and A. M. Roth (2011). Golden-winged Warbler (*Vermivora chrysoptera*). The Birds of North America. Number 20. The Academy of Natural Sciences; Washington D.C.: The American Ornithologists Union.

Confer, J. L., J. L. Larkin and P. E. Allen (2003). Effects of vegetation, interspecific competition, and brood parasitism on Golden-winged Warbler (*Vermivora chrysoptera*) nesting success. The Auk 120:138-144.

Corrêa, M. R., Y. M. Bellagamba, A. P. de Magalhães, J. P. Martins, A. J. D. R. Cruz, A. R. Kozovitz ... and C. S. de Azevedo (2018). Microhabitat structure and food availability modelling a small mammal assemblage in restored riparian forest remnants. Mammalia 82:315-327.

DeGraaf, R. M., and M. Yamasaki (2003). Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. Forest Ecology and Management 185:179-191.

Dobson, A. P., A. D. Bradshaw, and A. Á. Baker (1997). Hopes for the future:

restoration ecology and conservation biology. Science 277: 515-522.

Donner, D. M., J. R. Probst, and C. A. Ribic (2008). Influence of habitat amount, arrangement, and use on population trend estimates of male Kirtland's warblers. Landscape Ecology 23:467-480.

Dyer, J. 2006 Revisiting the Deciduous Forests of Eastern North America. BioScience 56:341-352.

Einum, S., K. H. Nislow, J. D. Reynolds, and W. J. Sutherland (2008). Predicting population responses to restoration of breeding habitat in Atlantic salmon. Journal of Applied Ecology 45:930-938.

Ficken, M. S., and R. W. Ficken (1967). Singing behaviour of blue-winged and golden-winged warblers and their hybrids. Behaviour 28:149-181.

Fiss, C. J. (2018). Multiscale Habitat Selection and Movement of Fledgling Golden-Winged Warblers (*Vermivora chrysoptera*) in Two Managed Mixed-Oak Forest Communities of Northern Pennsylvania (Unpublished masters thesis). Indiana University of Pennsylvania, Indiana, Pennsylvania, USA.

Fogg, A., L. Roberts and R. Burnett (2014). Occurrence patterns of Black-backed Woodpeckers in green forest of the Sierra Nevada Mountains, California, USA. Avian Conservation and Ecology 9:2

Forest Inventory and Analysis Database, St. Paul, MN: U.S. Department of Agriculture, Forest Service, Northern Research Station (2019). [Available only on internet: http://apps.fs.fed.us/fiadb-downloads/datamart.html]

Fry, J., G. Xian, S. Jin, J. Dewitz, C. Homer, L. Yang, C. Barnes, N. Herold, and J. Wickham. (2011). Completion of the 2006 National Land Cover Database for the conterminous United States. Photogrammetric Engineering and Remote Sensing 77:858-864.

Gill, F. B. (2004). Blue-winged Warblers (*Vermivora pinus*) versus Golden-winged Warblers (*V. chrysoptera*). The Auk 121:1014-1018.

Gill, F. B. (1980). Historical aspects of hybridization between Blue-winged and Golden-winged warblers. The Auk 97:1-18.

Haines, A. L., T. T. Kennedy and D. L. McFarlane (2011). Parcelization: forest change agent in northern Wisconsin. Journal of Forestry 109:101-108.

Highsmith, R. T. (1989). The singing behavior of golden-winged warblers. Wilson Bulletin 101:36-50.

Hill, N. P. and J. M. Hagan III (1991). Population trends of some northeastern North American landbirds: a half-century of data. The Wilson Bulletin 103:165-182.

Huxel, G. R. and A. Hastings (1999). Habitat loss, fragmentation, and restoration. Restoration Ecology 7:309-315.

James, F. C., and H. H. Shugart Jr. (1970). A quantitative method of habitat description. Audubon Field Notes 24:727-736.

Johnson, P. S., S. R. Shifley, and R. Rogers. (2009). Ecology and Silviculture of Oaks. 2nd Edition. CAB International Publishing. Cambridge, Massachusetts, USA.

Jones, H. P. and O. J. Schmitz (2009). Rapid recovery of damaged ecosystems. PloS one 4:e5653.

Kéry, M., and J. A. Royle (2015). Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 1: Prelude and Static Models. Academic Press, Cambridge, Massachusetts, USA.

King, D. I., Nislow, K. H., Brooks, R. T., DeGraaf, R. M. and Yamasaki, M. (2011). Early-successional forest ecosystems: far from “forgotten”. Frontiers in Ecology and the Environment 9:319-320.

Klaus, N. A. and D. A. Buehler (2001). Golden-winged Warbler breeding habitat characteristics and nest success in clearcuts in the southern Appalachian Mountains. Wilson Bulletin 113:297-301.

Kubel, J. E. and R. H. Yahner (2007). Detection probability of Golden-winged Warblers during point counts with and without playback recordings. Journal of Field Ornithology 78:195-205.

Leuenberger, W., D. J. McNeil, J. Cohen and J. L. Larkin (2017). Characteristics of Golden-winged Warbler territories in plant communities associated with regenerating forest and abandoned agricultural fields. Journal of Field Ornithology 88:169-183.

Litvaitis, J. A. (2001). Importance of early successional habitats to mammals in eastern forests. Wildlife Society Bulletin 29:466-473.

McCaskill, G. L., W. H. McWilliams, C. A. Alerich, B. J. Butler, S. J. Crocker, G. M. Domke … and J. A. Westfall (2009). Pennsylvania’s Forests 2009. U.S. Department of Agriculture, Forest Service, Northern Research Station. Newtown Square, Pennsylvania, USA.

McClure, C. J. and G. E. Hill (2012). Dynamic versus static occupancy: How stable are habitat associations through a breeding season?. Ecosphere 3:1-13.

McIntosh, E. J., S. Chapman, S. G. Kearney, B. Williams, G. Althor, J. P. Thorn ...

and R. Grenyer (2018). Absence of evidence for the conservation outcomes of systematic conservation planning around the globe: a systematic map. Environmental Evidence 7:22.

McNeil, D. J., C. R. V. Otto and G. J. Roloff (2014). Using audio lures to improve golden-winged warbler (*Vermivora chrysoptera*) detection during point-count surveys. Wildlife Society Bulletin 38:586-590.

McNeil, D. J., K. R. Aldinger, M. H. Bakermans, J. A. Lehman, A. C. Tisdale, J. A. Jones, and J. L. Larkin (2017). An evaluation and comparison of conservation guidelines for an at-risk migratory songbird. Global Ecology and Conservation 9:90-103.

McNeil, D. J., C. J. Fiss, E. Wood, J. Duchamp, M. H. Bakermans, and J. L. Larkin (2018). Using a natural reference system to evaluate songbird habitat restoration. Avian Conservation and Ecology 13:1

Nyland, R. D. (2002). Silviculture: Concepts and Applications. 2nd Edition. CBS Publisher and Distributor. Daryaganj, New Delhi, India.

Omernik, J. M. and G. E. Griffith (2014). Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. Environmental Management 54:1249-1266.

Otto, C. R. and G. J. Roloff (2012). Songbird response to green-tree retention prescriptions in clearcut forests. Forest Ecology and Management 284:241-250.

Palmer, M. A., R. F. Ambrose and N. L. Poff (1997). Ecological theory and community restoration ecology. Restoration ecology 5:291-300.

Patton, L. L., D. S. Maehr, J. E. Duchamp, S. Fei, J. W. Gassett and J. L. Larkin (2010). Do the Golden-winged Warbler and Blue-winged Warbler exhibit species-specific differences in their breeding habitat use? Avian Conservation and Ecology 5:2.

Perring, M. P., R. J. Standish, J. N. Price, M. D. Craig, T. E. Erickson, K. X. Ruthrof, A. S. Whiteley, L. E. Valentine, and R. J. Hobbs. (2015). Advances in restoration ecology: rising to the challenges of the coming decades. Ecosphere 6:1-25.

Piqueray, J., L. Saad, J. P. Bizoux and G. Mahy (2013). Why some species cannot colonise restored habitats? The effects of seed and microsite availability. Journal for Nature Conservation 21:189-197.

Probst, J. R., D. M. Donner, C. I. Bocetti, and S. Sjogren (2003). Population increase in Kirtland's warbler and summer range expansion to Wisconsin and Michigan's Upper Peninsula, USA. Oryx, 37(3), 365-373.

R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ralph, C. J., J. R. Sauer and S. Droege (1995). Monitoring bird populations by point counts. General Technical Report PSW-GTR-149. U.S. Forest Service, Pacific Southwest Research Station, Albany, California, USA. http://dx.doi.org/10.2737/PSW-GTR-149

Rohrbaugh, R. W., D. A. Buehler, S. B. Swarthout, D. I. King, J. L. Larkin, K. V. Rosenberg, A. M. Roth, R. Vallender, and T. Will. (2016). Conservation perspectives: Review of new science and primary threats to Golden-winged Warblers. Pp. 207–215 in H. M. Streby, D. E. Andersen, and D. A. Buehler (Eds). Golden-winged Warbler ecology, conservation, and habitat management. Studies in Avian Biology (no. 49), CRC Press, Boca Raton, Florida, USA.

Roth, A.M., R.W. Rohrbaugh, T. Will, and D.A. Buehler, editors. (2012). Golden-winged Warbler Status Review and Conservation Plan. www.gwwa.org/

Roth, A. M., Flaspohler, D. J., & Webster, C. R. (2014). Legacy tree retention in young aspen forest improves nesting habitat quality for Golden-winged Warbler (Vermivora chrysoptera). Forest Ecology and Management, 321, 61-70.

Sauer, J. R., D. K. Niven, J. E. Hines, D. J. Ziolkowski, Jr, K. L. Pardieck, J. E. Fallon, and W. A. Link. (2017). The North American Breeding Bird Survey, Results and Analysis 1966 - 2015. Version 2.07.2017 USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Scott, T. A., W. Wehtje and M. Wehtje (2001). The need for strategic planning in passive restoration of wildlife populations. Restoration ecology 9:262-271.

Snäll, T., P. J. Ribeiro Jr and H. Rydin (2003). Spatial occurrence and colonisations in patch-tracking metapopulations: local conditions versus dispersal. Oikos, 103:566-578.

Sokal, R. R. and F. J. Rohlf. (1969). The principles and practice of statistics in biological research. W.H. Freeman and Company, San Francisco, California, USA.

Streby, H. M., and D. E. Andersen (2013). Movements, cover-type selection, and survival of fledgling Ovenbirds in managed deciduous and mixed coniferous-deciduous forests." Forest Ecology and Management 287:9-16.

Streby, H. M., S. M. Peterson, and D. E. Andersen. (2016). Survival and habitat use of fledgling Golden-winged Warblers in the western Great Lakes region. Pp. 127–140 in H. M. Streby, D. E. Andersen, and D. A. Buehler (Eds.). Golden-winged Warbler ecology, conservation, and habitat management. Studies in Avian Biology (no. 49), CRC Press, Boca Raton, Florida, USA.

Sudduth, E. B., B. A. Hassett, P. Cada, and S. E. Bernhardt (2011). Testing the field of dreams hypothesis: functional responses to urbanization and restoration in stream ecosystems. Ecological Applications 21:1972-1988.

Suding, K. N. (2011). Toward an era of restoration in ecology: successes, failures, and opportunities ahead. Annual review of ecology, evolution, and systematics, 42, 465-487.

Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto ... and F. J. Swanson (2011). The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9:117-125.

Török, P. and A. Helm (2017). Ecological theory provides strong support for habitat restoration. Biological Conservation 206:85-91.

Trani, M. K., R. T. Brooks, T. L. Schmidt, V. A. Rudis and C. M. Gabbard (2001). Patterns and trends of early successional forests in the eastern United States. Wildlife Society Bulletin 29:413-424. [Editor's note: Victor A. Rudis, Southern

Research Station scientist, co-authored this publication.].

Triska, M. D., M. D. Craig, V. L. Stokes, R. P. Pech, and R. J. Hobbs (2016). The relative influence of in situ and neighborhood factors on reptile recolonization in post-mining restoration sites. Restoration Ecology 24: 517-527.

Wilson, A. M., D. W. Brauning and R. S. Mulvihill (2012). Second Atlas of Breeding Birds in Pennsylvania. The Pennsylvania State University. State College, Pennsylvania, USA.

Wood, E. M., S. E. Barker Swarthout, W. M. Hochachka, J. L. Larkin, R. W. Rohrbaugh, K. V. Rosenberg and A. D. Rodewald (2016). Intermediate habitat associations by hybrids may facilitate genetic introgression in a songbird. Journal of Avian Biology 47:508-520.

Wood, P. B., J. Sheehan, P. Keyser, D. Buehler, J. Larkin, A. Rodewald, S. Stoleson, T.B., Wigley, J. Mizel, T. Boves, G. George, M. Bakermans, T. Beachy, A. Evans, M. McDermott, F. Newell, K. Perkins, and M. White. (2013). Management guidelines for enhancing Cerulean Warbler breeding habitat in Appalachian hardwood forests. American Bird Conservancy. The Plains, Virginia, USA.

Working Lands for Wildlife. (2016a). Healthy Forests for Golden-winged Warbler. FY 17-21 Conservation Strategy. 20pp. nrcs.usda.gov/wildlife.

Figures and Tables

Table 2.1: Micro-habitat models of occupancy and density for Golden-winged Warblers within restored early-successional forests in the Appalachian Mountains (top) and Great Lakes (bottom). The top ten models are shown in each candidate set. All models include a detection probability (p) with associated detection covariates: Julian date (“date”), minutes since sunrise (“mssr”), Beautfort wind index (“wind”), and percent cloud cover (“cloud”). Additionally, models include components for occupancy (Ψ) and density (λ) with associated covariates: latitude (lat), longitude (long) and elevation (elev), site size (hectares), site age (growing seasons), basal area, sapling cover, shrub cover, Rubus cover, forb cover, grass cover, and % plots with 1-2m woody stems (% 1-2m woody). Also shown are the number of model parameters (k), model weight (w), and Δ Akaike’s Information Criterion adjusted for small sample size (ΔAICc).

Detection models – Occupancy (Appalachian Mountains)

Model	k	ΔAIC_c	w
p(date + mssr + wind), Ψ(long + lat + elev + growing seasons)	9	0.00	0.95
p(date + mssr + wind), Ψ(long + elev + growing seasons)	8	5.79	0.05
p(date + mssr + wind), Ψ(long + elev + % 1-2m woody)	8	106.85	0.00
p(date + mssr + wind), Ψ(long + lat + elev + % 1-2m woody)	9	108.63	0.00
p(date + mssr + wind), Ψ(long + elev + hectares)	8	119.70	0.00
p(date + mssr + wind), Ψ(long + lat + elev + hectares)	9	120.37	0.00
p(date + mssr + wind), Ψ(long + elev + sapling cover)	8	124.79	0.00
p(date + mssr + wind), Ψ(long + lat + elev + sapling cover)	9	126.51	0.00
p(date + mssr + wind), Ψ(long + elev + shrub cover)	8	131.56	0.00
p(date + mssr + wind), Ψ(long + lat + elev + shrub cover)	9	133.11	0.00

Detection models – Hierarchical Distance (Great Lakes)

p(wind), λ(long^2 + lat^2 + elev + growing seasons)	12	0.00	0.98
p(wind), λ(long^2 + lat^2 + elev + % 1-2m woody)	12	8.99	0.01
p(wind), λ(long^2 + lat^2 + elev + grass cover)	12	11.08	0.00
p(wind), λ(long^2 + lat + elev + growing seasons)	11	11.27	0.00
p(wind), λ(long^2 + lat^2 + elev + shrub cover)	12	14.75	0.00
p(wind), λ(long^2 + lat + elev + % 1-2m woody)	11	18.58	0.00
p(wind), λ(long^2 + lat + elev + grass cover)	11	20.44	0.00
p(wind), λ(long^2 + lat^2 + elev + *Rubus* cover)	12	28.90	0.00
p(wind), λ(long^2 + lat + elev + shrub cover)	11	31.96	0.00
p(wind), λ(long^2 + lat^2 + elev + basal area)	12	34.29	0.00

Table 2.2: Landscape-scale models of occupancy and density for Golden-winged Warblers within restored early-successional forests in the Appalachian Mountains (top) and Great Lakes (bottom). The top ten models are shown in each candidate set. All models include a detection probability (*p*) with associated detection covariates: Julian date (“date”), minutes since sunrise (“mssr”), Beaufort wind index (“wind”), and percent cloud cover (“cloud”). Additionally, models include components for occupancy (Ψ) and density (λ) with associated covariates: latitude (lat), longitude (long) and elevation (elev), deciduous forest, mixed forest, coniferous forest, shrubland, forested wetland, emergent wetland, pasture, row crops, human development, aspen-birch forest, 2. maple-beech forest, 3. oak-hickory forest, and 4. Spruce-fir forest. Also shown are the number of model parameters (k), model weight (w), and Δ Akaike’s Information Criterion adjusted for small sample size (ΔAIC_c).

Detection models – Occupancy (Appalachian Mountains)

Model	k	ΔAIC_c	w
p(date + mssr + wind), Ψ(lat + long + elev + deciduous forest)	9	0.00	0.95
p(date + mssr + wind), Ψ(lat + long + elev + mixed forest)	8	5.79	0.05
p(date + mssr + wind), Ψ(long + elev + deciduous forest)	8	106.85	0.00
p(date + mssr + wind), Ψ(lat + long + elev + row crop)	9	108.63	0.00
p(date + mssr + wind), Ψ(long + elev + row crop)	8	119.70	0.00
p(date + mssr + wind), Ψ(long + elev + mixed forest)	9	120.37	0.00
p(date + mssr + wind), Ψ(lat + long + elev + oak-hickory)	8	124.79	0.00
p(date + mssr + wind), Ψ(long + elev + oak-hickory)	9	126.51	0.00
p(date + mssr + wind), Ψ(long + elev + human development)	8	131.56	0.00
p(date + mssr + wind), Ψ(lat + long + elev + human development)	9	133.11	0.00
Detection models – Hierarchical Distance (Great Lakes)			
p(wind), λ($long^2$ + lat^2 + elev + mixed forest)	12	0.00	0.98
p(wind), λ($long^2$ + lat^2 + elev + deciduous forest)	12	8.99	0.01
p(wind), λ($long^2$ + lat^2 + elev + oak-hickory)	12	11.08	0.00
p(wind), λ($long^2$ + lat^2 + elev + spruce-fir)	11	11.27	0.00
p(wind), λ($long^2$ + lat^2 + elev + aspen-birch)	12	14.75	0.00
p(wind), λ($long^2$ + lat + elev + oak-hickory)	11	18.58	0.00
p(wind), λ($long^2$ + lat + elev + aspen-birch)	11	20.44	0.00
p(wind), λ($long^2$ + lat^2 + elev + row crop)	12	28.90	0.00
p(wind), λ($long^2$ + lat + elev + mixed forest)	11	31.96	0.00
p(wind), λ($long^2$ + lat^2 + elev + pasture)	12	34.29	0.00

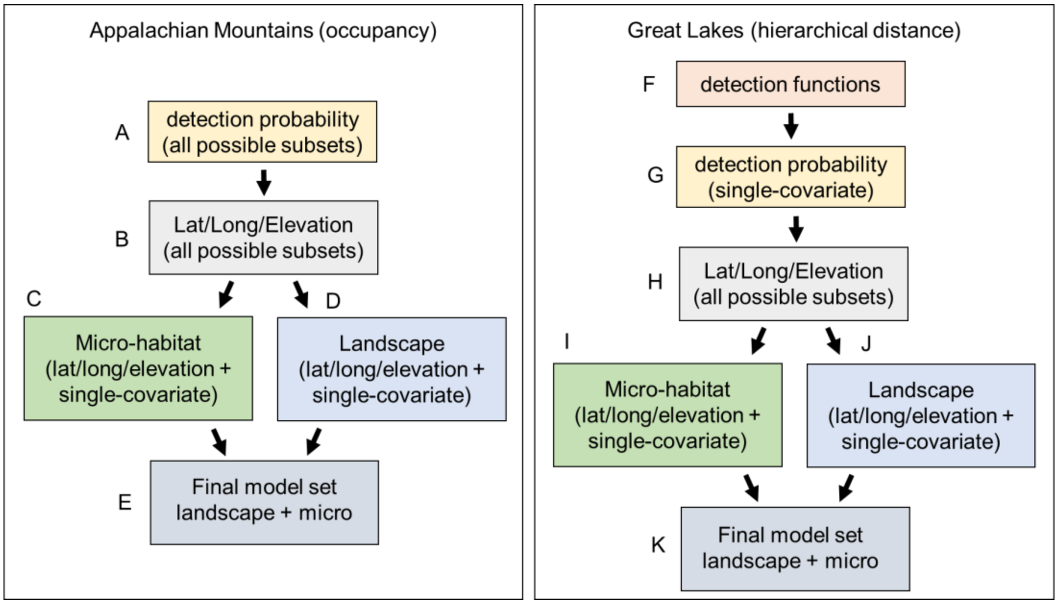

Figure 2.1. A workflow diagram depicting components of occupancy- and hierarchical distance modeling for the Appalachian Mountains (left) and Great Lakes (right), respectively

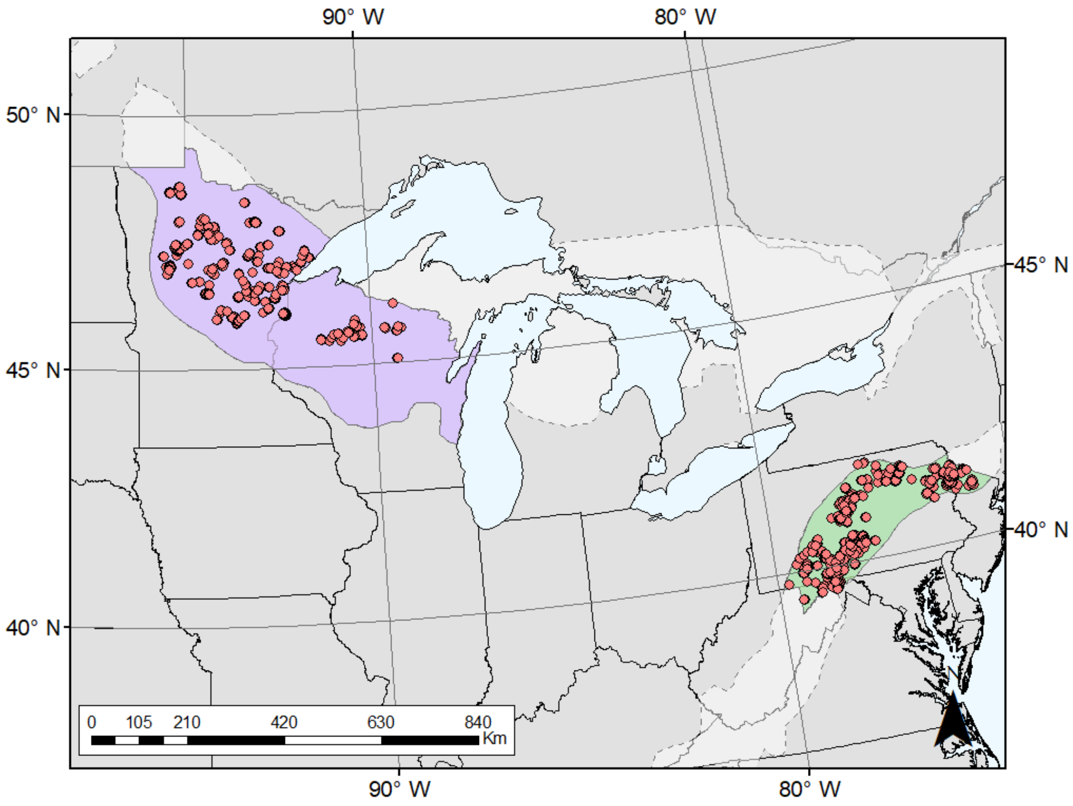

Figure 2.2. A map depicting locations where we conducted surveys (red points) for Golden-winged Warblers on restored early-successional habitats (*i.e.*, overstory removals). We sampled portions of both the Great Lakes (violet) and Appalachian Mountain (green) Conservation Regions. All points are shifted ± 1km in a random direction to maintain private landowner anonymity.

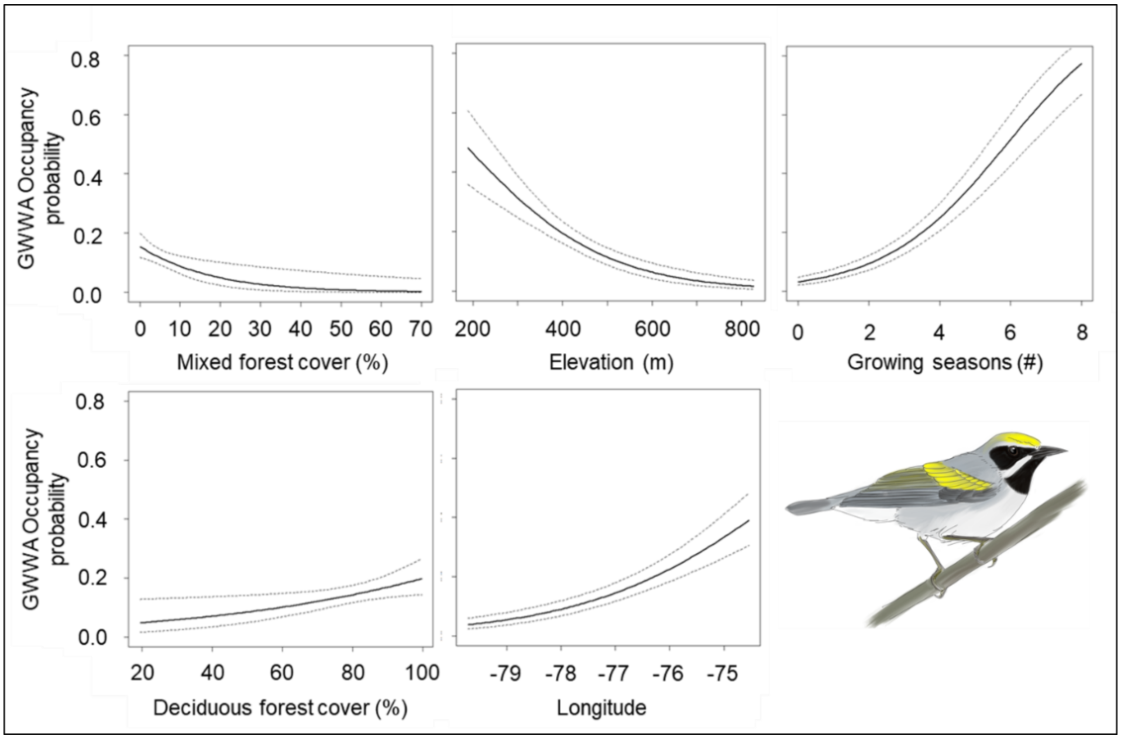

Figure 2.3. Functional relationships between Golden-winged Warbler occupancy within regenerating overstory removals across the sampled Appalachian Conservation Region. Shown are all covariate relationships for our top-ranked occupancy model.

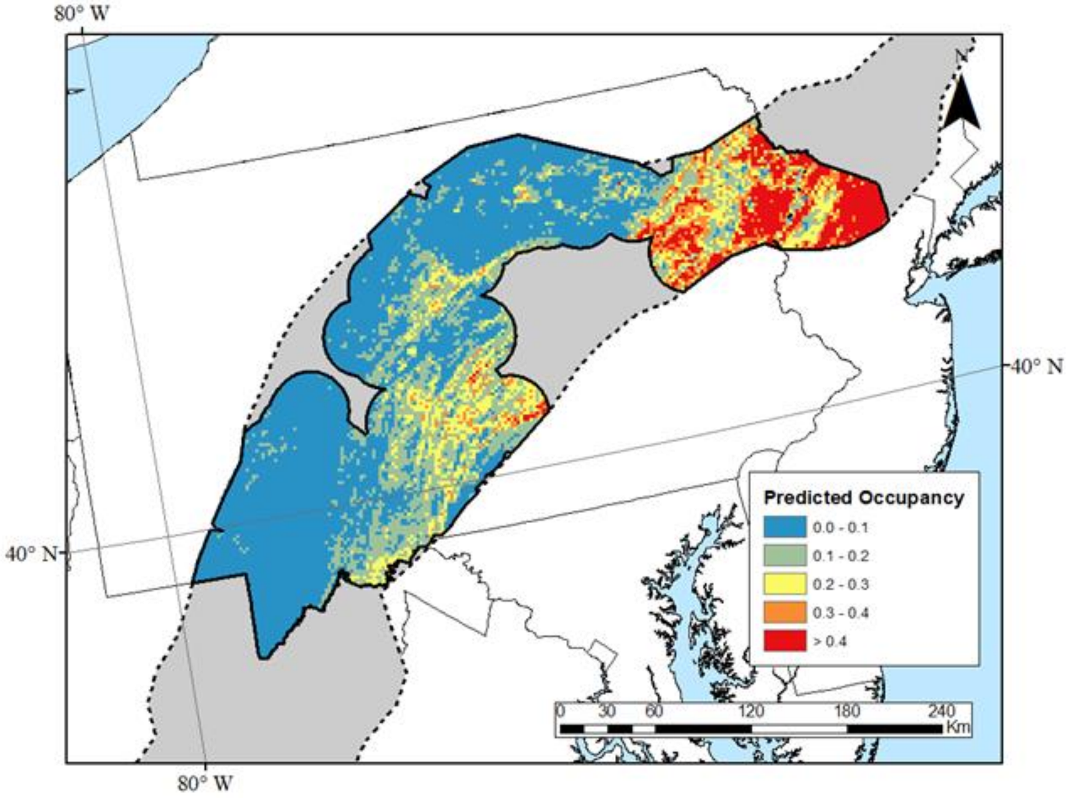

Figure 2.4. Patterns of Golden-winged Warbler predicted occupancy probability in restored habitats across sampled portions of the Appalachian Mountains Conservation Region. We predicted occupancy only within a 24 km radius of sampled survey locations using our top model that considered latitude, longitude, elevation, and percent mixed forest within a 1 km radius. Portions of the Appalachian Mountains Conservation Region outside our predicted area are shown in gray.

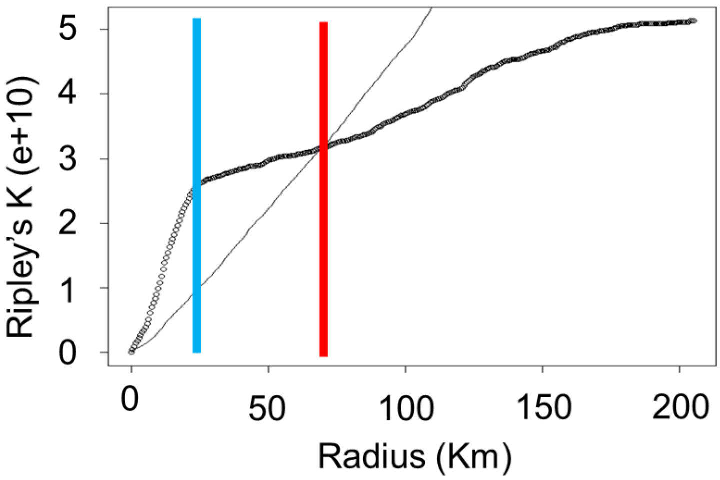

Figure 2.5. Values of Ripley's K for sampling points where Golden-winged Warblers were detected (circles) as compared to all our sampling locations (thin black line). An inflection point occurs around the 24 km radius and this is denoted with a blue vertical line, though clustering occurred out to a 70 km radius (red vertical line

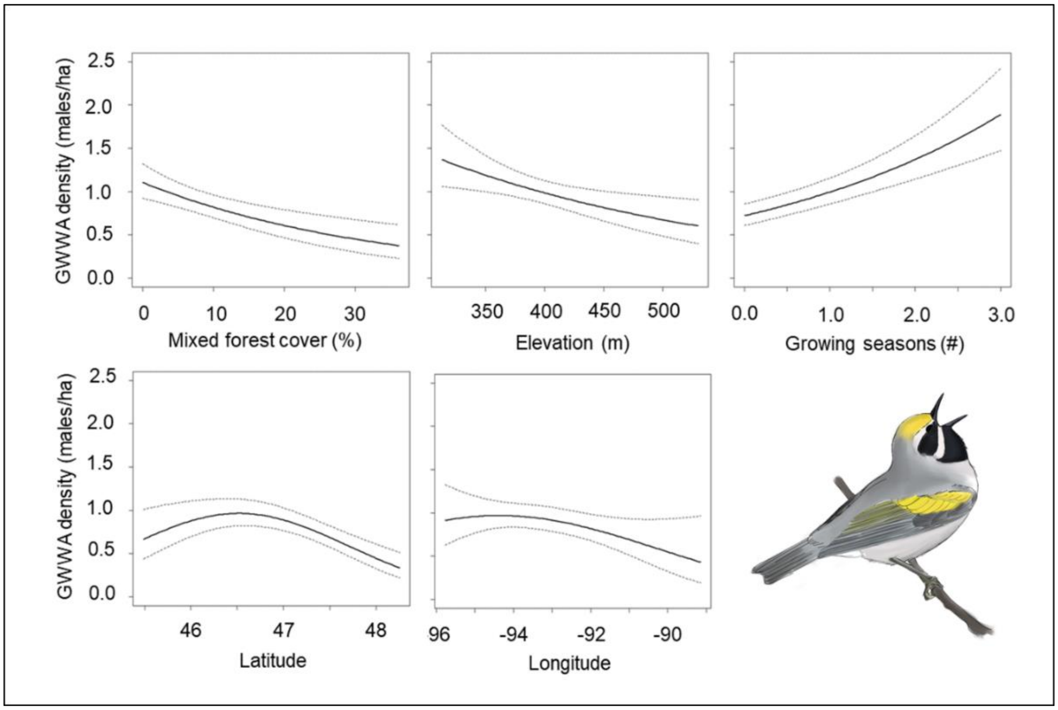

Figure 2.6. Functional relationships between Golden-winged Warbler density (males/ha) within regenerating overstory removals across the sampled Great Lakes Conservation Region. Shown are all covariate relationships for our top-ranked hierarchical distance model.

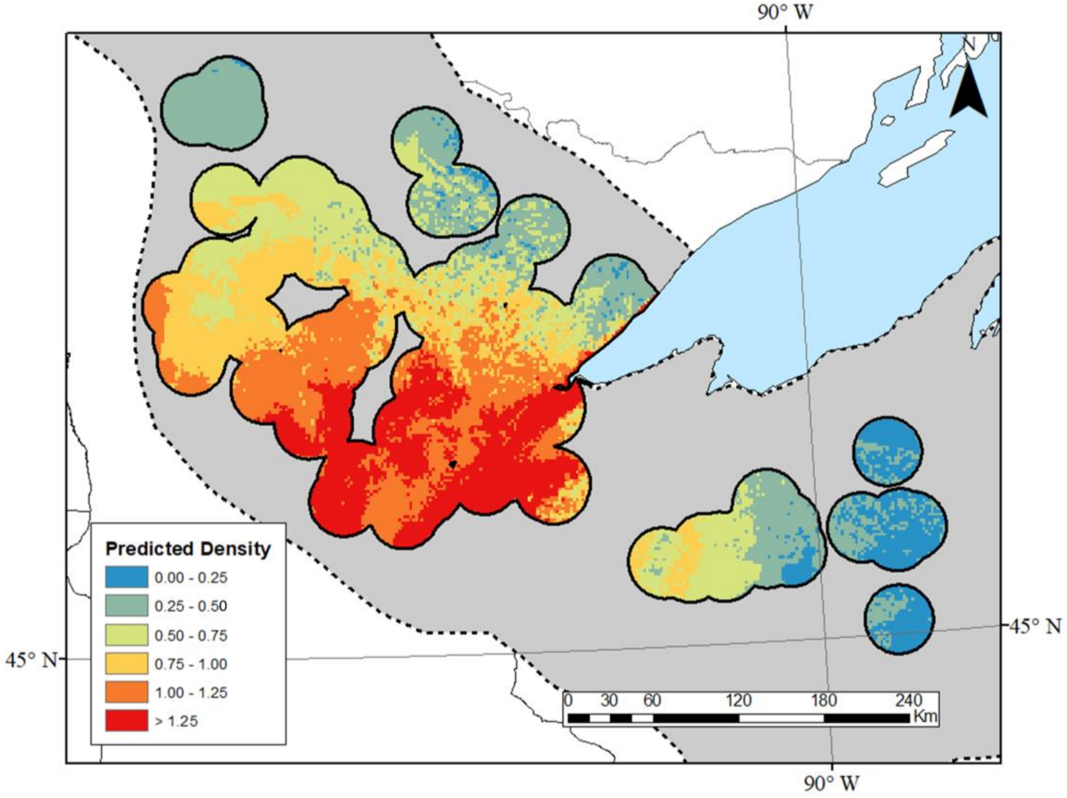

Figure 2.7. Patterns of Golden-winged Warbler predicted density (males/hectare) in restored habitats across sampled portions of the Great Lakes Conservation Region. We predicted occupancy only within a 24 km radius of sampled survey locations using our top model that considered latitude, longitude, elevation, and percent mixed forest within a 1 km radius. Portions of the Great Lakes Conservation Region outside our predicted area are shown in gray.

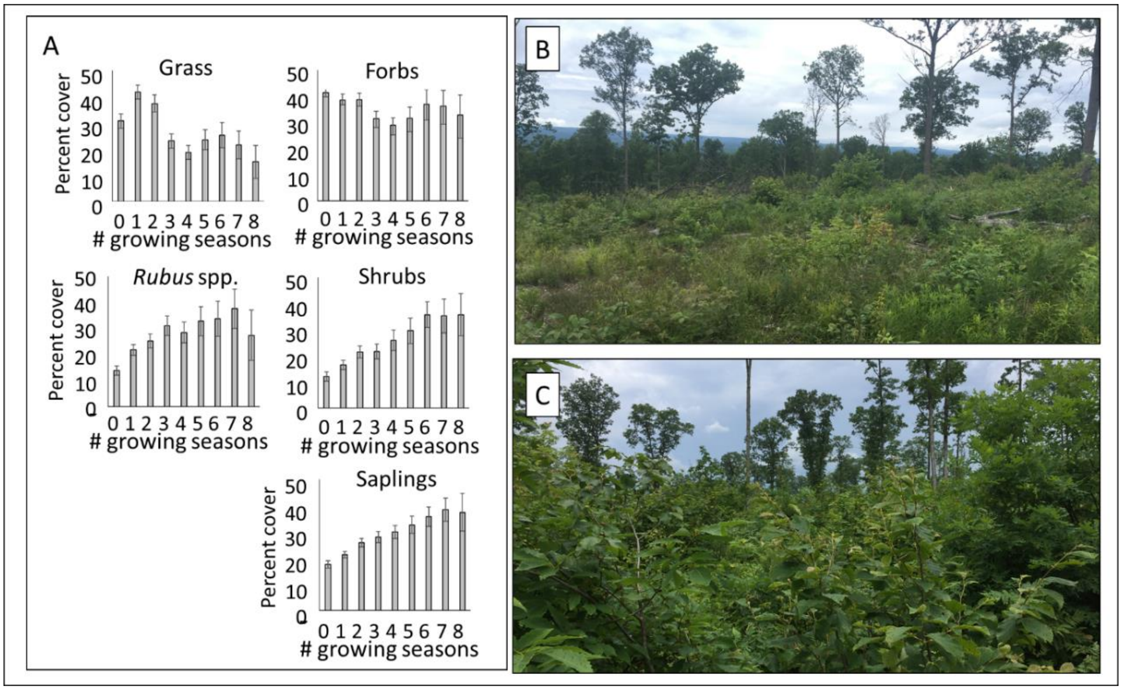

Figure 2.8. Patterns of vegetative succession within restored Golden-winged Warbler habitat over growing seasons. As sites aged, grass- and forb cover generally declined while non-herbaceous stem cover like *Rubus* spp, shrubs, and saplings increased in kind (A). These changes are particularly stark between recently-treated sites (*e.g.*, first growing season; B) and those with advanced understory regeneration (*e.g.*, ninth growing season; C).

CHAPTER 3

REGIONAL ABUNDANCE AND LOCAL BREEDING PRODUCTIVITY EXPLAIN OCCUPANCY OF RESTORED HABITATS IN A MIGRATORY SONGBIRD

Abstract

Ecological restoration is a key tool in offsetting the habitat loss and degradation that threatens biodiversity worldwide, but few projects are rigorously evaluated to determine if conservation objectives are achieved. We identified local and regional drivers of restoration outcomes for an imperiled bird, the Golden-winged Warbler (Vermivora chrysoptera; GWWA), across its breeding range. From 2015-18, we surveyed birds at 595 points located in recently-restored successional habitats. Demographic contributions of restorations were examined by using new- and published data on the survival of 341 nests and 258 fledglings to estimate full-season productivity (hereafter, “productivity”). Occupancy and colonization of restored habitat patches were three- and eight times higher in the Great Lakes than Appalachian Mountains (respectively), a pattern that mirrored variation in abundance and coarse population trends. Likewise, local extinction rates were five times higher in the Appalachian Mountains. At local scales, productivity was high in Eastern Pennsylvania (> 3 independent juveniles/pair/year) but low in Central Pennsylvania (1 independent juvenile/pair/year) while both Western- and Central Minnesota hosted intermediate productivity (1-2 juveniles/pair/year). Local variation in productivity matched that of occupancy in the Appalachian Mountains, while occupancy was high in the Great Lakes, in spite of intermediate productivity. These differences have profound implications for local population dynamics, as Golden-winged Warbler pairs possessed robust capacity to respond to habitat restoration in both regions, but this capacity was conditional upon local productivity where the species is rare. Our findings suggest that, even when restoration efforts are focused on a single species and used comparable prescriptions, complex interactions among processes governing habitat selection, settlement, and productivity can yield variable restoration outcomes.

Introduction

Habitat loss and degradation remain among the greatest threats to global biodiversity, worldwide (Andrén 1994, Wilcove et al. 1998, Butchart et al. 2010, Jantz et al. 2015). As the global human population continues to grow toward 10 billion, anthropogenic impacts on natural systems are only expected to increase (Foley et al. 2005, Crist et al. 2017). Although land conversion drives most habitat loss (Purvis et al. 2000) and fragmentation (Wilson et al. 2016), habitats may be degraded or otherwise rendered unsuitable for species due to changes in natural disturbance regimes that once created or maintained native disturbance-dependent ecosystems (e.g., wildfire; Askins 2001, DeGraaf and Yamasaki 2003). The field of restoration ecology was born partly to address these system-level impacts (Palmer et al. 2016), with habitat restoration being the most common approach to be used on the ground (Suding 2011).

Restoration is a popular tool to mitigate or ameliorate loss or degradation of important habitats (Lerner et al. 2007, Cullinane et al. 2016, Török and Helm 2017), but surprisingly few studies have evaluated how species respond to interventions (Menz et al. 2013). Several habitat restoration efforts have successfully led to the recoveries of species of conservation concern (Scott et al. 2001, Suding 2011), including Kirtland's Warbler (*Setophaga kirtlandii*; Probst et al. 2003), Black-capped Vireo (*Vireo atricapilla*; Wilsey et al. 2014), and black-footed ferret (*Mustela nigripes*; Jachowski and Lockhart 2009). Few habitat restoration efforts have yielded greater success than those initiated as part of the North American Waterfowl Management Plan, which have recovered or steadied populations of many once-ailing waterbirds (Nichols et al. 1995, Williams et al. 1999, Sauer et al. 2017, USFWS 2017). Restoration efforts, however, do not always fit a binary view of success versus failure (Scott et al. 2001), and most are considered to be partially successful (i.e., mixed measures of recovery; Jones and Schmitz 2009). Thus, despite the conceptually-appealing lens of "if you build it, they will come" (i.e., the 'Field of Dreams' Hypothesis, Palmer et al. 1997, Sudduth et al. 2011), restoration outcomes are highly variable and require more rigorous monitoring and evaluation (Suding 2011, Piqueray et al. 2013).

Few studies have explicitly studied how processes operating across a broad range of spatial and temporal scales, such as habitat selection, dispersal, and demography, can influence restoration outcomes (George and Zack 2001, Scott et al. 2001). With passive wildlife restoration efforts (i.e., those relying upon natural colonization rather than active reintroduction), successful occupancy of restored patches is understood to reflect hierarchical decisions about habitat selection made by dispersing individuals (Hildén 1965, Hutto 1985). Even for habitats restored to suitable conditions for a focal species, demographic and dispersal attributes of patches remain key determinants of colonization potential (Scott et al. 2001). For instance, restored sites near densely populated areas are often more quickly colonized than isolated sites or those in sparsely-occupied parts of the species range (Skellam 1951, Adrén 1994, Paracuellos and Tellería 2006). Likewise, local demography should affect colonization, by way of source-sink dynamics (Pulliam 1988, Stout et al. 2007). Nevertheless, predictions about population responses to habitat restoration are largely grounded in theory (Huxel and Hastings 1999, Brudvig 2011) rather than empirical demonstrations at appropriate spatial scales (Menz et al. 2013; McIntosh et al. 2018).

With persistent constraints on human and fiscal resources, the conservation community must ensure that restorations achieve, or at least make meaningful progress towards, conservation goals (Scott et al. 2001, Cullinane et al. 2016). Meeting this challenge requires careful and rigorous evaluation of behavioral and demographic responses of focal species to restoration across multiple spatiotemporal scales. In this study, we examined whether occupancy of restored habitats by a habitat-limited songbird will rise with (a) regional abundance or (b) local breeding productivity (i.e., annual production of juveniles). We considered support for either pattern to be inconsistent with the Field of Dreams hypothesis.

Methods

Focal Species

The Golden-winged Warbler (*Vermivora chrysoptera;* hereafter, “GWWA”) provided an excellent opportunity to examine restoration outcomes because altered disturbance regimes have dramatically reduced the availability of the early-successional habitat on which the species depends (Confer et al. 2011, Rosenberg et al. 2016). The widespread loss of early-successional habitat (King and Schlossberg 2014) has caused the species to become rare and patchily-distributed across most parts of its breeding range, Rosenberg et al. 2016, Sauer et al. 2017). Indeed, GWWAs have experienced a mean annual rate of decline at 2.28%/year, with the most pronounced declines in the Appalachian portion of the breeding range while those in the Great Lakes somewhat more stable (Sauer et al. 2017). Additionally, the population of GWWAs breeding in the Great Lakes is estimated to be ~ 20 times larger than the Appalachian GWWA population (Roth et al. 2012).

Habitat Guidelines and Restoration Implementation

In hopes of stemming persistent population declines, researchers and practitioners developed an evidence-based conservation plan for the GWWA (hereafter, 'the Conservation Plan'; Bakermans et al. 2011, Roth et al. 2012). The Conservation Plan synthesized numerous past studies on GWWA habitat ecology and management to develop a series of regionally- and habitat-specific best management guidelines, which, in turn, have been implemented by multiple agencies and NGOs as part of restoration activities. The most ambitious effort, Working Lands for Wildlife (WLFW; Ciuzio et al. 2013, WLFW 2016b), was launched in 2012 by the Natural Resource Conservation Service (NRCS). Over the ensuing six years, the WLFW effort, in concert with the Regional Conservation Partnership Program, RCPP, facilitated the creation of > 6,000 hectares of early-successional habitat across the Appalachian and Great Lakes portions of the GWWA's breeding range (WLFW 2016a). The WLFW program aims to restore an additional 6,000 hectares of breeding habitat from 2017-21 to offset habitat losses via natural ecological succession (WLFW 2016a).

Point Count Surveys

To assess the extent to which habitat restoration programs like WLFW and RCPP serve as GWWA habitat, we counted male GWWA using standard point count surveys within each restoration site across Conservation Regions and focal landscapes (see Study Area section, below). Our point placement and GWWA survey protocol were identical to those described by McNeil et al. (2018). Briefly, we conducted standard point count surveys for GWWAs at 1-2 locations within all restoration sites (Ralph et al. 1995). Survey locations were placed randomly within each restoration patch >80 m from the untreated habitat edge and > 250 m from the nearest neighboring point location (McNeil et al. 2018). Point counts were sampled twice/breeding season by a single observer using a combined passive/playback sampling protocol understood to maximize GWWA detection probability (Kubel and Yahner 2007, McNeil et al. 2014). We counted males from mid-May through June 2015-18 (Appalachians: 15 May-15 June; Great Lakes: 25 May – 25 June) during fair weather and took place from 0.5 hr pre-sunrise and continued for 4.5 hours daily. Before conducting surveys, we recorded survey conditions including the (1) Beautfort wind index (0–5) and (2) sky condition (% cloud cover) as well as (3) time, and (4) date. We removed all GWWA records for males observed outside the boundaries of managed sites. We also visually identified the plumage phenotype for each bird to avoid false positive identifications based on *Vermivora* song mismatch (Ficken and Ficken 1969, Highsmith 1989).

Nest and Fledgling Monitoring

To assess the role of breeding success on GWWA capacity to respond to habitat restoration, we considered nest and fledgling survival data from multiple focal landscapes within each Conservation Region (see Study Area section, below). Nest and fledgling survival data within the Great Lakes Conservation Region were collected from 2011-12 by Peterson (2014) and associated data were published by Streby et al. (2019; DOI: 10.7717/peerj.4319/supp-2). To compliment Great Lakes data, this study contributes analogous nest and fledgling data from two focal landscapes in the Appalachian Conservation Region: Central Pennsylvania (2016-17) and Eastern Pennsylvania (2014-15). Across these landscapes, we searched for GWWA nests using standard nest searching and monitoring methods (Martin and Greupel 1993). This included following females with nesting material, adults provisioning young, and, to a lesser extent, systematic searching. We monitored nests every 1-3 days and until either failure or success (*i.e.*, at least one nestling fledged the nest; Williams and Wood 2002, Streby and Andersen 2013). As nestlings approached fledging (~7-8 days old), we randomly removed 1-3 from each nest to tag with radio-transmitters (Rappole and Tipton 1991). Our fledgling survival monitoring approach was identical to protocols described by Peterson (2014) and is detailed by Fiss et al. (2016). Briefly, we randomly marked two brood-mates from each GWWA brood with radio transmitters either shortly before fledging (7-8 days old) or immediately after fledging (9 days old). We attached transmitters using a figure-eight style harness (Rappole and Tipton 1991) and the combined mass of transmitter and harness together did not exceed 5% of each fledgling's mass. We tracked each fledgling daily using the homing method and recorded survival/mortality.

Study Area

We employed a study design that required consideration of species response to habitat restoration across multiple scales: “Conservation Regions”, “Focal Landscapes”, and “sites”. Regions were defined by the two conservation regions delineated by the Conservation Plan. Within these two Conservation Regions, we identified four Focal Landscapes within which nest and fledgling survival data were available. Within both Conservation Regions and Focal Landscapes, we monitored restoration “sites” that had recently been treated with GWWA best management practices (see “Habitat Guidelines and Restoration Implementation” section, above).

i. Conservation Regions.

The Conservation Plan considers the range of the GWWA across two distinct “Conservation Regions”: Great Lakes (high latitude) and Appalachian Mountains (high elevation). Both Conservation Regions are dominated by deciduous forest cover and comprised of landscapes thought to minimize the likelihood of sympatry and, hence opportunity for hybridization with Blue-winged Warblers (*V. cyanoptera*; Confer and Larkin 2003, Bakermans et al. 2015, Wood et al. 2016). We studied GWWA response to habitat restoration within 17 counties of Minnesota and five counties of Wisconsin, which ranged from 249 - 540 m above sea level. The Western Great Lakes Conservation Region hosts an estimated 95% of breeding GWWAs (Roth et al. 2012), and the population is more stable than the Appalachian population (Sauer et al. 2017). The Great Lakes region is dominated by eastern deciduous, boreal-hardwood transition, and aspen forests (Dyer 2006, Omernik and Griffith 2014) interspersed with mosaics of upland and wetland vegetation communities (Fry et al.

2011), both of which serve as breeding habitat for GWWAs (Roth et al. 2012, Roth et al. 2014). Common tree species within the communities we sampled were red maple (*Acer rubrum*), birches (*Betula* spp.), aspens (*Populus* spp.), and oaks (*Quercus* spp.). Understory species varied but among the most common were alder (*Alnus* spp.), willow (*Salix* spp.), and dogwood (*Cornus* spp.).

In contrast to the Great Lakes, the 10 states comprising the Appalachian Mountains Conservation Region support only ~5% of the global breeding population of GWWAs, which has continued to steadily decline for > 50 years (Roth et al. 2012, Sauer et al. 2017). We studied restored sites within two counties of Maryland, 26 counties of Pennsylvania, and two counties of New Jersey. Our Appalachian sites occurred at 416 - 677 m above sea level within landscapes dominated by Appalachian oak and northern hardwood forest communities (Dyer 2006; Fry et al. 2011), though wetland communities are common within the Pocono Mountains of northeastern Pennsylvania (McNeil et al. 2017). Common tree species within the communities we sampled were maples (*Acer* spp.) birches, hickories (*Carya* spp.), and oaks. Understory species varied but among the most common were mountain laurel (*Kalmia latifolia*), witch-hazel (*Hamamelis virginiana),* and blueberries (*Vaccinium* spp.). Because sites in the Poconos were distinct from other Appalachian sites in terms of habitat and landscape attributes, we treated it as a separate region in our analysis of productivity.

ii. Focal Landscapes.

We examined four focal landscapes across the two Conservation Regions: Western Minnesota (Great Lakes Conservation Region), Eastern Minnesota (Great Lakes

Conservation Region), Central Pennsylvania (Appalachian Mountains Conservation Region), and Eastern Pennsylvania (Appalachian Mountains Conservation Region). We selected these four focal landscapes based on the availability of GWWA breeding productivity data combined with availability of WLFW/RCPP restoration sites. We defined the centroid of each focal landscape using the centroid of each landscape's nest/fledgling monitoring sites (see "Nest/Fledgling Monitoring Sites" section, below). We defined the spatial extent of a 'landscape' using a 35 km radius circle because this distance represents the typical natal dispersal distance for species like the GWWA (Tittler et al. 2009). Finally, as analyses progressed, we quickly noticed that a 35 km buffer appeared inappropriate for our Central- and Eastern Pennsylvania Focal Landscapes as nearly 100% of GWWA detections occurred within 15 km of the centroids (but this was not true for either Landscape within the Great Lakes). We therefore refined our occupancy buffers in the two Appalachian Landscapes to 15 km and report the results of both analyses.

Our Eastern Pennsylvania Focal Landscape occurred within the heavily-forest Pocono Mountains region of northeastern Pennsylvania (Shultz 1999). This region is moderately high elevation (300-600 m) with rolling hills and many naturally-occurring wetlands throughout (Davis 1993) within which GWWAs often nest (McNeil et al. 2018). The Pocono Mountains support abundant secondary mature deciduous forests with oak, maple, eastern hemlock (*Tsuga canadensis*) among the most abundant species (McCaskill et al. 2009). A more detailed description of the Eastern Pennsylvania Focal Landscape can be found within McNeil et al. (2018) and Fiss (2018). The Central Pennsylvania Focal Landscape was located within the

Appalachian Plateau of the northcentral Appalachian Mountains. This landscape supports a series of high-elevation ridges (500-750 m) along the Allegheny Front (Shultz 1999) that are, like the Pocono Mountains, dominated by secondary deciduous forest (McCaskill et al. 2009). Unlike the Eastern Pennsylvania Focal Landscape, the Central Pennsylvania Focal Landscape hosts very few natural wetlands (Davis 1993, Shultz 1999) and the nesting GWWAs are largely restricted to upland habitats. See Fiss (2018) for a more detailed description of the Central Pennsylvania Focal Landscape. Our Western and Eastern Minnesota Focal Landscapes occurred within the northern hardwood transition zone in the Western Great Lakes. Both Focal Landscapes are characterized by moderate elevation (300-600 m) across mosaics of natural shrublands, wetlands, and forest communities, all of which support nesting GWWAs (Confer et al. 2011, Peterson 2014). Like our Focal Landscapes in the Appalachia Mountains, those in Minnesota support widespread secondary mature deciduous forests with aspen, oak, and maple among the most abundant taxa. See Peterson (2014) for a more detailed description of both Minnesota Focal Landscapes.

iii. Sites.

To select restored habitats for monitoring, we obtained ArcGIS shapefiles (ESRI 2011) from NRCS regional conservation planners delineating privately-owned restored habitats from 2012-15. These shapefiles included all restoration sites treated with habitat- and regionally-specific best management practices as detailed by the Conservation Plan through NRCS conservation programs through 2015 (E. Bellush, pers. comm.). All NRCS sites in both Conservation Regions monitored were treated using silviculture practices (0-5 years, post-treatment). Additionally, we included a comparable sample of sites managed using GWWA best management practices on nearby public lands in each Conservation Region (Roth et al. 2012, McNeil et al. 2017). All public land sites in the Appalachian Mountains Conservation Region were treated using silvicultural practices (0-9 years, post-treatment) and all those in the Great Lakes Conservation Region were treated using shrub management practices (0-3 years, post-treatment). Although sites treated with shrub management may support Golden-winged Warblers prior to treatment, this treatment is intended to enhance Golden-winged Warbler abundance (Roth et al. 2012). Silviculture sites, in contrast, are applied to mature forest wherein Golden-winged Warblers do not breed (Bakermans et al. 2011, Roth et al. 2012).

1. *Perennial Point Count Sites*. Within restored sites, we conducted point counts for Golden-winged Warblers for 1 – 3 consecutive years (See “Surveys of Singing Males”, above). A subset of our point count locations were monitored *every* year from 2015-17 (hereafter, “perennial point count sites”). This dataset consisted of 430 point locations including 275 points in the Appalachian Mountains Conservation Region and 155 sites in the Great Lakes Conservation Region (Figure 3.1). More specifically, we perennially sampled 149 private silviculture sites and 126 public silviculture sites in the Appalachian Mountains and 80 private silviculture sites and 75 public shrub management sites in the Great Lakes. We conducted dynamic occupancy analyses (see “Statistical Analyses”, below) using only the perennial point count dataset. Of the 430 perennial point count sites, 160 sites also fell within our four focal landscapes: Western Minnesota (n=28), Eastern Minnesota (n=13), Central Pennsylvania (n=52), and Eastern Pennsylvania (n=67).

2. *Annual Point Count Sites.* While some sites were visited every year from 2015-17 (perennially), the remainder of our sites were only monitored monitor for 1-2 years (2016 and/or 2017; hereafter, “annual point count sites”). Additionally, we sampled shrub management sites within the two Minnesota Focal Landscapes in 2018. All annual point count sites were a combination of newly-managed NRCS habitats, those with newly-granted survey permission, and comparably-managed nearby public lands. The addition of annual point counts was important to bolstered our point count sample within the boundaries of our four Focal Landscapes as this analysis ultimately consisted of both a) all perennial point count sites that fell within Focal Landscape boundaries and b) annual point count sites. As our analyses at the Focal Landscape scale were conducted using static occupancy each sample consisted of a unique point count-by-year combination (see “Occupancy Modeling” section, below). Our final sample of annual point count-by-year combinations included 103 samples in the two Pennsylvania Focal Landscapes (52 Central- and 51 Eastern-) and 62 samples in the two Minnesota Focal Landscapes (39 Western- and 23 Eastern-). When we narrowed the radii for our Pennsylvania Focal Landscapes to 15 km, the sample of annual point count-by-year combinations was reduced to 58 with 31 and 27 for Central- and Eastern Pennsylvania, respectively.

3. *Nest/fledgling Monitoring Sites.* The cores of our four Focal Landscapes were defined by the centroids of all combined sites within each landscape wherein we monitored nests and fledglings (both Pennsylvania Landscapes) or the landscape

coordinates provided by Peterson (2014; both Minnesota Landscapes). Within the Eastern Pennsylvania Focal Landscape, we sampled nests and fledglings within six regenerating timber harvests across a large tract of public land: Delaware State Forest of Pike and Monroe Counties, Pennsylvania. Our Central Pennsylvania sampling occurred across 11 timber harvests across Sproul State Forest and Pennsylvania State Game Lands 100 of Centre and Clinton Counties, Pennsylvania. Within the Western Minnesota Focal Landscape, Peterson (2014) collected data across Minnesota's Tamarac National Wildlife Refuge of Becker County, Minnesota. Within the Eastern Minnesota Focal Landscape data were collected data across Rice Lake National Wildlife Refuge of Aitkin County, Minnesota.

Statistical Analyses

Occupancy modeling

We modeled Golden-winged Warbler detections using occupancy models in the R package unmarked (Fiske & Chandler, 2011, R Core Team, 2018). This package allows the user to fit linear models within a maximum likelihood framework and can be combined with an Information Theoretic approach (Andersen 2007) for model selection (e.g., using Akaike's Information Criterion; AIC; Burnham and Andersen, 2002). We conducted two occupancy analyses: A Conservation Region comparison (Great Lakes vs. Appalachian Mountains; each modeled separately) and a Focal Landscape comparison (Western Minnesota vs. Eastern Minnesota vs. Central Pennsylvania vs. Eastern Pennsylvania). We conducted our Conservation Region comparison using multi-season ('dynamic') occupancy models with the standard parameterization ('detection probability (p), initial occupancy (Ψ_1), colonization (γ), and extinction (ε)', MacKenzie et al. 2006). We varied detection probability as a function of all possible combinations (0-4) of our survey covariates (i. minutes since sunrise (mssr), ii. Julian date, iii. Beaufort wind index and iv. cloud cover [%]). To reduce the number of categories within the Beaufort wind index, we simplified values of ≤ 2 to 'calm' and those >2 to 'windy'. We modeled our three state variables (Ψ_1, γ, and ε) using all possible combinations of two covariates (i. region, ii. management type (shrub management/timber harvest) and iii. site age [number of growing seasons post-management]). We also considered models that included full time dependency to account for potential annual variation in our two dynamic variables (γ, and ε). To create a set of candidate dynamic occupancy models, we created all possible combinations of detection- and state models using our most parameterized (global) model: 'p (mssr + Julian date + wind + cloud cover), Ψ_1 (site age + management type), γ/ε (site age + survey year + management type)' using the *dredge* function in the R package MuMIn (Barton 2018, R Core Team, 2018). We followed a similar approach for our Focal Landscape comparison except each Landscape was modeled separately and we used static occupancy models with a stacked dataset because sub-regional datasets were smaller samples and dynamic parameters (*i.e.*, γ, and ε) were not essential to this second analysis (McClure and Hill 2012, Fogg et al. 2014). Our global model for this analysis was: 'p (mssr + Julian date + wind + cloud cover), Ψ (site age + management type + survey year)'.

ii. Full season productivity

To estimate productivity of juveniles within restored habitats, we multiplied estimated rates of nest productivity (NP) and fledgling survival (FS) to calculate full-season productivity (FSP; Peterson 2014). Nest productivity was the product of fledglings/successful nest (fledgling productivity) and nest success rate (NS; % nests that fledged young). GWWA pairs attempt to rear a single brood of young each season but will re-nest at least once in response to early nest failures (Confer et al. 2011). We calculated NS while accounting for two nesting attempts using the formula: (1-[1-NS]^2) and propagated error using the delta method (Powell 2007). We calculated NS using nest daily survival rate (DSR) over a 25-day nesting cycle as: DSR^{25} (Aldinger 2018). We generated estimates of DSR using logistic exposure models in program MARK (Dinsmore and Dinsmore 2007). Fledgling productivity was the regional mean output of fledglings for nests that successfully fledged young. Both Focal Landscapes in Minnesota were reported to have mean fledgling productivity = 4.00, however, no error was associated with this value so we used the largest observed variance between the two Pennsylvania Focal Landscapes to conservatively incorporate uncertainty. Fledgling survival was the fraction of fledglings that survived from fledging (day 1 post-fledging) to independence from parental care (~day 30 post-fledging).

Results

Occupancy of Restored Habitats

We detected Golden-winged Warblers at 173 of 430 points (naïve occupancy = 0.40) across the Great Lakes (naïve occupancy = 0.75) and (naïve occupancy = 0. 20) Appalachian Conservation Regions over three years. Most detections in the Appalachian Mountains were concentrated around either central Pennsylvania (*i.e.*, Centre, Clinton Counties) or eastern Pennsylvania (*i.e.*, Pike, Monroe Counties) while the species was nearly homogeneous across the Great Lakes Region. Using these data, we created a candidate set of 4096 and 512 models for our Great Lakes- and Appalachian Mountains Conservation Regions, respectively (Table 3A). A detection model with covariates for ‘wind’ and ‘Julian date’ was best supported in our Great Lakes model set, however, a model with a ‘minutes since sunrise’ covariate was also competing ($\Delta AIC_c < 2.0$). A model with all four survey covariates was best-ranked for Appalachian data with all competing models containing ‘wind’, ‘minutes since sunrise’, and ‘Julian date’ (Table 3A). Occupancy was best explained by ‘time since management’ in both the Great Lakes and Appalachian Conservation Regions. Similarly, extinction (but not colonization) in the Appalachian Mountains was explained by time since management’ while this was not true in the Great Lakes Conservation Region. After accounting for the effects of detection probability, site age, and management type, occupancy ($\widehat{\Psi_1}$ = 0.78; 95% CI: 0.71 – 0.85) and colonization ($\hat{\gamma}$= 0.56; 95% CI: 0.41 – 0.70) were both higher in the Great Lakes than in the Appalachians ($\widehat{\Psi_1}$= 0.23; 95% CI: 0.17 – 0.31; $\hat{\gamma}$ = 0.07; 95% CI: 0.04– 0.11; Fig. 3.2A). In contrast, Appalachian sites were more likely to experience extinction events ($\hat{\varepsilon}$ = 0.21; 95% CI: 0.12 – 0.34) than sites in the Great Lakes ($\hat{\varepsilon}$ = 0.04; 95% CI: 0.02 – 0.09).

We created 128 candidate models for each Minnesota Focal Landscape and 64 candidate models for each of our Pennsylvania Focal Landscapes. A model with ‘wind’ + ‘minutes since sunrise’ covariates on detection and ‘time since management’ + ‘management type’ covariates on occupancy was best supported in the Western Minnesota Focal Landscape (35 km; Table 3B). In contrast, a model with only ‘date’ on detection and an intercept-only for occupancy was best supported in Eastern Minnesota (35 km). A model with a ‘minutes since sunrise’ covariate on detection and ‘time since management’ + ‘survey year’ covariates on occupancy was best supported in the Central Pennsylvania Focal Landscape (15 km). ‘Wind’ and ‘time since management’ best explained detection and occupancy (respectively) in the Eastern Pennsylvania Focal Landscape (15km; Table 3B). Occupancy rates in restored habitats in Western Minnesota (timber harvests $\hat{\Psi}$ = 0.86; 95% CI: 0.55 – 0.97, shrub management $\hat{\Psi}$ = 0.98; 95% CI: 0.92 – 1.00), Eastern Minnesota ($\hat{\Psi}$ = 0.97; 95% CI: 0.88 – 0.99), and Central Pennsylvania ($\hat{\Psi}$ = 0.28; 95% CI: 0.15 – 0.46) Landscapes resembled broader patterns of occupancy at the Conservation Region scale (Figs. 3.2 – 3.3; Table 3B). In contrast, occupancy rates of restored habitats in Eastern Pennsylvania were high ($\hat{\Psi}$ = 0.83; 95% CI: 0.72 – 0.90) and more closely resembled occupancy rates observed in the Great Lakes Conservation Region than the Conservation Region within which this Landscape occurred (Fig. 3.3; Table 3B).

Full-season Productivity

We monitored 77 nests in the Eastern Pennsylvania Focal Landscape (2014-15) and 79 nests in the Central Pennsylvania Focal Landscape (2016-17). During the 2017 nesting season, a highly localized hail storm within the Pennsylvania Wilds resulted in 100% nest failure at one site (n = 11 nests; Fiss et al., *in press*) so excluded those nests from our analyses. From those nests, 46/77 (60%) and 23/68 (34%) nests fledged young in the Eastern- and Central Pennsylvania Focal Landscapes, respectively. Daily survival rates were expectedly higher in Eastern Pennsylvania (DSR: 0.97; 95% CI: 0.96 – 0.98) than in Central Pennsylvania (DSR: 0.95; 95% CI: 0.94 – 0.97). Successful nests in Eastern Pennsylvania produced more fledglings (4.28/successful nest, 95% CI: 3.91 – 4.65) than those in the Central Pennsylvania (3.17/successful nest, 95% CI: 2.67 – 3.67). When we accounted for re-nesting attempts, nest productivity was 4.19 fledglings/pair/year (95% CI: 4.07 – 4.30) and 2.28 fledglings/pair/year (95% CI: 2.20 – 2.38) in each respective Focal Landscape. From successful nests, we marked 64 and 63 fledglings in the Eastern- and Central Pennsylvania Focal Landscape, respectively. A higher number of fledglings from Eastern Pennsylvania (n=47; 74%, 95%CI: 63 – 84%) survived to independence (30 days post-fledging) as compared to fledglings from Central Pennsylvania (n=30; 48%, 95% CI: 35 – 60%). These values combined to yield FSP values of 3.07 (95% CI: 2.62 – 3.53) juveniles/pair/year in Eastern Pennsylvania and 1.08 (95% CI: 0.80 – 1.37) juveniles/pair/year in Central Pennsylvania (Fig. 3.3).

We analyzed data from 58 nests and 42 fledglings in the Eastern Minnesota Focal Landscape (2011-12) and 138 nests and 89 fledglings in the Central Minnesota Focal Landscape (2011-12). Daily survival rates were expectedly similar between Eastern- (DSR: 0.96; 95% CI: 0.94 – 0.97) and Western Minnesota (DSR: 0.95; 95% CI: 0.94 – 0.96). When we accounted for re-nesting attempts, nest productivity was 3.48 fledglings/pair/year (95% CI: 3.33 – 3.63) and 3.09 fledglings/pair/year (95% CI: 3.00 – 3.17) in Eastern- and Western Minnesota, respectively. A higher number of fledglings from Western Minnesota (53/89; 60%, 95% CI: 49 – 70%) survived to independence as compared to fledglings from Central Minnesota (19/42; 45%, 95% CI: 30 – 60%). These values combined to yield FSP values of 1.84 (95% CI: 1.52 – 2.16) juveniles/pair/year in Western Minnesota and 1.57 (95% CI: 1.04 – 2.10) juveniles/pair/year in Eastern Minnesota (Fig. 3.3).

Discussion

As large-scale habitat restorations efforts become increasingly common (Suding 2011), we face an imperative to better monitor species response and understand the drivers of successful outcomes (Brudvig 2011, Menz et al. 2013), particularly at ecologically meaningful scales (McIntosh et al. 2018). Our study represents one of only a handful of comprehensive evaluations of national and regional restoration programs to support species of conservation concern. Our results do not support the Field of Dreams hypothesis (*i.e*., "if you build it, they will come"), thereby indicating that restoration does not guarantee colonization, even for a habitat-limited species. Instead, occupancy of restored habitats was three times higher and colonization eight times greater in regions with abundant versus rare GWWAs. Likewise, local extinction of restored sites was seven times more likely in the low-abundance region. Thus, habitat restoration efforts are most likely to achieve goals in regions with source populations to accelerate colonization and occupancy.

Not only did regional abundance explain restoration outcomes, but we also found compelling evidence that occupancy of restored habitats is related to breeding productivity (i.e., FSP), even within a region of overall population decline. A positive association between occupancy and local breeding productivity makes sense as landscapes with high FSP necessarily export more dispersing juveniles than those with low FSP (Greenwood and Harvey 1982). Still, even this pattern varied by region; while FSP and occupancy were linked in the Appalachian Conservation Region, both landscapes in the Great Lakes exhibited intermediate FSP paired with high occupancy

(Fig. 3.3). Although understanding the factors that drive regional variation in this pattern requires further study, it seems likely that regional abundance plays an important role here, as well. Across the Appalachian Mountains, GWWAs have become rare and patchily-distributed while the species remains common in the Great Lakes (Roth et al. 2012). Restored sites in the Appalachians therefore rely upon one of only a small handful of sub-populations to produce dispersing colonists while those in the Great Lakes may be colonized by juveniles produced nearly anywhere across the entire region (Sauer et al. 2017). To this end, success of programs like WLFW and RCPP may require patience in regions where GWWAs have become rare due to persistent breeding habitat loss over the past century (Rosenberg et al. 2016).

Less clear is why FSP (and associated capacity to colonize new habitats) was high in Eastern Pennsylvania and both Minnesota Landscapes but low in central Pennsylvania. GWWA pairs replaced themselves (with independent juveniles) *every* year in Eastern Pennsylvania while pairs appeared to require two years to do so in Central Pennsylvania. Although it remains unknown why Eastern Pennsylvania continues to support high output of young while other areas have lost this capacity, one contributor may be the regionally-unique abundance of natural wetlands (McNeil et al. 2018). While many formerly-occupied landscapes across the Appalachian Mountains have seen local extirpation of this species (Wilson et al. 2012, Rosenberg et al. 2016), those with abundant natural shrub-wetlands (like the Great Lakes and Eastern Pennsylvania) have retained GWWA populations within these habitats (Confer et al. 2011, Peterson et al. 2016, McNeil et al. 2018). A recent study from another Appalachian landscape lacking shrub wetlands, eastern Tennessee, found low

FSP within anthropogenic habitats, comparable to those we observed in Central Pennsylvania (FSP = 0.66; Lehman 2017). While our study did not assess the occupancy of restoration sites in Tennessee, our results suggest that implementation would be unlikely to yield high rates of successful colonization in the state.

Regardless of where implementation occurs, early-successional habitat management requires expenditure of limited conservation funds (Cullinane et al. 2016, WLFW 2016a, 2016b). Maximization of restoration success is therefore critical for ensuring that scarce resources provide maximum benefit to imperiled species (Scott et al. 2001). Our finding that Appalachian GWWAs were largely concentrated within a few small portions of the region suggests that regional habitat restoration should be focused within close proximity to known populations. Moreover, the observation of very few detections occurring beyond 15 km of each sub-region’s core suggests that GWWAs may be quite dispersal-limited, even more than reported for similar species (Tittler et al. 2009). Studies of simulated data have suggested that habitat management is most successful when focused near population centers (Huxel and Hastings 1999), however, few have tested this idea at meaningful spatial scales (McIntosh et al. 2018). Our results support this idea and suggests that restoration efforts in the Appalachians implemented > 15 km from population centers are unlikely to be colonized by GWWAs, at least until these populations spread beyond what we observed in our study

Conservation of migratory species like GWWAs presents an inherent challenge to conservation because such organisms encounter a varying suite of threats across different portions of the lifecycle (Martin et al. 2007, Hostetler et al. 2015). Long-distance migratory species, in particular, constitute an exceptional challenge because disparate breeding- and non-breeding areas frequently span wide political and ecological boundaries (Marra et al. 2011), yet effective conservation requires protection of both (Rosenberg et al. 2016, Bennett et al. 2016). With this in mind, the value of breeding grounds conservation to GWWA populations has been challenged recently (John 2018, Kramer et al. 2017, Streby et al. 2019). In spite of stark differences in their capacity to occupy restored habitats, GWWAs breeding in Central- and Eastern Pennsylvania winter together in northern South America (Kramer et al. 2016). Although females and males have different habitat requirements on the non-breeding grounds (Bennett et al. 2016), sexual segregation would not explain differential demographic patterns between these two breeding populations. This suggests that, while preservation of non-breeding habitat is paramount to the long-term survival of migratory species like the GWWA, maintaining high quality breeding habitat is critical for conservation.

While our findings constitute a promising exploration of how species response to habitat restoration varies with respect to local abundance and reproductive output, our results are not without limitation. Measurements of FSP, while an improvement over nest-only analyses (Cox et al. 2014), do not account for overwinter survival of hatch-year birds and therefore are not analogous to ‘recruitment’. In fact, Aldinger (2018) suggested that overwinter survival rates for hatch-year GWWAs is fairly low, ~half that expected for adults. Still, unless over-winter survival rates vary greatly among regions, we expect recruitment patterns in each region to be consistent with patterns of FSP. Given that survival rates for adult GWWAs are constant across even large geographic extents (Peterson et al. 2015), such a disparity in overwinter survival seems unlikely. We also recognize that our proxy for habitat quality, time-since-management, is imperfect. Future work incorporating detailed habitat data (e.g., within-stand vegetation, landscape composition, etc.) would be very useful for informing adaptive habitat management for this species. With this in mind, we do not believe a systematic bias in habitat quality to be present within the context of our sites and believe site age serves as a suitable proxy for site quality. Importantly, estimates of colonization and extinction presented here were generated using mean values of site age while these rates vary with site age (Table 3A). Though extinction rates exceeded colonization rates in the Appalachian Mountains for average site, naïve occupancy of sites monitored all three years increased over time (from 0.12 in 2015 to 0.20 in 2017) suggesting a positive occupancy trend in the region. An important caveat is that our study is not a comprehensive assessment of how species respond to habitat restoration, our work provides new insights into factors driving the colonization of restored habitats by an imperiled species, especially with respect to local abundance and reproductive output.

Acknowledgments

This project was primarily funded by the United States Department of Agriculture - Natural Resource Conservation Service ‘Conservation Effects Assessment Project’ (CEAP) grant. Additionally, we are grateful for funding from the PA Game Commission (PGC), National Fish and Wildlife Foundation, and American Bird Conservancy. We also thank the PA Bureau of Forestry, the PGC, MD Dep’t of Natural Resources, Rice Lake National Wildlife Refuge (NWR), and Tamarack NWR

for logistical assistance and access to their lands. We are grateful to Sharon Petzinger and the NJ Department of Fish & Wildlife for their assistance with field work. Finally, this effort would not be possible without the efforts of many volunteers and paid field technicians. All work was conducted in accordance with USGS banding permit # 23277 and the guidelines of the Institutional Animal Care and Use Committees of both Cornell Univ. (#2013-029) and Indiana Univ. of PA (#14-1314).

Works Cited

Aldinger, K. R. (2018). Ecology and Management of Golden-Winged Warblers (*Vermivora chrysoptera*) and Associated Avian Species in the Allegheny Mountains of West Virginia (Unpublished doctoral dissertation). West Virginia University, Morgantown, West Virginia, USA.

Anderson, D. R. (2007). Model based inference in the life sciences: a primer on evidence. Berlin, Germany: Springer Science & Business Media.

Andrén, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355-366.

Askins, R. A. (2001). Sustaining biological diversity in early successional communities: the challenge of managing unpopular habitats. Wildlife Society Bulletin 20:407-412

Bakermans, M. H., J. L. Larkin, B. W. Smith, T. M. Fearer, and B. C. Jones. 2011. Golden-winged Warbler habitat best management practices in forestlands in Maryland and Pennsylvania. American Bird Conservancy, The Plains, Virginia, USA.

Bakermans, M., B. W. Smith, B. C. Jones and J. L. Larkin (2015). Stand and within-stand factors influencing Golden-winged Warbler use of regenerating stands in the central Appalachian Mountains. Avian Conservation and Ecology 10:10. http://dx.doi.org/10.5751/ACE-00747-100110

Barton, K. (2018) MuMIn: Multi-Model Inference. R package version 1.42.1.

https://CRAN.R-project.org/package=MuMIn

Bennett, R.E., A. Rothman, K.V. Rosenberg, F. Rodriguez. (2016). Golden-winged Warbler non-breeding season conservation plan. In Roth, A.M., R.W. Rohrbaugh, T. Will, and D.A. Buehler (Eds.). Golden-winged Warbler Status Review and Conservation Plan. www.gwwa.org/

Burnham, K. P., & Anderson, D. R. (2002). Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media, Berlin, Germany.

Butchart, S. H., M. Walpole, B. Collen, A. Strien, J. P. Scharlemann, R. E. Almond, ... and K. E. Carpenter (2010). Global biodiversity: indicators of recent declines. Science 328:1164-1168.

Brudvig, L. A. (2011). The restoration of biodiversity: where has research been and where does it need to go?. American Journal of Botany 98:549-558.

Ciuzio, E., W. L. Hohman, B. Martin, M. D. Smith, S. Stephens, A. M. Strong, T. Vercauteren (2013). Opportunities and challenges to implementing bird conservation on private lands. Wildlife Society Bulletin 37:267–277.

Confer, J. L., J. L. Larkin and P. E. Allen (2003). Effects of vegetation, interspecific competition, and brood parasitism on Golden-winged Warbler (*Vermivora chrysoptera*) nesting success. The Auk 120:138-144.

Confer, J. L., P. Hartman and A. M. Roth (2011). Golden-winged Warbler (*Vermivora chrysoptera*). The Birds of North America. Number 20. The Academy of Natural Sciences; Washington D.C, USA.

Crist, E., C. Mora, C., and R. Engelman (2017). The interaction of human population, food production, and biodiversity protection. Science 356:260-264.

Cullinane, T. C., C. Huber, K. Skrabis and J. Sidon. (2016). Estimating the economic impacts of ecosystem restoration—Methods and case studies: U.S. Geological Survey Open-File Report 2016–1016. http://dx.doi.org/10.3133/ofr20161016.

Davis, A. F. (1993). Rare Wetland Plants and Their Habitats in Pennsylvania. Proceedings of the Academy of Natural Sciences of Philadelphia 144: 254-262.

DeGraaf, R. M. and M. Yamasaki (2003). Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. Forest Ecology and Management 185:179-191.

Dinsmore, S. J. and J. J. Dinsmore (2007). Modeling avian nest survival in program MARK. Studies in Avian Biology No. 34:73–83

Dyer, J. (2006) Revisiting the Deciduous Forests of Eastern North America. BioScience 56:341-352.

Environmental Systems Research Institute. (2011). ArcGIS Desktop: Release 10. ESRI, Redlands, California, USA.

Fiske, I. and R. B. Chandler (2011). unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Fiss, C. J., D. J. McNeil, F. Rodruigez, A. D. Rodewald, and J. L. Larkin. In Press. Hail-induced Nest Failure and Adult Mortality in a Declining Ground-nesting Forest Songbird. The Wilson Journal of Ornithology.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter ... and J. H. Helkowski (2005). Global consequences of land use. Science 309:570-574.

Fry, J., G. Xian, S. Jin, J. Dewitz, C. Homer, L. Yang, C. Barnes, N. Herold, and J. Wickham. (2011). Completion of the 2006 National Land Cover Database for the conterminous United States. Photogrammetric Engineering and Remove Sensing 77:858-864.

George, T. L. and S. Zack (2001). Spatial and temporal considerations in restoring habitat for wildlife. Restoration Ecology 9:272-279.

Greenwood, P. J., and P. H. Harvey (1982). The natal and breeding dispersal of birds. Annual review of ecology and systematics 13:1-21.

Highsmith, R. T. (1989). The singing behavior of golden-winged warblers. Wilson Bulletin 101:36-50.

Hildén, O. (1965). Habitat selection in birds: a review. Annales Zoologici Fennici 2:53-75.

Hostetler, J. A., T. S. Sillett and P. P. Marra (2015). Full-annual-cycle population models for migratory birds. The Auk 132:433-449.

Hutto, R. L. (1985). Habitat selection by nonbreeding, migratory land birds. Pages 455–473 in M. L. Cody (Ed.). Habitat selection in birds. Academic Press, New York, New York, USA.

Huxel, G. R. and A. Hastings (1999). Habitat loss, fragmentation, and restoration. Restoration Ecology 7:309-315.

Jachowski, D. S., and J. M. Lockhart (2009). Reintroducing the black-footed ferret *Mustela nigripes* to the Great Plains of North America. Small Carnivore Conservation 41:58-64.

Jantz, S. M., B. Barker, T. M. Brooks, L. P. Chini, Q. Huang, R. M. Moore … and G.

C. Hurtt (2015). Future habitat loss and extinctions driven by land-use change in biodiversity hotspots under four scenarios of climate-change mitigation. Conservation Biology 29:1122-1131.

John, J. (2018, 21 March). Warblers in trouble due to South American deforestation. The Wildlife Society, Retrieved from http://wildlife.org/

Johnson, C. N., A. Balmford, B. W. Brook, J. C. Buettel, M. Galetti, L. Guangchun, J. M. Wilmshurst (2017). Biodiversity losses and conservation responses in the Anthropocene. Science 356:270-275.

Jones, H. P. and O. J. Schmitz (2009). Rapid recovery of damaged ecosystems. PloS one 4:e5653.

King, D. I. and S. Schlossberg (2014). Synthesis of the conservation value of the early-successional stage in forests of eastern North America. Forest Ecology and Management 324:186-195.

Kramer, G. R., D. E. Andersen, D. A. Buehler, P. B. Wood, S. M. Peterson, J. A. Lehman, ... and J. P. Loegering (2018). Population trends in *Vermivora* warblers are linked to strong migratory connectivity. Proceedings of the National Academy of Sciences 115:E3192-E3200.

Kramer, G. R., H. M. Streby, S. M. Peterson, J. A. Lehman, D. A. Buehler, P. B. Wood ... and D. E. Andersen (2017). Nonbreeding isolation and population-specific migration patterns among three populations of Golden-winged Warblers. The Condor 119:108-121.

Lehman, J. A. (2017). Survival and Habitat Selection of Golden-Winged Warblers (*Vermivora chrysoptera*) during Nesting and Post-fledging Periods at North

Cumberland Wildlife Management Area (unpublished masters thesis). University of Tennessee, Knoxville. Knoxville, Tennessee, USA.

Lerner, J., J. Mackey and F. Casey (2007). What's in Noah's wallet? Land conservation spending in the United States. AIBS Bulletin 57:419-423.

Lutter, S. H., A. A. Dayer, E. Heggenstaller and J. L. Larkin (2018). Effects of biological monitoring and results outreach on private landowner conservation management. PloS One 13:e0194740.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines (2006). Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Academic Press, Cambridge, Massachusetts, USA.

Marra, P. P., D. Hunter and A. M. Perrault (2011). Migratory connectivity and the conservation of migratory animals. Environmental Law 41:317-354.

Martin, T. E. and G. R. Geupel (1993). Nest-Monitoring Plots: Methods for Locating Nests and Monitoring Success. Journal of field Ornithology 64:507-519.

Martin, T. G., I. Chadès, P. Arcese, P. P. Marra, H. P. Possingham and D. R. Norris (2007). Optimal conservation of migratory species. PloS one 2:e751.

McCaskill, G. L., W. H. McWilliams, C. A. Alerich, B. J. Butler, S. J. Crocker, G. M. Domke … and J. A. Westfall (2009). Pennsylvania’s Forests 2009. U.S. Department of Agriculture, Forest Service, Northern Research Station. Newtown Square, Pennsylvania, USA.

McClure, C. J. and G. E. Hill (2012). Dynamic versus static occupancy: How stable are habitat associations through a breeding season?. Ecosphere 3:1-13.

McIntosh, E. J., S. Chapman, S. G. Kearney, B. Williams, G. Althor, J. P. Thorn, ... and R. Grenyer (2018). Absence of evidence for the conservation outcomes of systematic conservation planning around the globe: a systematic map. Environmental Evidence 7:22.

McNeil, D. J., C. R. V. Otto and G. J. Roloff (2014). Using audio lures to improve golden-winged warbler (*Vermivora chrysoptera*) detection during point-count surveys. Wildlife Society Bulletin 38:586-590.

McNeil, D. J., K. R. Aldinger, M. H. Bakermans, J. A. Lehman, A. C. Tisdale J. A. Jones ... and J. L. Larkin (2017). An evaluation and comparison of conservation guidelines for an at-risk migratory songbird. Global Ecology and Conservation 9:90-103.

McNeil, D. J., C. J. Fiss, E. Wood, J. Duchamp, M. H. Bakermans, and J. L. Larkin (2018). Using a natural reference system to evaluate songbird habitat restoration. Avian Conservation and Ecology 13:1

Menz, M. H., K. W. Dixon and R. J. Hobbs (2013). Hurdles and opportunities for landscape-scale restoration. Science 339:526-527.

Nichols, J. D., F. A. Johnson, and B. K. Williams (1995). Managing North American waterfowl in the face of uncertainty. Annual review of ecology and systematics 26:177-199.

Omernik, J. M. and G. E. Griffith. (2014). Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. Environmental Management 54:1249-1266.

Palmer, M. A., R. F. Ambrose, and N. L. Poff (1997). Ecological theory and community restoration ecology. Restoration Ecology 5:291-300.

Palmer, M. A., J. B. Zedler and D. A. Falk (2016). Foundations of restoration ecology. Island Press. Washington D. C., USA.

Paracuellos, M and J. L. Tellería (2004). Factors affecting the distribution of a waterbird community: the role of habitat configuration and bird abundance. Waterbirds 27:446-453.

Peterson, S. M. (2014). Landscape productivity and the ecology of brood division in Golden-winged Warblers in the Western Great Lakes Region (Unpublished Masters Thesis). University of Minnesota, Saint Paul, Minnesota, USA.

Peterson, S. M., H. M. Streby, G. R. Kramer, J. A. Lehman, D. A. Buehler, D. E. Andersen (2015). Geolocators on Golden-winged Warblers do not affect migratory ecology. The Condor 117:256-261.

Piqueray, J., L. Saad J. P. Bizoux, and G. Mahy (2013). Why some species cannot colonise restored habitats? The effects of seed and microsite availability. Journal for Nature Conservation 21:189-197.

Powell, L. A. (2007). Approximating variance of demographic parameters using the delta method: a reference for avian biologists. The Condor 109:949-954.

Probst, J. R., D. M. Donner, C. I. Bocetti and S. Sjogren (2003). Population increase in Kirtland's warbler and summer range expansion to Wisconsin and Michigan's Upper Peninsula, USA. Oryx 37:365-373.

Pulliam, H. R. (1988). Sources, sinks, and population regulation. The American Naturalist 132:652-661.

Purvis, A., K. E. Jones G. M. Mace (2000). Extinction. BioEssays, 22:1123-1133.

R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ralph, C. J., J. R. Sauer, and S. Droege. (1995). Monitoring bird populations by point counts. General Technical Report PSW-GTR-149. U.S. Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Roth, A.M., R.W. Rohrbaugh, T. Will, and D.A. Buehler, Eds. (2012). Golden-winged Warbler Status Review and Conservation Plan. www.gwwa.org/

Roth, A. M., D. J. Flaspohler, C. R. Webster (2014). Legacy tree retention in young aspen forest improves nesting habitat quality for Golden-winged Warbler (*Vermivora chrysoptera*). Forest Ecology and Management 321:61-70.

Sauer, J. R., D. K. Niven, J. E. Hines, D. J. Ziolkowski, Jr, K. L. Pardieck, J. E. Fallon, and W.A. Link. (2017). The North American Breeding Bird Survey, Results and Analysis 1966 - 2015. Version 2.07.2017 USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Scott, T. A., W. Wehtje and M. Wehtje (2001). The need for strategic planning in passive restoration of wildlife populations. Restoration Ecology 9:262-271.

Shultz, C. H. (1999). The Geology of Pennsylvania. Pennsylvania Geological Survey, Harrisburg, Pennsylvania, USA.

Skellam, J. G. (1951). Gene dispersion in heterogeneous populations. Heredity 5:433-435.

Stout, W. E., R. N. Rosenfield, W. G. Holton, and J. Bielefeldt (2007). Nesting biology of urban Cooper's Hawks in Milwaukee, Wisconsin. The Journal of

Wildlife Management 71:366-375.

Streby, H. M., and D. E. Andersen (2013). Testing common assumptions in studies of songbird nest success. Ibis 155:327-337.

Streby, H. M., G. R. Kramer, S. M. Peterson and D. E. Andersen. (2019). Correction: Evaluating outcomes of management targeting the recovery of a migratory songbird of conservation concern. PeerJ 6:e4319-correction.

Sudduth, E. B., B. A. Hassett, P. Cada and E. S. Bernhardt (2011). Testing the field of dreams hypothesis: functional responses to urbanization and restoration in stream ecosystems. Ecological Applications 21:1972-1988.

Suding, K. N. (2011). Toward an era of restoration in ecology: successes, failures, and opportunities ahead. Annual Review of Ecology, Evolution, and Systematics 42:465-487.

Tittler, R., M. A. Villard and L. Fahrig (2009). How far do songbirds disperse?. Ecography 32:1051-1061.

Török, P. and A. Helm (2017). Ecological theory provides strong support for habitat restoration. Biological Conservation 206:85-91.

U.S. Fish and Wildlife Service. 2017. Waterfowl population status, 2017. U.S. Department of the Interior, Washington, D.C. USA.

Van Horne, B. (1983). Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

White, G. C., and K. P. Burnham (1999). Program MARK: survival estimation from populations of marked animals. Bird study, 46(sup1), S120-S139.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips and E. Losos (1998). Quantifying threats to imperiled species in the United States. BioScience 48:607-615.

Williams, B. K., M. D. Koneff and D. A. Smith (1999). Evaluation of waterfowl conservation under the North American waterfowl management plan. The Journal of Wildlife Management 63:417-440.

Williams, G. E. and P. B. Wood (2002). Are traditional methods of determining nest predators and nest fates reliable? An experiment with Wood Thrushes (*Hylocichla mustelina*) using miniature video cameras. The Auk 119:1126-1132.

Wilsey, C. B., J. J. Lawler, D. Cimprich and N. H. Schumaker (2014). Dependence of the endangered black-capped vireo on sustained cowbird management. Conservation Biology 28:561-571.

Wilson, M. C., X. Y. Chen, R. T. Corlett, R. K. Didham, P. Ding, R. D. Holt ... and W. F. Laurance (2016). Habitat fragmentation and biodiversity conservation: key findings and future challenges. Landscape Ecology 31:219-227.

Wilson, A. D., D. W. Brauning, R. D. Mulvhill. (2012). Second Atlas of Breeding Birds in Pennsylvania. Pennsylvania State University Press. State College, Pennsylvania, USA.

Working Lands for Wildlife. (2016a). Healthy Forests for Golden-winged Warbler. FY 17-21 Conservation Strategy. 20pp. nrcs.usda.gov/wildlife.

Working Lands for Wildlife. (2016b). Sustainably Managing Forests Creates Golden-winged Warbler Breeding Habitat. Golden-winged Warbler. 4pp. nrcs.usda.gov/wildlife.

Tables and

Figures

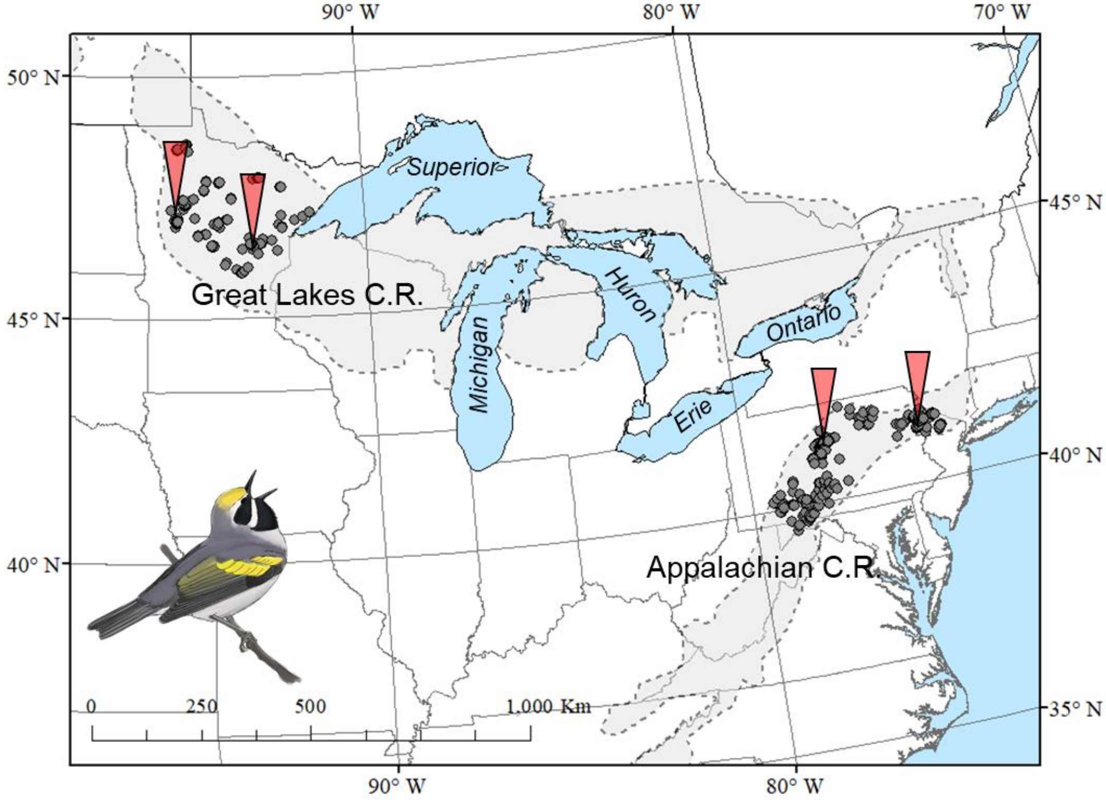

Figure 3.1. Point count locations (perennial; gray circles) where we monitored occupancy response of Golden-winged Warblers to habitat restoration efforts across the Great Lakes and Appalachian Conservation Regions (gray polygons with dashed boarders). Also noted (red arrows) are four Focal Landscapes where full-season productivity (FSP) estimates were made; West-to-East: Tamarac National Wildlife Refuge (NWR, Western Minnesota; Peterson et al. 2016), Rice Lake NWR (Eastern Minnesota; Peterson et al. 2016), Sproul State Forest (SF)/State Game Lands 100 (Central Pennsylvania; this study) and Delaware SF (Eastern Pennsylvania; this study).

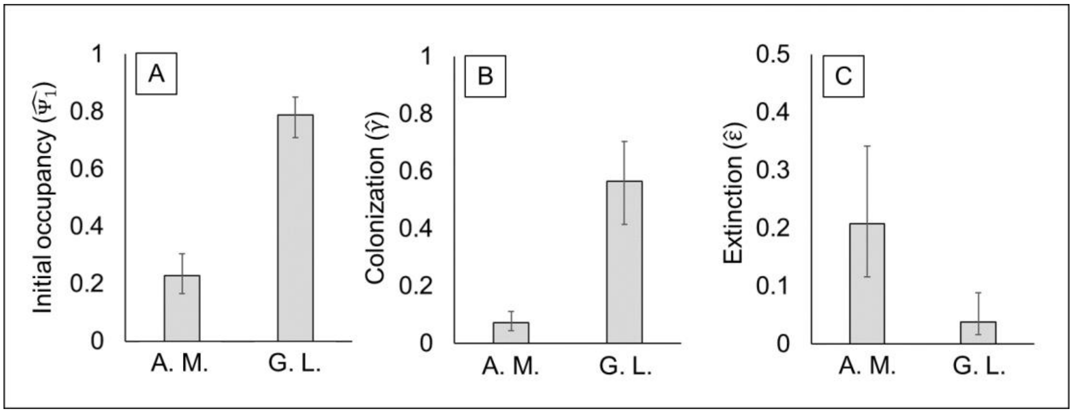

Figure 3.2. Parameter estimates (gray bars) associated with Golden-winged Warbler use of managed early-successional communities across both Conservation Regions delineated in the Golden-winged Warbler Conservation Plan: Appalachian Mountains (A.M.) and Great Lakes (G.L.). Shown are Region-specific differences in initial occupancy ($\widehat{\Psi_1}$; A), colonization ($\hat{\gamma}$; B), and local extinction ($\hat{\varepsilon}$; C). Error bars represent 95% confidence intervals.

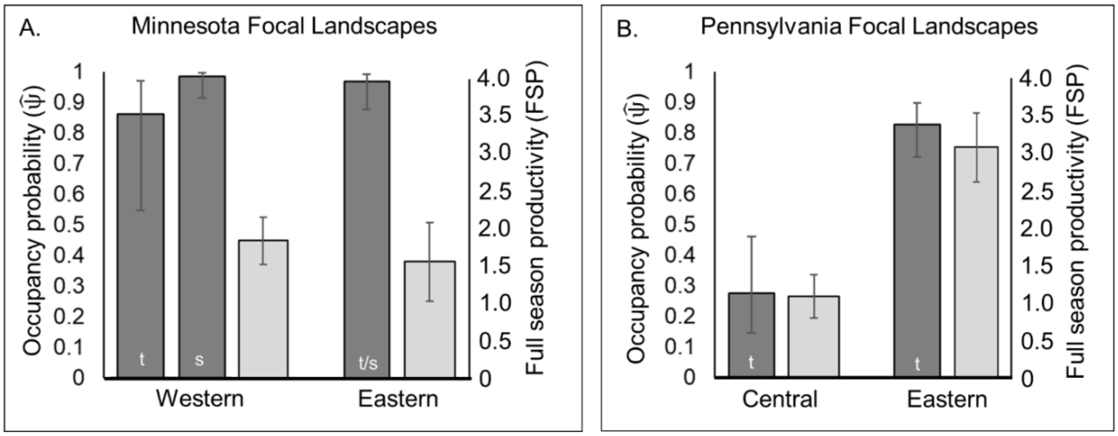

Figure 3.3. Occupancy (Ψ; dark gray bars, left vertical axis) of habitats managed for Golden-winged Warblers across Focal Landscapes (n=4) in Minnesota (A) and Pennsylvania (B). Focal Landscapes were chosen based on the availability of full season productivity data (FSP; light gray bars, right vertical axis). Habitats managed in Pennsylvania were solely timber harvests (t) whereas both timber harvests and shrub shearing (s) were monitored in the Great Lakes. Our best-supported model for Western Minnesota suggested timber harvests and shrub shearing sites hosted different rates of occupancy while this was not true for Eastern Minnesota. Error bars represent 95% confidence intervals.

CHAPTER 4

DYNAMIC BREEDING-SEASON HABITAT NEEDS OF EASTERN NORTH AMERICAN FOREST BIRDS

Abstract

The post-fledging period is a distinct stage in both annual and full life cycles of passerine birds with profound implications for conservation. Recent tracking studies indicate some forest birds drastically shift habitats between nesting- and post-fledging periods indicating diverse habitat needs over a breeding season, however, the extent to which forest birds shift habitats remains unclear. We reviewed the literature on habitat use/selection, survival and movements during the post-fledging period for forest birds in eastern North America using 32 published papers or graduate theses/dissertations on 25 forest bird populations. Our review included 11 species, but three quarters of the 1,626 fledglings studied were constituted by only three species: Wood Thrush (*Hylocichla mustelina*), Golden-winged Warbler (*Vermivora chrysoptera*), and Ovenbird (*Seiurus aurocapilla*). Collectively, this body of literature indicates that micro-habitat needs commonly shift between the nesting- and post-fledging periods. Most (83%) populations, for which micro-habitat selection was explicitly analyzed, indicated positive selection for dense understory vegetation structure. While all populations with sufficient data showed evidence of shifting microhabitat use, a shift in cover type or macrohabitat was detected for only 29% of populations. Many populations (56%) also included analyses of multi-scale habitat selection. Habitat selection patterns differed among species and even populations within a species, underscoring the need for regionally-specific studies. Our review highlights the consistent need for structural complexity within habitats and suggests that proximity to multiple cover types may be warranted for some species and populations. Although studies across a broader suite of species/nesting guilds will provide a more comprehensive picture of avian breeding habitat needs, our results provide the first empirical evidence that forest bird nesting habitat conditions are consistently distinct from post-fledging habitat conditions and thus require independent consideration.

Introduction

Quantifying reproductive output has been fundamental to understanding bird-habitat relationships, and measures of reproductive productivity are often used as proxies of habitat quality (Van Horne 1983). Although ecologists recognize the importance of all stages in the annual and life-cycles of birds, most common demographic metrics focus on the nesting period; examples include pairing success (Probst and Hayes 1987, Van Horn 1995), clutch or brood size (Lack 1954, Pettifor et al. 1988), nesting success (Mayfield 1975, Johnson 1979, 1980, Dhondt et al. 1992, Kilpi and Lindström 1997), and the number of young fledged per nest (Drury 1961, Ricklefs 1970, Balogh et al. 2011). While breeding productivity depends in large part on events during the nesting period, the scientific community now recognizes that productivity must be viewed through a broader lens that also includes post-nesting periods, especially the period between fledging and independence, hereafter the “post-fledging period” (Streby et al. 2011b, Vitz and Rodewald 2011, Jones et al. 2017).

As wildlife tracking technology has advanced in recent decades (Sykes et al.

1990, Bridge 2011) transmitters have become small enough to allow daily relocations of very small passerine fledglings (*e.g.*, < 10 g; Norris and Marra 2007, Faaborg et al. 2010). This has facilitated a proliferation of songbird post-fledging studies, with dozens of publications over the past two decades (Cox et al. 2014, Naef-Daenzer and Grüebler 2016). One of the key insights from early studies of the post-fledging period is that mortality of dependent fledglings can be extremely high – upwards of 60-70% in some cases (Cox et al. 2014) – which can limit population growth in some cases (Thomson et al. 1997, Robinson et al. 2004, Streby and Anderson 2011), particularly R-selected species (Stahl and Oli 2006). In this more comprehensive view of avian reproduction, 'breeding productivity' is considered to be the product of nest productivity (number of young fledged/nest) and fledgling survival (Cox et al. 2014, Peterson et al. 2016).

Given the importance of the post-fledging period to many songbird populations (Cox et al. 2014), conservationists must understand the habitat needs of fledglings (Faaborg et al. 2010). Post-fledging habitat selection is understood to be driven by the need to balance access to food (Vitz & Rodewald 2007, McDermott & Wood 2010) and cover (King et al. 2006, Vitz & Rodewald 2011), with movement constrained by the nest location (Streby et al. 2014). The consequences of habitat selection are not trivial, and fledgling survival often correlates strongly with habitat attributes, such as vegetation density (King et al. 2006, Vitz and Rodewald 2011, Ausprey and Rodewald 2011). To this end, productivity might be improved by manipulating habitat conditions associated with fledgling survival (Moore et al. 2010).

As studies investigating songbird post-fledging ecology become more common, the suite of species examined continues to expand, in kind. One guild that has become increasingly well-studied are those that breed in North America's eastern deciduous forests (hereafter, 'forest birds', *i.e.*, Anders et al. 1998, Moore et al. 2010, Jenkins et al. 2017). In response to population declines in many forest bird populations (Sauer et al. 2017), several state and federal agencies and their partners have initiated habitat management programs targeted at benefiting forest-dependent bird populations in the eastern United States (Ciuzio et al. 2013, McNeil et al. 2017). Indeed, thousands of hectares of breeding habitat have been restored using forest bird management prescriptions over the past decade through several forest bird conservation initiatives (*e.g.*, USDA-NRCS "Working Lands For Wildlife"; Ciuzio et al. 2013, WLFW 2016). With this in mind, conservation guidelines for forest birds rarely account for post-fledging habitat needs (Rosenberg et al. 2003, Roth et al. 2012, Wood et al. 2013), and failures to account for habitat needs across the entire breeding cycle may thwart conservation efforts aimed at stemming population declines (Faaborg et al. 2010, Rohrbaugh et al. 2016).

Meeting the needs of migratory passerines that depend on forest habitats for breeding requires an understanding of how the entire reproductive cycle (*i.e.*, nesting and post-fledging) fit together, yet a synthesis of post-fledging habitat associations of eastern forest birds has never been produced. These are critical knowledge gaps that likely hinder conservation efficacy in eastern forests. In this paper, we review nesting and post-fledging habitat requirements, habitat use, and juvenile survival rates for 11 species of eastern forest birds. Using a literature review, we examine forest-nesting species for which has post-fledging ecology been assessed to (1) identify the spatial scales at which birds alter habitat use and selection between nesting and post-fledging periods, and (2) determine the extent to which habitat use and/or selection affect survival.

Methods

Avian Breeding Cycle Terminology

Hatch-year (young) and after-hatch-year (adult) birds experience a series of important life stages after nesting, but these stages are described inconsistently in published literature. The period between the time a bird leaves its nest ("fledging") until nutritional independence from caring adults (Cox et al. 2014, though sometimes called the "natal period" (*e.g.*, Vega Rivera 1998), is defined here as the "post-fledging period" (Figure 4.1). Under this definition, dependent "fledglings" graduate to the level of independent "juveniles" at the cessation of parental care (Faaborg et al. 2010). We note that some authors define the post-fledging period as extending until Fall migration (*e.g.*, Cox et al. 2014) but we define this latter period (between independence and migration) as the 'post-breeding period' (Faaborg et al. 2010). The onset of nutritional independence marks the "post-breeding" period for hatch-year birds (now called "juveniles"), sometimes also called the "post-natal period" (*e.g.*, Vega Rivera 1998). Adults may also enter the post-breeding period after young are independent, with the exception of multi-brooded species which return to nesting stages. Our study focuses only on the post-fledging period, though we discuss aspects of the post-breeding period.

Literature Review

To quantify patterns of habitat use, selection, movements and survival among forest birds during the post-fledging period, we reviewed both published scientific articles and unpublished theses/dissertations on the topic of post-fledging ecology. We restricted our review to only forest-nesting passerines in eastern North America and only studies conducted using telemetry-based monitoring. We considered a species to be ‘forest-nesting’ if it was described as nesting within communities dominated by trees, including regenerating saplings (Rodewald 2015). We searched Google Scholar, Google, Birds of North America Online, and Web of Science databases for articles using all combinations of the following keywords: “North America”, “forest”, “fledgling”, “post-fledging”, “radio” “telemetry”, “habitat”, “use”, “selection”, “survival”, “movement”, “songbird”, and “passerine”. We also reviewed the references of each relevant publication for other articles using our keywords. Within each paper, we recorded the number of fledglings marked, number of fledglings survived, nesting habitat cover type, fledgling cover types, and whether studies quantified the following: fledgling micro-habitat use (yes/no) and nest micro-habitat conditions (yes/no). We considered micro-habitat to be local vegetation structure around each nest/fledgling as measured by researchers in the field (*e.g.*, vegetation density, canopy cover, etc.). We considered a cover type to be a broad habitat category as described/suggested within each paper (*e.g.*, mature forest, early-successional, etc.) and considered a cover type shift to be fledgling use of cover types other than those used by nesting adults in the study. Likewise, a micro-habitat shift was the use of micro-habitat conditions that differed from conditions measured at nest sites.

In addition to *habitat use*, we summarized whether *habitat selection* (use with respect to availability) and habitat effects on survival were quantified using at least one micro-habitat feature or macro-habitat feature within each bird population. Although our review is not focused on fledgling survival (see Cox et al. 2014), we briefly discuss major patterns here. Macro-habitat was a broad category that included both 'cover types' and other metrics measured beyond the scale of micro-habitat (*e.g.*, distance to nearest un-forested edge). For studies that quantified micro-habitat selection, we also noted the presence of selection (positive or negative) for 'understory vegetation structure', which was defined as any micro-habitat metric constituted by woody stems (*e.g.*, shrub cover, sapling density, etc.) or any metric characterizing the density of understory structure (*e.g.*, vegetation density). We considered effects to be significant if they were accompanied by rigorous statistical support as defined within each article.

Results

We identified 32 telemetry-based papers on North American forest birds during the post-fledging period, which collectively studied 25 populations of 11 species across 14 states or provinces (Figs. 4.2-4.3; Table 1). Among these 25 populations, 1,626 fledglings were marked with nearly three quarters (n = 1,180 fledglings; 73%) constituted by only three species: Wood Thrush, Golden-winged Warbler, and Ovenbird (Fig. 4.2). The least-studied species represented in our sample were Veery (n=29 total fledglings) and Cerulean Warbler (n=21 total fledglings). All species were monitored while nesting within closed-canopy forest, except Golden-winged Warblers which nested within regenerating forests and/or shrublands (Table 4.1). Differences in cover type between nests and fledglings were reported for 6 of 21 (29%) populations that allowed comparison for the following species: Golden-winged Warbler, Ovenbird, Worm-eating Warbler, and Wood Thrush. For populations that included comparisons of micro-habitat features between nest- and fledgling locations (n=13), 100% reported differences, usually suggesting denser understory vegetation structure near fledgling sites. Nest/fledgling micro-habitat differences were reported for Acadian Flycatcher, Cerulean Warbler, Golden-winged Warbler, Hooded Warbler, Northern Cardinal, Ovenbird, and Worm-eating Warbler (Table 4.1). The only species for which we found no evidence for a difference between nesting- and post-fledging habitat (at either cover type or micro-habitat) was the Veery.

Of the 25 eastern forest bird populations with published fledgling telemetry data, 14 populations (56%) had habitat selection patterns described for fledglings (Table 4.2). These included 12 populations (48%) that evaluated micro-habitat patterns and 10 populations (40%) that evaluated macro-habitat patterns. Additionally, 10 (83%) of the 12 populations that assessed micro-habitat selection suggested positive selection for greater understory vegetation structure and none suggested selection against this feature. Thirteen populations (52%) included assessments of daily movement rates and all reported daily increases as fledglings aged. Finally, we found habitat effects on survival for 18 populations (72%) including 11 populations (44%) that assessed micro-habitat impacts and 16 populations (64%) that assessed macro-habitat impacts on survival.

Discussion

Forest Bird Post-Fledging Habitat Shifts

Our literature review suggests that habitat use and/or selection commonly shifts between nesting and post-fledging periods in eastern forest birds, though these shifts occur more often at micro-habitat scales than at cover-type scales (Table 4.1). Indeed, distinct habitat shifts were reported by some of the earliest telemetry studies of fledglings on the Wood Thrush (Anders et al. 1997, Vega Rivera et al. 1998, 1999), however, habitat shifts were only apparent after independence from parental care (*i.e.*, post-breeding) and thus are not considered ‘post-fledging’ habitat shifts. Shortly thereafter, both passive netting studies (*e.g.*, Pagan et al. 2000) and single-species telemetry studies (*e.g.*, on the Ovenbird; King et al. 2006) revealed distinct habitat shifts at both micro-habitat and cover-type scales for dependent fledglings. Although many early telemetry studies that reported post-fledging habitat shifts focused on ground nesters from mature forests like Ovenbirds and Worm-eating Warblers (King et al. 2006, Vitz and Rodewald 2010, 2011), species nesting within early-successional communities are also demonstrated to shift habitats during post-fledging (*e.g.*, Golden-winged Warblers; Streby et al. 2016, Fiss 2018). To this end, habitat shifts after fledging seem to be the rule among forest bird species while static habitat associations appear uncommon (Tables 4.1, 4.2).

Post-fledging habitat shifts were ubiquitous at micro- scales, but cover type shifts were much less common (29% of populations). For example, fledgling Ovenbirds in New Hampshire remained within mature forest cover types, consistent with broad nesting habitat (King et al. 2006), but fledglings used micro-habitats with fewer large trees and denser vegetation structure than typical of nest sites (also see Vitz and Rodewald 2011). Further, the propensity to shift cover-types after fledging varied by populations *within a species* (*e.g.*, Golden-winged Warblers in the Great Lakes shifted cover types but those in Tennessee did not; Streby et al. 2016, Lehman 2017) whereas all populations shifted micro-habitats (Table 2). This suggests that, when post-fledging cover type shifts do occur, they may actually be driven by changing micro-habitat needs that occasionally facilitate shifts into different cover types depending on the landscape around the nesting site. Several have hypothesized that post-fledging habitat selection is driven, in part, by the need to avoid predators (McDermott and Wood 2010, Vitz and Rodewald 2010, 2011). Our finding that fledglings sometimes shifted cover types but always shifted micro-habitats after leaving the nest is consistent with a predator-avoidance hypothesis, especially given that sites used by fledglings were usually characterized by denser vegetation structure than at nest sites, regardless of cover type (Vitz and Rodewald 2010, Ausprey and Rodewald 2010, 2011, but see Moore et al. 2010).

Fledging Habitat Selection

Habitat selection is generally viewed as superior to *habitat use* because preference may serve as a proxy for habitat quality (Johnson 1980, Cody 1985, Garshelis 2000, Jones 2001). Indeed, over half (56%) of the post-fledging populations in our assessment included evidence for non-random habitat selection at one or more scales. Further, most such analyses (83%) indicated positive selection for metrics of understory vegetation structure (*e.g.*, stem densities, woody cover, etc.). For example, Cerulean Warbler fledglings selected locations with higher sapling cover than random locations, especially in the first few days post-fledging (Raybuck 2016). Although our review did not quantitatively assess all factors selected by fledglings across the 25 populations (*e.g.*, canopy cover, snag density, cover types), selection patterns often varied across species, populations, and spatial scales. For example, at macro-scales, Golden-winged Warbler fledglings in the Great Lakes selected for mature forest and sapling-dominated clear-cuts (Streby et al. 2016), whereas those in Pennsylvania selected for mature- and early-successional forest but not sapling-dominated stands (Fiss 2018). In other cases, patterns were congruent among populations as with Ovenbird selection of locations with less canopy in both New Hampshire (King et al. 2006) and Ohio (Vitz and Rodewald 2011). With this in mind, selection patterns within some populations differed as fledglings aged (*e.g.*, Raybuck 2016, Jenkins et al. 2017) or even among individuals (*e.g.*, Dellinger 2007). The complex interactions between population-specific habitat selection and multi-scale habitat composition therefore necessitate that fledgling habitat selection patterns be assessed on a population-by-population basis.

Fledgling Movement Dynamics

Dynamic habitat associations through time are, in part, necessarily explained by increased mobility as fledglings age (Raybuck 2016, Jenkins et al. 2017, Ladin et al. 2018). Basic movement data were presented for only about half of populations, which is consistent with the largely still-descriptive nature of this line of inquiry. Movement rates are expected to differ among habitats of different quality (Rosenzweig 1981, Charnov 1967), but few studies have explicitly compared movement rates among different habitats. Jenkins et al. (2017), as one exception, observed that Ovenbirds travelled at significantly slower rates when within densely-vegetated microhabitats where foraging opportunities and protection from predators was expected to be high (Vitz and Rodewald 2007, McDermott and Wood 2010, Streby and Anderson 2013a, b). Additionally, although mixed-species flocking is common among fledgling songbirds (Sullivan 1988, Vega Rivera et al. 1998, Chandler et al. 2016), the extent to which flocking affects fledgling movements remains almost entirely unknown.

Habitat and Survival

Despite the fact that habitat use/selection or movement provide insight into habitat needs and preferences, fledgling survival rates may be a more direct measure of habitat quality (Van Horne 1983, Faaborg et al. 2010, Cox et al. 2014), especially given that some bird populations are very sensitive to variation in fledgling survival (Thomson et al. 1997, Robinson et al. 2004). Understanding the factors that impact fledgling survival may therefor bear profound impact on our understanding of avian population demography, including source/sink dynamics (Balogh et al. 2011). Furthermore, quantifying factors associated with high fledgling survival is important for conservation of imperiled species for which ongoing conservation efforts include breeding habitat management (*e.g.*, Roth et al. 2012, Rohrbaugh et al. 2016). Another challenge is that few studies have compared fledgling survival rates among habitat management alternatives (including un-managed habitats; but see Moore et al. 2010, Eng et al. 2011). Although similar comparisons have been made using nest survival (*e.g.*, Confer et al. 2010, Boves et al. 2015, McNeil et al. 2017), assessments involving both nests and fledglings would allow more holistic assessments of relative habitat quality. Like habitat selection, factors that affect fledgling survival are also well-known to vary across regions and multi-region studies are thus needed (King et al. 2006, Vitz and Rodewald 2011, Streby et al. 2013b, Haché et al. 2014).

Conservation Implications

Our observation that habitat shifts between nesting- and post-nesting periods were common in forest birds appears to signify a conundrum for forest managers wishing to maintain habitat for a variety of species. That species like Wood Thrushes and Ovenbirds require multiple habitat types (nesting + post-nesting) necessitates greater consideration and more deliberate forest planning than would be the case for single-habitat species (Freemark and Merriam 1986). Though on the surface, this seems to substantially complicate landscape needs for a suite of forest birds, one straightforward solution is the creation and maintenance of diverse forests (Oliver and Larson 1996). Forest age class diversification, implemented through carefully-planned forestry, would facilitate the presence of a mosaic of old- and young age classes that provide nesting- post-fledging- and post-breeding habitat for the majority of species (Thompson 1993, Thompson et al. 1993). Although the extent to which dynamic forest management may benefit bird communities has not been well-tested, literature suggests that a diverse array of forest age classes best resembles the landscape within which eastern forest birds evolved (Yahner 2003). An important test of this idea would require assessing how management activities that increase diversity of microhabitat conditions and diversifies stand age classes across local landscapes impact breeding bird abundance and productivity across a suite of species.

Though our knowledge of post-fledging ecology of forest birds has improved by orders of magnitude in recent years, many fundamental questions remain unanswered. For example, many studies are regionally-focused and therefore difficult to apply outside the region within which data were collected. Birds studied within multiple regions of their breeding ranges have demonstrated marked differences in their post-fledging habitat needs (Streby et al. 2016, Lehman 2017, Fiss 2018). This highlights the importance of limiting inference of post-fledging research to the study area(s) wherein data were collected. Likewise, patterns may change annually (Schmidt et al. 2008) and studies should therefore collect data over multiple years to account for inter-annual variation in demographic rates. Most studies have been biased toward a relatively small handful of species (*e.g.*, Wood Thrush, Ovenbird, Worm-eating Warbler, Golden-winged Warbler), which seriously constrains conservation efforts. Studies on post-breeding ecology of adults are also sorely needed, as data on this portion of the avian lifecycle are largely restricted to anecdotal observations or passive mist-netting (Vega-Rivera et al. 1999, Vega-Rivera et al. 2003, Vitz and Rodewald 2007).

Acknowledgments

This project would not have been possible without funding through the U.S. Department of Agriculture (USDA) - Natural Resource Conservation Service (NRCS). We are also grateful for funding from the Cornell Lab of Ornithology – Athena Fund. We are also grateful to the doctoral committee of D.J.M.: A. Rodewald (chair), J.

Larkin, A. Dhondt, R. Stedman, and V. Ruiz-Gutierrez.

Works Cited

Akresh, M. E., K. Dinse, J. Foufopoulos, S. C. Schubel and T. Kowalczyk (2009). Passerine breeding and post-fledgling habitat use in riparian and upland temperate forests of the American Midwest. The Condor 111:756-762.

Aldinger, K. R., T. Terhune, P. B. Wood, D. A. Buehler, M. H. Bakermans, J. L. Confer, … and A. Roth (2015). Variables associated with nest survival of Golden-winged Warblers (*Vermivora chrysoptera*) among vegetation communities commonly used for nesting. Avian Conservation and Ecology 10:1.

Aldinger, K. R. (2018). Ecology and Management of Golden-Winged Warblers (*Vermivora chrysoptera*) and Associated Avian Species in the Allegheny Mountains of West Virginia (Unpublished doctoral dissertation). West Virginia University, Morgantown, West Virginia, USA.

Anders, A. D., D. C. Dearborn, J. Faaborg and F. R. T. Iii (1997). Juvenile survival in a population of Neotropical migrant birds. Conservation Biology 11:698-707.

Anders, A. D., J. Faaborg, and F. R. Thompson III (1998). Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. The Auk 115:349-358.

Balogh, A. L., T. B. Ryder and P. P. Marra (2011). Population demography of Gray Catbirds in the suburban matrix: sources, sinks and domestic cats. Journal of Ornithology 152:717-726.

Boves, T. J., A. D. Rodewald, P. B. Wood, D. A. Buehler, J. L. Larkin, T. B. Wigley, and P. D. Keyser (2015). Habitat quality from individual-and population-level perspectives and implications for management. Wildlife Society Bulletin 39:443-447.

Bridge, E. S., K. Thorup, M. S. Bowlin, P. B. Chilson, R. H. Diehl, R. W. Fléron, … and M. Wikelski (2011). Technology on the move: recent and forthcoming innovations for tracking migratory birds. BioScience 61:689-698.

Buehler, D. A., P. B. Hamel, and T. Boves (2013). Cerulean Warbler (*Setophaga cerulea*), version 2.0. In The Birds of North America (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA.

Burke, D. M. and E. Nol (1998). Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. The Auk 115:96-104.

Burke, A. D., F. R. Thompson III and J. Faaborg (2017). Variation in early-successional habitat use among independent juvenile forest breeding birds. The Wilson Journal of Ornithology 129:235-246.

Chandler, R. B., S. Tolfree, J. Gerwin, C. Smalling, L. Chavarría-Duriaux, G. Duriaux, and D. I. King. 2016. Conservation implications of Golden-winged Warbler social and foraging behaviors during the nonbreeding season. Pp. 175–192 in H. M. Streby, D. E. Andersen, and D. A. Buehler (Eds.). Golden-winged Warbler ecology, conservation, and habitat management. Studies in Avian Biology (no. 49), CRC Press, Boca Raton, Florida, USA.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. Theoretical Population Biology 9:129-136.

Chollet, S. and J. L. Martin (2013). Declining woodland birds in North America:

should we blame Bambi?. Diversity and Distributions 19:481-483.

Ciuzio, E., W. L. Hohman, B. Martin, M. D. Smith, S. Stephens, A. M. Strong, and T. Vercauteren (2013). Opportunities and challenges to implementing bird conservation on private lands. Wildlife Society Bulletin 37:267-277.

Clark, M. E., & Martin, T. E. (2007). Modeling tradeoffs in avian life history traits and consequences for population growth. Ecological Modelling, 209(2-4), 110-120.

Cody, M. L. (Ed.). (1985). Habitat selection in birds. Academic Press, Cambridge Massachusetts, USA.

Confer, J. L., K. W. Barnes and E. C. Alvey (2010). Golden-and Blue-winged warblers: Distribution, nesting success, and genetic differences in two habitats. The Wilson Journal of Ornithology 122:273-278.

Cox, W. A., F. R. Thompson III, A. S. Cox, and J. Faaborg (2014). Post-fledging survival in passerine birds and the value of post-fledging studies to conservation. The Journal of Wildlife Management 78:183-193.

Dellinger, T. A. (2007). Post-fledging ecology and survival of Neotropical migratory songbirds on a managed Appalachian forest (Unpublished Master's Thesis). West Virginia University, Morgantown, West Virginia, USA.

Dhondt, A. A., B. Kempenaers and F. Adriaensen (1992). Density-dependent clutch size caused by habitat heterogeneity. Journal of Animal Ecology 61:643-648.

Donovan, T. M., F. R. Thompson III, J. Faaborg and J. R. Probst (1995). Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology, 9:1380-1395.

Drury, W. H. (1961). Studies of the breeding biology of horned lark, water pipit, Lapland longspur, and snow bunting on Bylot Island, Northwest Territories, Canada. Bird-Banding 32:1-46.

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.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux ... and S. C. Latta (2010). Conserving migratory land birds in the New World: Do we know enough?. Ecological applications 20:398-418.

Fair, J., E. Paul, and J. Jones (2010). Guidelines to the Use of Wild Birds in Research. Ornithological Council. Washington, D.C., USA

Fiss, C. J. (2018). Multiscale Habitat Selection and Movement of Fledgling Golden-Winged Warblers (*Vermivora chrysoptera*) in Two Managed Mixed-Oak Forest Communities of Northern Pennsylvania (Unpublished Master's Thesis). Indiana University of Pennsylvania, Indiana, Pennsylvania, USA.

Foster, M. S. (1967). Molt cycles of the Orange-crowned Warbler. The Condor 69: 169-200.

Freemark, K. E. and H. G. Merriam (1986). Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biological Conservation 36:115-141.

Garshelis, D. L. (2000). Delusions in habitat evaluation: Measuring use, selection, and importance. In L. Boitani, and T. K. Fuller (Eds.). Research Techniques in Animal Ecology: Controversies and Consequences. Columbia University Press, New York, New York, USA.

Goguen, C. B. (2019). Survival, Movements, and Habitat Use of Fledgling Veeries (*Catharus fuscescens*) in Northeastern Pennsylvania. The American Midland Naturalist 181:18-29.

Guzy, M. J. and G. Ritchison (1999). Common Yellowthroat (*Geothlypis trichas*), version 2.0. In The Birds of North America. A. F. Poole and F. B. Gill (Eds.). Cornell Lab of Ornithology, Ithaca, New York, USA.

Haché, S., E. M. Bayne, and M. A. Villard (2014). Postharvest regeneration, sciurid abundance, and postfledging survival and movements in an Ovenbird population. The Condor 116:102-112.

Hunter, W. C., D. A. Buehler, R. A. Canterbury, J. L. Confer and P. B. Hamel (2001). Conservation of disturbance-dependent birds in eastern North America. Wildlife Society Bulletin 29:440-455 [Editor's note: Paul B. Hamel, Southern Research Station scientist, co-authored this publication.].

Humphrey, P. S. and K. C. Parkes (1959). An approach to the study of molts and plumages. The Auk 76:1-31.

Hoover, J. P. and M. C. Brittingham (1998). Nest-site selection and nesting success of Wood Thrushes. The Wilson Bulletin 110:375-383.

Holmes, R. T. and T. W. Sherry (2001). Thirty-year bird population trends in an unfragmented temperate deciduous forest: Importance of habitat change. The Auk 118:589-609.

Holway, D. A. (1991). Nest-site selection and the importance of nest concealment in the Black-throated Blue Warbler. The Condor 93:575-581.

Howell, S. N. G. (2010). Molt in North American Birds. Houghton Mifflin Harcourt, Boston, Massachusetts, USA.

Jackson, A. K., J. P. Froneberger and D. A. Cristol (2013). Habitat near nest boxes correlated with fate of eastern bluebird fledglings in an urban landscape. Urban Ecosystems 16:367-376.

Johnson, D. H. (1979). Estimating nest success: the Mayfield method and an alternative. The Auk 96:651-661.

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Jenkins, J. M., M. Hart, L. S. Eggert and J. Faaborg (2017). Sex-Specific Movements in Postfledging Juvenile Ovenbirds (*Seiurus aurocapilla*). The Wilson Journal of Ornithology 129:846-850.

Jones, T. M., M. P. Ward, T. J. Benson and J. D. Brawn (2017). Variation in nestling body condition and wing development predict cause-specific mortality in fledgling dickcissels. Journal of Avian Biology 48:439-447.

Jones, J. and R. J. Robertson (2001). Territory and nest-site selection of Cerulean Warblers in eastern Ontario. The Auk118:727-735.

Jones, J. (2001). Habitat Selection Studies in Avian Ecology: A Critical Review. The Auk 118:557-562.

Kilpi, M. and K. Lindström (1997). Habitat-specific clutch size and cost of incubation in common eiders, *Somateria mollissima*. Oecologia 111:297-301.

Kirby, J. S., A. J. Stattersfield, S. H. Butchart, M. I. Evans, R. F. Grimmett, V. R. Jones ... and I. Newton (2008). Key conservation issues for migratory land-and waterbird species on the world's major flyways. Bird Conservation

International 18:49-73.

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.

Lack, D. L. (1954). The natural regulation of animal numbers. The Clarendon Press; Oxford, UK.

Lack, D. L. (1966). Population Studies of Birds. The Clarendon Press; Oxford, UK.

Ladin, Z. S., S. Van Nieuland, S. A. Adalsteinsson, V. D’Amico, J. L. Bowman, J. J. Buler ... and W. G. Shriver (2018). Differential post-fledging habitat use of Nearctic-Neotropical migratory birds within an urbanized landscape. Movement ecology 6:17.

Lindenmayer, D. B., J. F. Franklin and J. Fischer (2006). General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological conservation 131:433-445.

Litvaitis, J. A., K. Titus, and E. M. Anderson. (1996). Measuring Vertebrate Use of Terrestrial Habitats and Foods. In T. A. Bookhout (Ed.). Research and Management Techniques for Wildlife and Habitats. The Wildlife Society. Bethesda, Maryland, USA.

Lloyd, P., T. E. Martin, R. L. Redmond, U. Langner, and M. M. Hart (2005). Linking demographic effects of habitat fragmentation across landscapes to continental source–sink dynamics. Ecological Applications 15:1504-1514.

MacArthur, R. H. (1958). Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599-619.

Marshall, M.R., J. A. DeCecco, A. B. Williams, G. A. Gale, and R. J. Cooper (2003). Use of regenerating clearcuts by late-successional bird species and their young during the post-fledging period. Forest Ecology and Management 183:127–135.

Martin, T. E. and G. R. Geupel (1993). Nest-Monitoring Plots: Methods for Locating Nests and Monitoring Success. Journal of field Ornithology 64:507-519.

Mayfield, H. F. (1960). The Kirtland's warbler (Vol. 40). Cranbrook Institute of Science, Bloomfield Hills, Michigan, USA.

Mayfield, H. F. (1961). Nesting success calculated from exposure. The Wilson Bulletin 73:255-261.

Mayfield, H. F. (1975). Suggestions for calculating nest success. The Wilson Bulletin 87:456-466.

Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney (2009). Habitat selection at multiple scales. Ecoscience 16:238-247.

McDermott, M. E. and P. B. Wood (2010). Influence of cover and food resource variation on post-breeding bird use of timber harvests with residual canopy trees. Wilson Journal of Ornithology 122:545-555.

McNeil, D. J., K. R. Aldinger, M. H. Bakermans, J. A. Lehman, A. C. Tisdale, J. A. Jones, ... and J. L. Larkin (2017). An evaluation and comparison of conservation guidelines for an at-risk migratory songbird. Global Ecology and Conservation 9:90-103.

Moore, L. C., B. J. Stutchbury, D. M. Burke, and K. A. Elliott (2010). Effects of forest management on postfledging survival of Rose-breasted Grosbeaks (*Pheucticus* *ludovicianus*). The Auk 127:185-194.

Morris, D. W. (1987). Ecological scale and habitat use. Ecology 68:362-369.

Morton, M. L. (1991). Post-fledging dispersal of Green-tailed Towhees to a subalpine meadow. The Condor 93:466–468.

Mumme, R. L. (2018). The trade-off between molt and parental care in Hooded Warblers: Simultaneous rectrix molt and uniparental desertion of late-season young. The Auk 135:427-438.

Naef-Daenzer, B. and M. U. Grüebler (2016). Post-fledging survival of altricial birds: ecological determinants and adaptation. Journal of Field Ornithology 87:227-250.

Newell, F. L. and A. D. Rodewald (2012). Management for oak regeneration: Short-term effects on the bird community and suitability of shelterwood harvests for canopy songbirds. The Journal of Wildlife Management 76:683-693.

Nice, M. M. (1957). Nesting success in altricial birds. The Auk 74:305-321.

Nolan Jr, V. (1978). The ecology and behavior of the prairie warbler, *Dendroica discolor*. Ornithological monographs; no. 26.

Nolan Jr, V., E. D. Ketterson, and C. A. Buerkle (2014). Prairie Warbler (*Setophaga discolor*), version 2.0. In The Birds of North America (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, New York, USA.

Norris, R. D. and P. P. Marra, (2007). Seasonal interactions, habitat quality, and population dynamics in migratory birds. The Condor 109:535-547.

Ogden, L. J. E., and B. J. Stutchbury (1996). Constraints on double brooding in a

Neotropical migrant, the Hooded Warbler. Condor 98:736-744.

Ogden, L. J. E. and B. J. Stutchbury (1997). Fledgling care and male parental effort in the Hooded Warbler (*Wilsonia citrina*). Canadian Journal of Zoology 75:576-581.

Oliver, C. D. and B. C. Larson (1996). Forest Stand Dynamics. John Wiley and sons, Hoboken, New Jersey, USA.

Pagen, R. W., F. R. Thompson III and D. E. Burhans (2000). Breeding and post-breeding habitat use by forest migrant songbirds in the Missouri Ozarks. The Condor 102:738-747.

Peterson, S. M., H. M. Streby, and D. E. Andersen. (2016). Spatially explicit models of full-season productivity and implications for landscape management of Golden-winged Warblers in the western Great Lakes region. Pp. 141–160 in H. M. Streby, D. E. Andersen, and D. A. Buehler (Eds.). Golden-winged Warbler ecology, conservation, and habitat management. Studies in Avian Biology (no. 49), CRC Press, Boca Raton, Florida, USA.

Pettifor, R. A., C. M. Perrins and R. H. McCleery (1988). Individual optimization of clutch size in great tits. Nature 336:160.

Porneluzi, P. A., R. Brito-Aguilar, R. L. Clawson and J. Faaborg (2014). Long-term dynamics of bird use of clearcuts in post-fledging period. The Wilson Journal of Ornithology 126:623-634.

Porneluzi, P., M. A. Van Horn, and T. M. Donovan (2011). Ovenbird (*Seiurus aurocapilla*), version 2.0. In The Birds of North America. A. F. Poole (Ed.). Cornell Lab of Ornithology, Ithaca, New York, USA.

Probst, J. R. and J. P. Hayes (1987). Pairing success of Kirtland's Warblers in marginal vs. suitable habitat. The Auk 104:234-241.

Pulliam, H. R. (1988). Sources, sinks, and population regulation. The American Naturalist 132:652-661.

Pyle, P. and S. N. Howell (1997). Identification guide to North American birds. Slate Creek Press. Bolinas, California, USA.

Rappole, J. H. and A. R. Tipton (1991). New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62:335-337.

Raybuck, D. W. (2016). Migration and the post-fledging period: Examining two critical stages of the Cerulean Warbler life cycle. (Unpublished Master's Thesis). Arkansas State University, Jonesboro, Arkansas, USA.

Ricklefs, R. E. (1970). The estimation of a time function of ecological use. Ecology 51:508-513.

Rimmer, C. C. (1988). Timing of the definitive prebasic molt in Yellow Warblers at James Bay, Ontario. Condor 90:141-156.

Robinson, R. A., R. E. Green, S. R. Baillie, W. J. Peach, and D. L. Thomson (2004). Demographic mechanisms of the population decline of the Song Thrush *Turdus philomelos* in Britian. Journal of Animal Ecology 73:670–682.

Robinson, S. K., F. R. Thompson, T. M. Donovan, D. R. Whitehead, and J. Faaborg (1995). Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987-1990.

Robinson, S. K. and W. D. Robinson (2001). Avian nesting success in a selectively harvested north temperate deciduous forest. Conservation Biology 15:1763-

1771.

Robbins, C. S., J. R. Sauer, R. S. Greenberg and S. Droege (1989). Population declines in North American birds that migrate to the Neotropics. Proceedings of the National Academy of Sciences 86:7658-7662.

Rodewald, P. (Editor). (2015). The Birds of North America: https://birdsna.org. Cornell Laboratory of Ornithology, Ithaca, New York, USA.

Rohrbaugh, R. W., D. A. Buehler, S. B. Swarthout, D. I. King, J. L. Larkin, K. V. Rosenberg, A. M. Roth, R. Vallender, and T. Will. (2016). Conservation perspectives: Review of new science and primary threats to Golden-winged Warblers. Pp. 207–215 in H. M. Streby, D. E. Andersen, and D. A. Buehler (Eds.). Golden-winged Warbler ecology, conservation, and habitat management. Studies in Avian Biology (no. 49), CRC Press, Boca Raton, Florida, USA.

Rosenberg, K. V., R. S. Hames, R. W. Rohrbaugh, Jr., S. Barker Swarthout, J. D. Lowe, and A. A. Dhondt. (2003). A Land Manager's Guide to Improving Habitat for Forest Thrushes. The Cornell Lab of Ornithology. Ithaca, New York, USA.

Rosenzweig, M. L. (1981). A theory of habitat selection. Ecology 62:327-335.

Ruhl, P. J., C. D. Delancey, and J. B. Dunning Jr. (2018). Roost preference, postfledging habitat use, and breeding phenology of adult female Worm-eating Warblers (*Helmitheros vermivorum*) on the breeding grounds. The Wilson Journal of Ornithology 130:397-409.

Rush, S. A. and B. J. Stutchbury (2008). Survival of fledgling Hooded Warblers

(*Wilsonia citrina*) in small and large forest fragments. The Auk 125:183-191.

Rushing, C. S., T. B. Ryder and P. P. Marra (2016). Quantifying drivers of population dynamics for a migratory bird throughout the annual cycle. Proceedings of the Royal Society B: Biological Sciences 283:20152846.

Sabo, S. R. and R. T. Holmes (1983). Foraging niches and the structure of forest bird communities in contrasting montane habitats. The Condor 85:121-138.

Sauer, J. R., D. K. Niven, J. E. Hines, D. J. Ziolkowski, Jr, K. L. Pardieck, J. E. Fallon and W. A. Link. (2017). The North American Breeding Bird Survey, Results and Analysis 1966 - 2015. Version 2.07.2017 USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Schlossberg, S., D. I. King, S. Destefano, and M. Hartley (2018). Effects of early-successional shrubland management on breeding wood thrush populations. The Journal of Wildlife Management 82:1572-1581.

Schmidt, K. A., S. A. Rush and R. S. Ostfeld (2008). Wood thrush nest success and post-fledging survival across a temporal pulse of small mammal abundance in an oak forest. Journal of Animal Ecology 77:830-837.

Stahl, J. T. and M. K. Oli (2006). Relative importance of avian life-history variables to population growth rate. Ecological modelling 198:23-39.

Streby, H. M., S. M. Peterson, and D. E. Andersen (2011). Invertebrate availability and vegetation characteristics explain use of non-nesting cover types by mature forest songbirds during the post-fledging period. Journal of Field Ornithology 82:406-414.

Streby, H. M. and D. E. Andersen (2011). Seasonal productivity in a population of migratory songbirds: why nest data are not enough. Ecosphere 2:1-15.

Streby, H. M. and D. E. Andersen (2013a). Survival of Fledgling Ovenbirds: Influences of Habitat Characteristics at Multiple Spatial Scales. The Condor 115:403-410.

Streby, H. M., and D. E. Andersen (2013b). Movements, cover-type selection, and survival of fledgling Ovenbirds in managed deciduous and mixed coniferous-deciduous forests. Forest Ecology and Management 287:9-16.

Streby, H. M., J. M. Refsnider, S. M. Peterson and D. E. Andersen (2014). Retirement investment theory explains patterns in songbird nest-site choice. Proceedings of the Royal Society of London B: Biological Sciences 281:20131834.

Streby, H. M., S. M. Peterson, and D. E. Andersen. (2016). Survival and habitat use of fledgling Golden-winged Warblers in the western Great Lakes region. Pp. 127–140 in H. M. Streby, D. E. Andersen, and D. A. Buehler (Eds.). Golden-winged Warbler Ecology, Conservation, and Habitat Management. Studies in Avian Biology (no. 49), CRC Press, Boca Raton, Florida, USA.

Sullivan, K. A. (1988) Ontogeny of Time Budgets in Yellow-eyed Juncos: Adaptation to Ecological Constraints. Ecology 69:118-124.

Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, ... and F. J. Swanson (2011). The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9:117-125.

Sykes, P. W., J. W. Carpenter, S. Holzman, and P. H. Geissler. (1990). Evaluation of three miniature radio transmitter attachment methods for small passerines.

Wildlife Society Bulletin 18:41-48.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager and F. Jeltsch (2004). Animal species diversity driven by habitat heterogeneity/ diversity: the importance of keystone structures. Journal of Biogeography 31:79-92.

Terhune II, T. M., K. R. Aldinger, D. A. Buehler, D. J. Flaspohler, J. L. Larkin, J. P. Loegering, K. L. Percy, A. M. Roth, C. Smalling, and P. B. Wood. (2016). Golden-winged Warbler nest-site habitat selection. Pp. 109–125 in H. M. Streby, D. E. Andersen, and D. A. Buehler (Eds.). Golden-winged Warbler Ecology, Conservation, and Habitat Management. Studies in Avian Biology (no. 49), CRC Press, Boca Raton, Florida, USA.

Thompson, F. R., J. R. Probst and M. G. Raphael (1993). Silvicultural options for Neotropical migratory birds. In: Finch, D. M. Stangel, P. W. (Eds.). Status and management of neotropical migratory birds: Estes Park, Colorado. Gen. Tech. Rep. RM-229. Fort Collins, Colorado: Rocky Mountain Forest and Range Experiment Station, US Dept. of Agriculture, Forest Service.

Thompson, F. R. (1993). Simulated responses of a forest-interior bird population to forest management options in central hardwood forests of the United States. Conservation Biology 7:325-333.

Thomson, D. L., S. R. Baillie and W. J. Peach (1997). The demography and age-specific annual survival of song thrushes during periods of population stability and decline. Journal of Animal Ecology 66:414-424.

Vitz, A. C. and A. D. Rodewald (2007). Vegetative and fruit resources as determinants of habitat use by mature-forest birds during the postbreeding period. The Auk 124:494-507.

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

Van Horne, B. (1983). Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Van Horn, M. A., R. M. Gentry and J. Faaborg (1995). Patterns of Ovenbird (*Seiurus aurocapillus*) pairing success in Missouri forest tracts. The Auk 112:98-106.

Vanderhoff, N. E., and P. K. Eason (2008). Influence of environmental variables on foraging by juvenile American Robins. Journal of Field Ornithology 79:186-192.

Vega Rivera, J. H., W. J. McShea, J. H. Rappole and C. A. Haas (1998a). Pattern and chronology of prebasic molt for the Wood Thrush and its relation to reproduction and migration departure. – Wilson Bull. 110: 384-392.

Vega Rivera, J. H., J. H. Rappole, W. J. McShea and C. A. Haas (1998b). Wood Thrush postfledging movements and habitat use in northern Virginia. Condor 100:69-78.

Vega Rivera, J. H., W. J. McShea, J. H. Rappole and C. A. Haas (1999). Postbreeding movements and habitat use of adult Wood Thrushes in northern Virginia. The Auk 116:458-466.

Vega Rivera, J. H., C. A. Haas, J. H. Rappole and W. J. McShea (2000). Parental care of fledgling Wood Thrushes. The Wilson Bulletin 112:233-237.

Vega Rivera, J. H., W. J. McShea and J. H. Rappole (2003). Comparison of breeding and postbreeding movements and habitat requirements for the Scarlet Tanager (*Piranga olivacea*) in Virginia. The Auk 120:632-644.

Weathers, W. W. and K. A. Sullivan (1989). Juvenile foraging proficiency, parental effort, and avian reproductive success. Ecological Monographs 59:223-246.

Weathers, W. W. and K. A. Sullivan (1991). Foraging efficiency of parent juncos and their young. Condor 93:346-353.

White, G. C. and R. A. Garrott (2012). Analysis of Wildlife Radio-tracking Data. Elsevier, Amsterdam, Netherlands.

White, J. D., T. Gardali, F. R.Thompson III, and J. Faaborg, (2005). Resource selection by juvenile Swainson's Thrushes during the postfledging period. The Condor 107:388-401.

Will, T. C. (1986). The behavioral ecology of species replacement: Blue-winged and Golden-winged warblers in Michigan (Unpublished Doctoral Dissertation). University of Michigan. Ann Arbor, Michigan, USA.

Wood, P.B., J. Sheehan, P. Keyser, D. Buehler, J. Larkin, A. Rodewald, S. Stoleson, T.B., Wigley, J. Mizel, T. Boves, G. George, M. Bakermans, T. Beachy, A. Evans, M. McDermott, F. Newell, K. Perkins, and M. White (2013). Management guidelines for enhancing Cerulean Warbler breeding habitat in Appalachian hardwood forests. American Bird Conservancy. The Plains, Virginia, USA.

Yahner, R. H. (2003). Responses of bird communities to early successional habitat in a managed landscape. The Wilson Journal of Ornithology 115:292-299.

Tables and Figures

Table 4.1. Eastern North American bird populations for which we found fledgling telemetry data. We found data on: Acadian Flycatcher (*Empidonax virescens*), Cerulean Warbler (*Setophaga cerulea*), Gray Catbird (*Dumetella carolinensis*), Golden-winged Warbler (*Vermivora chrysoptera*), Hooded Warbler (*S. citrina*), Northern Cardinal (*Cardinalis cardinalis*), Ovenbird (*Seiurus aurocapilla*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), Veery (*Catharus fuscescens*), Worm-eating Warbler (*Helmitheros vermivorum*), and Wood Thrush (*Hylocichla mustelina*). We include focal species (common name), broad study area, number of fledglings transmittered (n), broad nesting cover types, broad fledgling cover types, and citations for studies presenting data on each population.

#	Focal species	Study area	n	Nesting Cover Types	Fledgling Cover Types	Citations
1	Acadian Flycatcher	Missouri	45	Mature forest	Mature forest	Jenkins et al. 2016, Jenkins et al. 2017a, Jenkins et al. 2017b, Jenkins et al. 2017c
2	Acadian Flycatcher	Ohio	31	Mature forest fragments	Mature forest fragments	Ausprey 2010, Ausprey & Rodewald 2011
3	Cerulean Warbler	Pennsylvania	21	Mature forest	Mature forest	Raybuck 2016
4	Gray Catbird	Pennsylvania & Delaware	52	Mature forest fragments	*Unclear*	Ladin et al. 2018
5	Golden-winged Warbler	Minnesota & Manitoba	246	Shrub-dominated clear cuts, shrub-wetlands	Varied, including mature-, sapling-, early-successional forests	Streby et al. 2016, Peterson et al. 2016, Peterson 2016

Table 4.1, continued.

#	Focal species	Study area	n	Nesting Cover Types	Fledgling Cover Types	Citations
6	Golden-winged Warbler	Pennsylvania	127	Early-successional forest	Mature- and early-successional forest	Fiss 2018, McNeil 2019
7	Golden-winged Warbler	Tennessee	58	Reclaimed surface mines and early-successional forest	Reclaimed surface mines and early-successional forest	Lehman 2017
8	Hooded Warbler	Ontario	65	Mature Forest with selective logging	Mature Forest with selective logging	Eng et al. 2011
9	Hooded Warbler	Pennsylvania	52	Mature forest	Mature forest	Rush and Stutchbury 2008
10	Northern Cardinal	Ohio	45	Mature forest fragments	Mature forest fragments	Ausprey 2010, Ausprey & Rodewald 2011
11	Ovenbird	Minnesota	62	Mature forest (two types)	Varied, including mature, sapling, and early-successional forests.	Streby et al. 2013a, Streby et al. 2013b
12	Ovenbird	Missouri	62	Mature forest	Mature forest	Jenkins et al. 2016, Jenkins et al. 2017a, Jenkins et al. 2017b, Jenkins et al. 2017c

Table 4.1, continued.

#	Focal species	Study area	n	Nesting Cover Types	Fledgling Cover Types	Citations
13	Ovenbird	New Brunswick	55	Mature forest & mature forest with selective logging	Mature forest & mature forest with selective logging	Hache et al. 2014
14	Ovenbird	New Hampshire	41	Mature forest	Mature forest	King et al. 2006
15	Ovenbird	Ohio	52	Mature forest	Mature- and early-successional forest	Vitz and Rodewald 2010, Vitz and Rodewald2011, Vitz 2008
16	Rose-breasted Grosbeak	Ontario	42	Mature forest with selective logging	Mature forest with selective logging	Moore et al. 2010
18	Worm-eating Warbler	Ohio	60	Mature forest	Mature- and early-successional forest	Vitz and Rodewald 2010, Vitz and Rodewald2011, Vitz 2008
19	Worm-eating Warbler	Tennessee	4	Mature forest	Mature forest	Youngman 2017
20	Wood Thrush	Indiana	210	Multiple ages of forest	*Unclear*	Vernasco et al. 2018

Table 4.1, continued.

#	Focal species	Study area	n	Nesting Cover Types	Fledgling Cover Types	Citations
21	Wood Thrush	Missouri	49	Mature forest	Mature forest	Anders et al. 1997, Anders et al. 1998
22	Wood Thrush	New York	74	Mature forest	*Unclear*	Schmidt et al. 2008
23	Wood Thrush	Pennsylvania & Delaware	60	Mature forest fragments	*Unclear*	Ladin et al. 2018
24	Wood Thrush	Virginia	29	Mature forest	*Unclear*	Vega Rivera 1998
25	Wood Thrush	West Virginia	55	Mature forest	Mature- and early-successional forest	Dellinger 2007

Table 4.2. Eastern North American bird populations for which we found fledgling telemetry data. We found data on: Acadian Flycatcher (ACFL), Cerulean Warbler (CERW), Gray Catbird (GRCA), Golden-winged Warbler (GWWA), Hooded Warbler (HOWA), Northern Cardinal (NOCA), Ovenbird (OVEN), Rose-breasted Grosbeak (RBGR), Veery (VEER), Worm-eating Warbler (WEWA), and Wood Thrush (WOTH). Scientific names can be found in Table 4.1. For each population, we include focal population (species and study area), Whether populations included assessment of: micro-habitat selection, macro-habitat selection, micro-habitat impacts on survival, and macro-habitat impacts on survival (yes/no). Empty cells (marked with "-") indicate no data. Additionally, we noted whether populations exhibited selection for understory vegetation structure: 'pos' = positive association with increased structure, 'neg' = negative association with increased structure, and 'no' = no association with increased structure; asterisks imply non-significant patterns.

#	Focal Population	Micro-habitat selection?	Understory vegetation?	Macro-habitat selection?	Micro-habitat on survival?	Micro-habitat on survival?
1	ACFL, Missouri	no	-	no	yes	yes
2	ACFL, Ohio	yes	pos*	yes	yes	yes
3	CERW, Pennsylvania	yes	pos	yes	yes	yes
4	GRCA, Pennsylvania & Delaware	no	-	no	no	no
5	GWWA, Great Lakes	no	-	yes	no	yes
6	GWWA, Pennsylvania	yes	pos	yes	yes	yes
7	GWWA, Tennessee	yes	pos	yes	yes	yes

Table 4.2, continued.

#	Focal Population	Micro-habitat selection?	Understory vegetation?	Macro-habitat selection?	Micro-habitat on survival?	Micro-habitat on survival?
8	HOWA, Ontario	no	-	no	no	yes
9	HOWA, Pennsylvania	no	-	no	no	yes
10	NOCA, Ohio	yes	pos	yes	yes	yes
11	OVEN, Minnesota	yes	no	yes	yes	yes
12	OVEN, Missouri	no	-	no	yes	yes
13	OVEN, New Brunswick	no	-	no	no	no
14	OVEN, New Hampshire	yes	pos	yes	yes	yes
15	OVEN, Ohio	yes	pos	no	yes	no
16	RBGR, Ontario	no	-	yes	no	yes
17	VEER, Pennsylvania	yes	pos	no	no	no
18	WEWA, Ohio	yes	pos	no	yes	no

Table 4.2, continued.

#	Focal Population	Micro-habitat selection?	Understory vegetation?	Macro-habitat selection?	Micro-habitat on survival?	Micro-habitat on survival?
19	WEWA, Tennessee	yes	pos	no	no	no
20	WOTH, Indiana	no	-	no	no	yes
21	WOTH, Missouri	no	-	no	no	no
22	WOTH, New York	no	-	no	no	yes
23	WOTH, Pennsylvania + Delaware	no	-	no	no	no
24	WOTH, Virginia	no	-	no	no	no
25	WOTH, West Virginia	yes	pos	yes	no	yes

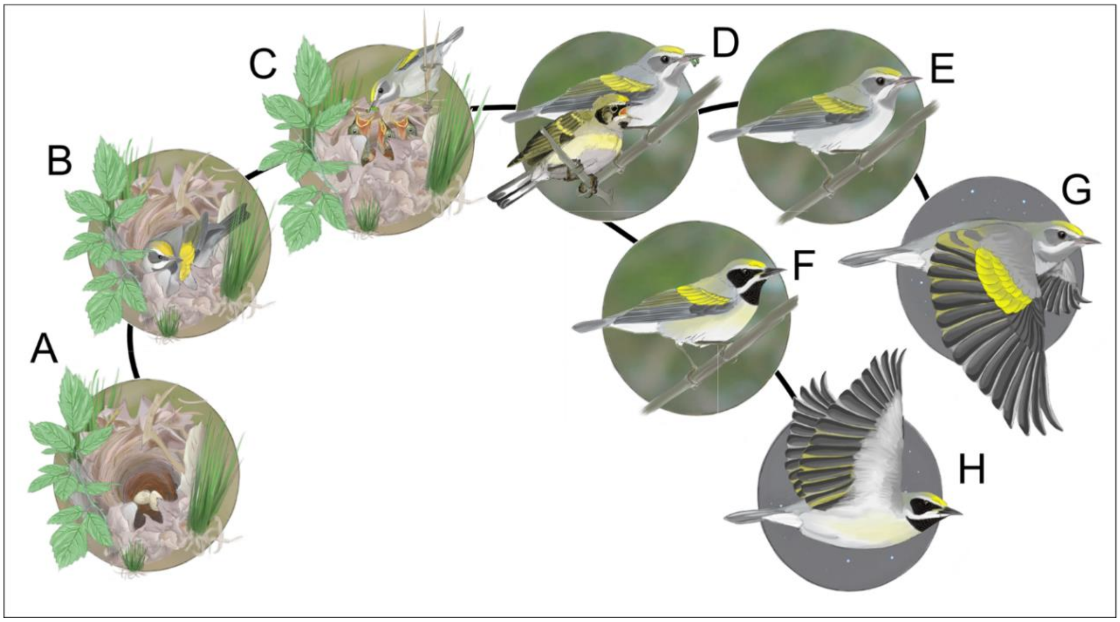

Figure 4.1. A schematic of the major stages in the breeding cycle of a typical forest passerine bird with circles depicting the relationships between adults and young: egg-laying (A), incubation (B), rearing nestlings (C), post-fledging (D), post-breeding adults (E) and juveniles (F), and migrating adults (G) and juveniles (H). Many past productivity studies have focused on the egg-laying, incubation, and nestling rearing stages (A-C) while stages beyond the post-fledging period (D-H) have only recently been examined in detail.

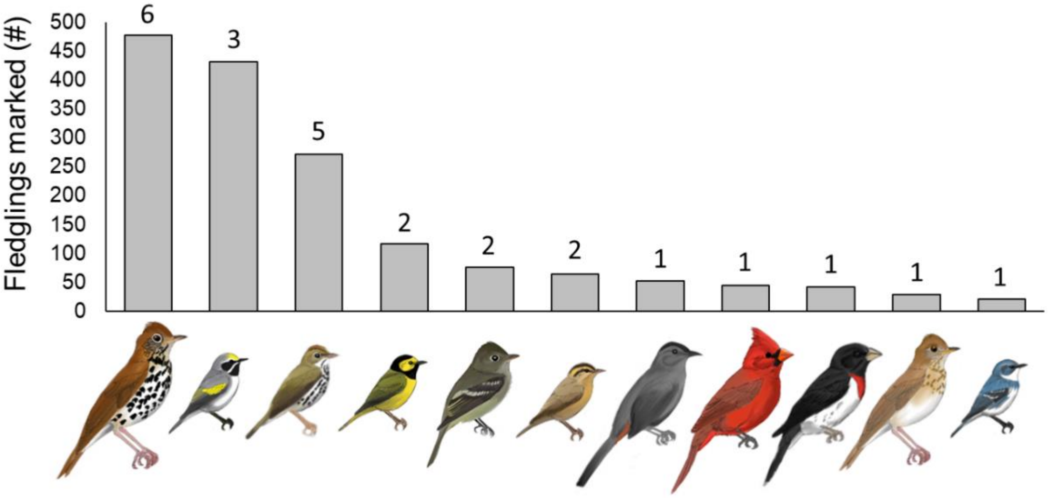

Figure 4.2. Number of fledglings marked by telemetry studies on eastern forest birds (gray bars) from left-to-right: Wood Thrush, Golden-winged Warbler, Ovenbird, Hooded Warbler, Acadian Flycatcher, Worm-eating Warbler, Gray Catbird, Northern Cardinal, Rose-breasted Grosbeak, Veery, and Cerulean Warbler. Scientific names are listed in Table 4.1. Values above bars indicate the number of populations studied.

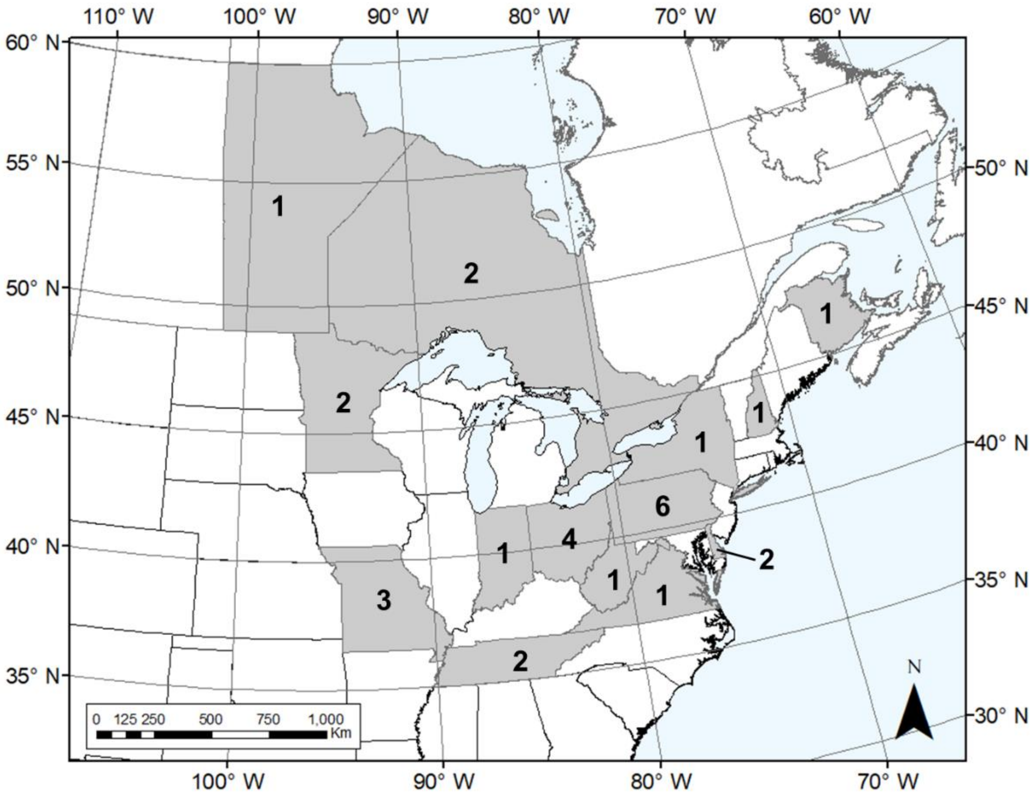

Figure 4.3. A map depicting locations where fledgling telemetry studies have been conducted on eastern North American forest birds. States/provinces where studies have been conducted are shaded and the number of forest bird populations within each is indicated numerically.

CHAPTER 5

DECOMPOSING HETEROGENEITY IN POPULATION DECLINES: LANDSCAPE-SPECIFIC VARIATION IN DRIVERS OF PRODUCTIVITY

Abstract

Population dynamics of many species are highly sensitive to variation in survival of immature individuals, yet few studies explicitly estimate survival across life stages. To better understand the demographic components of breeding productivity, we studied variation in nest and fledgling survival from 2014-17 in a migratory songbird, the Golden-winged Warbler (*Vermivora chrysoptera*), in habitats restored according to species-specific best management practices. We assessed potential effects of breeding phenology and habitat on nest- and fledgling survival and assessed the extent to which survival rates across key life stages (egg, nestling, and fledgling) differed between a high-productivity (Pocono Mountains) and a low-productivity landscape (Pennsylvania Wilds). Variation in nest survival was explained by breeding phenology rather than habitat structure, while both phenology and habitat impacted fledgling survival. Our results suggest that landscape-specific differences in productivity stemmed from marked disparities in survival of nestlings and young fledglings (< 10 days post-fledging; lowest in Pennsylvania Wilds), but not eggs or older fledglings (> 11 days post-fledging; similar in both landscapes). Additionally, these results demonstrate that variation in breeding phenology can create heterogeneity in local productivity via its asymmetric influence on demography across life stages. Our study

also illustrates how the lens through which we study breeding productivity can profoundly shape our conclusions regarding the relative contributions of different life stages to breeding performance. Low nestling- and fledgling survival in the Pennsylvania Wilds, coupled with high begging rates and low body mass, suggests food limitation as a potential driver of differences in productivity between our focal landscapes. Ultimately, our findings underscore the importance of meeting both nesting and post-fledging requirements for species of conservation concern.

Introduction

Although demography is traditionally viewed relative to four basic rates (*i.e.*, birth, death, immigration, and emigration; Pulliam 1988, Hanski and Gilpin1991), such a coarse view can obscure the variation that can occur within each, especially across different sexes, ages, and life stages (Silvertown et al. 1993, Heppell et al. 2000, Sæther and Bakke 2000, Clutton-Brock and Sheldon 2010). For example, adult survival can be modeled as a function of life-cycle stage (*e.g.*, Norris and Marra 2015), sex (Nichols et al. 2004), or other life history components (Menges 1992). Decomposing vital rates into distinct subcomponents and exploring how factors may differentially impact each is fundamental to both understanding population ecology and conserving species of concern (Greenberg and Marra 2005, Faaborg et al. 2010).

Survival during early life stages (*i.e.*, immatures) is among the most important drivers of population growth across many animal taxa (*e.g.*, insects [Radchuk et al. 2013], birds [Clark and Martin 2007], amphibians [Vonesh and De la Cruz 2002], mammals [Heppell et al. 2000], and others [Silvertown et al. 1993]). Survival rates of immatures may be described at even finer-scales, such as embryos, larvae, fledglings, independent juveniles, etc. (Meier et al. 2010, Radchuk et al. 2013). High sensitivity to variation in survival of immatures is particularly true for species with low adult survival and high-fecundity (*i.e.*, R-selected; Stahl and Oli 2006), though this has been poorly described for most species and populations (Bridge et al. 2011, Cox et al. 2014, Kays et al. 2015).

Birds, unlike many taxa, provide excellent opportunities to study a variety of demographic components because many species are easy to mark and follow (Newton 1998, Clutton-Brock and Sheldon 2010, Bridge et al. 2011). Components of nest productivity (*e.g.*, nest success, clutch size, etc.) have long been the primary tools used by ornithologists to measure productivity, (Mayfield 1975, Johnson 1979, Rotella et al. 2004). However, more recently, fledgling survival has been shown to be more important than nest productivity in driving some avian population trends (Thomson et al. 1997, Robinson et al. 2004). Further, nest and fledgling survival rates may be decoupled, emphasizing the need for independent consideration of all stages that comprise breeding productivity (Rush and Stutchbury 2008, Schmidt et al. 2008). While fledgling survival is a critical component of productivity and, ultimately, population recruitment, risks to fledglings remain relatively poorly studied in most species (Cox et al. 2014), largely due to prior logistical and technological limitations of tracking small fledglings (Sykes et al. 1990, Bridge et al. 2011). Fortunately, recent improvements to tracking technologies now allow quantification of demographic processes at finer-scales for even small animals (*e.g.*, <10 g; Cox et al. 2014, Kays et al. 2015).

To better understand the demographic components of productivity and the extent to which they vary among populations, we studied nest and fledgling survival in a migratory songbird, the Golden-winged Warbler (*Vermivora chrysoptera*) for which breeding productivity rates vary widely across the range (Peterson et al. 2016, Lehman 2017, Fiss 2018). Long-term population declines in the Golden-winged Warbler (Sauer et al. 2017) have prompted several large conservation efforts to restore breeding habitat for the species in hopes of stemming population losses (Ciuzio et al. 2013, McNeil et al. 2017). With this in mind, it remains largely unknown which factors drive various components of juvenile output in this species, especially within managed habitats created to help stabilize population declines (Bakermans et al. 2011, Roth et al. 2012). We investigated variation among key components of breeding productivity between two Golden-winged Warbler sub-populations – one with high and one with low breeding productivity. Specifically, we quantified 1) effects of breeding phenology and micro-habitat on nest survival, 2) influence of individual, phenological, micro-habitat, and stand-scale variables on fledgling survival, and 3) variation in survival rates across key life stages (egg, nestling, and fledgling).

Methods

Study Area

We focused our study within two of Pennsylvania's densest breeding populations of Golden-winged Warblers (Wilson et al. 2012): the Pocono Mountains (2014-15) and the Pennsylvania Wilds (2016-17). Although our landscapes were studied in different years, weather conditions sampled in each region were comparable (*i.e.*, one drought year and one non-drought year in each; Figure 5A). Within both landscapes, we sampled habitats treated using Golden-winged Warbler best management practices

(BMPs; Bakermans et al. 2011, Roth et al. 2012, Terhune et al. 2016). Specifically, habitats were deciduous overstory removal timber harvests (5-10 years post-harvest) leaving 2.2 – 8.9 m^2/ha of residual basal area (Roth et al. 2012). All habitats occurred at high-elevations (300 - 750 m.a.s.l.) and within heavily-forested landscapes (> 80 % forest cover).

Pocono Mountains

The Pocono Mountains lie within the Pocono Plateau of northeastern Pennsylvania and is characterized by moderate elevation (300-600 m.a.s.l.) rolling hills puncuated by abundant wetlands (White & Chance 1882, Cuff 1989, Shultz 1999). The Poconos landscape is dominated by mature forests of mixed coniferous-deciduous and deciduous composition, with northern hardwood and mixed-oak (*Quercus* spp.) communities most common (McCaskill et al. 2009). Golden-winged Warblers nest within two habitat types in the Poconos landscape: natural wetlands and managed early-successional forest (McNeil et al. 2018). Within the Poconos, we focused our survey efforts within Delaware State Forest, which includes 33,000 ha of publicly-owned forest in Pike, Monroe, Northampton, and Carbon Counties. Portions of Delaware State Forest are harvested on a rotational basis with the goal of diversifying forest age classes. We randomly selected six regenerating timber harvests ranging in size from 7 – 68 ha meeting the BMP criteria described above.

Pennsylvania Wilds

The Pennsylvania Wilds occur in North-Central Pennsylvania within the Ridge-and-Valley Province, which is characterized by high-elevation ridges (500-750 m.a.s.l.) separated by deep valleys. Like the Poconos, this landscape is dominated by mature forests with mixed- and deciduous (*e.g.*, Northern hardwood, mixed-oak) forest types most common (McCaskill et al. 2009). Unlike in the Poconos, wetlands are rare in the Pennsylvania Wilds (Cuff 1989, Fry et al. 2011) and Golden-winged Warblers are therefore restricted to upland habitats in this landscape (Fiss 2018). In the Pennsylvania Wilds landscape, we surveyed Sproul State Forest and Pennsylvania State Game Lands 100 (SGL 100), both of which are managed to diversify forest age classes for the benefit of forest- and wildlife health. Sproul State Forest and SGL 100 occur across a collective 194,000 ha of forest land in Centre and Clinton Counties. We randomly selected 11 timber harvests (18-262 ha in size) that met Golden-winged Warbler BMPs after removing from consideration those sites where Golden-winged Warblers were absent or at very low densities. Managed sites in the Pennsylvania Wilds ranged from 18 to 262 ha in size. Not only does geomorphology and land cover composition differ between the landscapes, but full-season productivity contrasts sharply as well: 3.07 juveniles/pair/year (95% CI: 2.62 – 3.53) in the Pocono Mountains versus 1.08 (95% CI: 0.80 – 1.37) in the Pennsylvania Wilds (DJM, unpublished data).

Nest Searching and Monitoring

Following methods of McNeil et al. (2017), we located nests using a combination of systematic sampling and opportunistic osbervation of adult behavior. Systematic sampling consisted of a trained field technician hiking through habitats physically searching through all vegetation within which nests could conceievably be placed (Confer et al. 2011). Opportunistic observations of adult behaviors involved following adults to their nests when cues were presented (*e.g.*, alarm calls, etc.). We monitored nests every 2-3 days, more frequently as fledging approached (Martin and Geupel 1993). Nest initiation began with ≥ 1 egg (*i.e.*, nests without eggs were not considered) and nests were considered ‘successful’ if at least one chick fledged (Streby and Anderson 2013)

Fledgling Telemetry

Nestling Golden-winged Warblers were randomly marked either (1) immediately prior to fledging (7 days old) or (2) on the day of fledging (9 days old). Similarly, 1-2 nestlings were randomly selected from each nest for measurement, banding (a USGS aluminum band and a single plastic color band), and transmitter attachment. Transmitters were attached using a figure-eight harness (Rappole and Tipton 1991) secured over the synsacrum using < 1 mm elastic cord (Streby and Anderson 2013). The combined mass of the transmitter, glue, and harness were 0.39 g: <5% of the mean mass of a fledgling (Fair et al. 2010). Processing for each fledgling was approximately 2-3 minutes. Radio transmitters used in our study (Blackburn Transmitters Inc., Nacogdoches, TX) had an expected battery life of ≥ 30 days. After transmitters were attached, each chick was returned to the initial capture location (*i.e.*, perch/nest). We tracked fledglings daily, until either mortality or transmitter failure, using the homing method, a Yagi H-type antenna and hand-held radio receiver. We recorded locations using a handheld GPS unit whereupon we conducted a vegetation survey. We also noted the extent of begging by each fledgling by estimating the percent of time spent vocalizing during our ~5-min observations.

Micro-habitat Quantification

At nest locations, we employed the nest vegetation sampling protocol recommended by the Golden-winged Warbler Working Group (see Aldinger et al. 2015). Although we do not detail the method here, briefly, we estimated percent cover of woody vegetation, *Rubus* spp., vines, forbs, grass, leaf litter, and bare ground within 1-m of the nest. Additionally we counted all 1-2 m tall shrubs, >2 m tall shrubs, and > 0.5 m tall saplings ≤ 5 m of the nest. We also visually estimated average sapling height (>0.5 m) and average shrub height (>1 m) within 11.3-m of the nest. Within a 11.3-m radius plot around each nest, we tallied and measured diameter-at-breast-height of all trees and snags and used an ocular tube (James and Shugart 1970) to measure the presence/absence of grass, forb and *Rubus* spp cover at 2.26-m intervals along four 11.3-m transects in each cardinal direction.

Within a 1-m radius of each fledgling location, we visually estimated percent cover of woody vegetation, *Rubus* spp., vines, forbs, grass, leaf litter, and bare ground. *Rubus* spp. and woody were combined into a ‘non-herbaceous’ class. Vines, forbs, and grass were combined into a ‘herbaceous’ class, whereas leaf litter and bare ground were combined into an ‘unvegetated’ class. We also measured ‘vertical vegetation cover’ at each fledgling location by reading a spherical densiometer in each cardinal direction centered at fledgling locations, held at 1-m in height (hereafter, ‘percent vertical vegetation cover’). We recorded ‘lateral vegetation density’ using a density board (Nudds 1977) read from a 5-m distance and 1-m from the ground (% squares > 50% covered; see Fiss 2019). Finally, we measured basal area at each fledgling location using a 10-factor basal area prism.

Forest Stand Quantification

To assess the influence of stand structure on fledgling survival, we used forest inventory data for Delaware State Forest, Sproul State Forest, and State Game Lands 100. Data included maps provided by regional foresters with the following categories: i) early-successional (< 20 yrs post-harvest), ii) sapling (> 50% stocked by trees < 15 cm diameter-at-breast-height; DBH), iii) thinned (< 50% stocked by trees > 15 cm in DBH), iv) mature (> 50% stocked by trees > 15 cm DBH), v) swamp (palustrine stands > 50% stocked by trees > 15 cm DBH), and vi) shrubland (palustrine or upland communities < 50% stocked by trees and dominated by shrubs). Using these forest inventory data, we analyzed 1) percent cover and 2) proximity (*e.g.*, minimum distance to-) for each fledgling/day with respect to each cover type. We calculated percent cover using *extract by mask* in ArcGIS 10.2 (ESRI 2011) within fledgling home ranges within 1-5 days of leaving the nest, which is when nearly all mortality occurs in the Poconos. Stand-scale habitat was described within 150-m-r buffers around each fledgling home range centroid (Vitz and Rodewald 2010). Because fledgling survival varied over the entire 30-day post-fledging period in the Pennsylvania Wilds, home ranges for fledglings in this landscape were based on either a 150 m radius buffer (using each bird's centroid location from days 1-30) or a minimum convex polygon around all observed locations, using whichever area was larger. Several covariates were too uncommon to allow parameter estimation and were discarded when this occured: percent sapling/thinned stand (too uncommon in both landscapes), distance to nearest early-successional stand (almost always 0, both landscapes), and 'percent swamp', 'distance to nearest swamp', and 'distanct to nearest sapling stand' covariates were only usable for our Poconos analyses (too uncommon in the Pennsylvania Wilds).

Nest Survival Analysis

We used an information theoretic approach (Burnham and Anderson 2002) to assess factors associated with nest survival. We specified logistic exposure models using the 'Nest Survival' interface in program MARK (ver.7.1, Colorado State University, Ft.Collins, Colorado, US; Rotella et al. 2004, Dinsmore and Dinsmore 2007). Models were compared with Akaike's Information Criterion adjusted for small sample size (AICc) with those within 2.0 ΔAICc considered to be equally supported (Burnham and Anderson 2002). The 'daily survival rate' (DSR) for each nest was estimated separately for each landscape for the following: 1) β_1(vegetation covariate), 2) β_1(Julian date) + β_2(vegetation covariate), and 3) β_1(Julian date) + β_2(Julian date^2) + β_3(vegetation covariate). Prior to analysis, we screened data for highly-correlated variables ($r \geq 0.7$; Sokal and Rohlf 1969). In addition to our nest DSR models, we predicted mean 'egg stage' survival and 'nestling stage' DSR for each landscape using intercept-only nest survival models for respective stages. A nest 'entered' the egg stage when it had ≥ 1 egg and was successful when ≥ 1 egg hatched. Likewise, nests entered the nestling stage when they contained ≥ 1 nestling and were successful when ≥ 1 nestling fledged.

Fledgling Survival Analysis

As with nests, we modeled the effects of vegetation covariates on fledgling DSR using an information theoretic approach implemented in Program MARK (Known Fate; White and Burnham 1999). We tested combinations of temporal patterns (*i.e.*, fledgling age) with 0-1 vegetation covariates using identical model selection criteria used in nest survival analyses, above. Specifically, we tested 1) β_1(vegetation covariate), 2) β_1(fledgling age) + β_2(vegetation covariate), and 3) β_1(fledgling age) + β_2(fledgling age^2) + β_3(vegetation covariate). We assessed a variety of patterns of fledgling age on survival because the first few days post-fledging are most dangerous in many species (Cox et al. 2014, Naef-Daenzer & Grüebler 2016), but the most appropriate pattern was unknown in our system. Prior to analyses, we noticed a distinct pattern of early fledgling mortality (days 0 – 11 post-fledging) and constant survival thereafter in the Poconos but not the Pennsylvania Wilds. We therefore modeled a quadratic relationship with age in the Pennsylvania Wilds and modeled an early quadratic (days 0 – 11 post-fledging) + constant survival thereafter (days 12 – 30) in the Poconos.

Incorporating the aformentioned temporal predictors, we tested all possible combinations of 0 – 1 ‘individual-level’ covariates on fledgling survival: fledge date, mass at banding, daily begging effort, daily movement distance, and year). We repeated this process for microhabitat covariates (*e.g.*, % cover variables, lateral/vertical vegetation density, etc.), and stand-scale covariates (*e.g.*, distance to nearest mature stand, percent shrubland, etc.). Finally, we used the set of covariates with the statistical support from each scale (individual-, microhabitat-, and stand-) to generate our final candidate model set by exploring all possible combinations of additive models using covariates from each . For example, if ‘fledge date’ and ‘percent herbaceous’ were important ‘individual’ and ‘‘microhabitat scale’ predictors, respectively, our final model set included all single-covariate models as well as models with ‘fledge date + herbaceous’. Percent early-successional forest was correlated with percent mature forest (R > 0.7) and was not analyzed.

Results

Nests

We monitored survival of 77 nests in the Pocono Mountains and 79 in the Pennsylvania Wilds. In 2017, an unusual, localized hail storm in the Pennsylvania Wilds resulted in complete failure of nests at one site (n = 11 nests; Fiss et al., 2019) so we censored those nests. Nests were initiated seven days earlier (Julian date 134) in the Poconos than in the Pennsylvania Wilds (141; Fig. 5B). Additionally, clutch sizes were larger in the Poconos (4.87 eggs; 95% CI: 4.72 – 5.02 vs 4.39 eggs; 95% CI: 4.21 – 4.58). Likewise, more fledglings were produced by successful nests in the Poconos (4.28; 95% CI: 3.91 – 4.65) than the Pennsylvania Wilds (3.17; 95% CI: 2.67 – 3.67).

Mean daily survival rates were higher for nests in the Poconos (DSR = 0.97, 95% CI: 0.96 – 0.98) than in the Pennsylvania Wilds (DSR = 0.95, 95% CI: 0.94 – 0.96). Further examination demonstrated that these differences stemmed from higher nestling survival in the Poconos (DSR: 0.96; 95% CI: 0.94 – 0.98) than in the Pennsylvania Wilds (DSR: 0.90; 95% CI: 0.84 – 0.93; Fig. 5.1), whereas egg survival rates were similar in both landscapes (Poconos DSR: 0.97; 95% CI: 0.96-0.98, Pennsylvania Wilds DSR: 0.96; 95% CI: 0.95 – 0.97). Nest survival declined as the season progressed in both landscapes (Table 1; Fig. 5.2). Although models with habitat covariates were top-ranked for both landscapes, models without habitat covariates were always competing and habitat 95% confidence intervals overlapped with zero, suggesting weak relationships with nest survival (Table 1).

Fledglings

Fledgling survival in the Poconos was initially low ($\theta = 0.84$, 95% CI: 0.74 – 0.91, n = 64 fledglings) but quickly approached 1.0 (~ day 5 post-fledging; Fig. 5.2). Fledglings in the Pennsylvania Wilds also experienced low initial survival ($\theta = 0.87$, 95% CI: 0.79 – 0.92, n = 63 fledglings), however, DSR only reached1.0 after 20 days post-fledging (Fig. 5.2). Survival varied with individual-, microhabitat, and stand-scale habitat factors (Table 2). Fledgling survival in the Poconos was a function of Julian date (+), un-vegetated cover (+), and distance to nearest swamp (-; Fig. 5.3). Fledgling survival in the Pennsylvania Wilds was a function of vertical vegetation density (+), and percent begging effort (-; Fig. 5.3).

Discussion

Here we illustrate how the lens through which biologists study breeding productivity can profoundly shape conclusions regarding the relative contributions of different life stages to breeding performance. For example, in our study, landscape-specific variation in phenology and demography among life stages drove differences in breeding productivity (Fig. 5.1). Though avian ecologists have long recognized the importance of stage-specific demography, most studies focus on a single life stage or fail to consider variation within a stage. Our work is among the first to explicitly identify sources of between-population variation in breeding productivity (*i.e.*, eggs, nestlings, and fledglings). Had we considered only nests, patterns of survival across a suite of habitat conditions would suggest that current management strategies are ideal for Golden-winged Warbler reproduction (Table 1; McNeil et al. 2017). In contrast, a fledgling-only view of productivity would suggest that current management strategies do not consistently support reproduction (Fig. 5.3). Simultaneous consideration of both components of productivity provides more nuanced insight into the habitat needs for species like the Golden-winged Warbler for which nest- and fledgling survival vary independently.

Despite comparable habitat conditions (within nesting habitat and adjacent post-fledging habitats; Fiss 2018) created using identical best management practices (Bakermans et al. 2011, Roth et al. 2012, Terhune et al. 2016), factors associated with fledgling survival differed between our two focal landscapes (Table 2). Survival of fledglings was related to both microhabitat and stand-scale factors versus microhabitat alone in the Pennsylvania Wilds. Though our results are generally consistent with the literature (King et al. 2006, Vitz and Rodewald 2007, 2011; Confer et al. 2010, McNeil et al. 2018), our findings of landscape-specific patterns underscore the importance of assessing survival across landscapes, even when a single habitat type/prescription is studied.

Although we did not directly measure prey availability, we suspect that food limitation may depress fledgling survival in the Pennsylvania Wilds, where birds were 10% lighter in the Pennsylvania Wilds, whether marked as nestlings (Pennsylvania Wilds: 7.64 g, 95% CI: 7.38 – 7.89; Poconos: 8.36 g, 95% CI: 8.22 – 8.50) or fledglings (Pennsylvania Wilds: 7.80, 95% CI: 7.62 – 7.99; Poconos: 9.02, 95% CI: 8.37 – 9.66). Interestingly, fledgling mass in the Poconos was comparable to that reported in the Great Lakes, where the population is relatively stable (8.6 g; Peterson et al. 2016). Moreover, fledglings begged for food twice as much in the Pennsylvania Wilds (mean [days 1-5]: 26%, 95% CI: 23 – 29%) compared to the Pocono Mountains (mean [days 1-5]: 13%, 95% CI: 11 – 16%). Begging, which reflects hunger (Hinde and Godfray 2011), is often considered a relatively risky behavior (Trivers 1985, Godfray and Johnstone 2000), perhaps even more so during the first few days post-fledging (Naef-Daenzer & Grüebler 2016, Peterson et al. 2016). Perhaps not surprisingly then, begging was negatively related to fledgling survival, though only in the Pennsylvania Wilds (Table 2; Fig. 5.3). Nevertheless, a food-limitation hypothesis is further supported by our finding that egg-stage nest DSR was equal between the landscapes while nestling-stage nest DSR was lower in the Pennsylvania Wilds (Fig. 5.1).

Temporal patterns of breeding phenology and survival differed widely between the two landscapes to yield sharply contrasting rates of juvenile output. One possible driver of lower nest survival in the Pennsylvania Wilds was a delay in nest initiation by 7 days (Fig. 5.2), especially when considering that nest survival declined over the breeding season in both landscapes (Hochachka 1990, Verhulst et al. 1995, Elmberg et al. 2009, Borgmann et al. 2013). Seasonal improvements in fledgling survival (Schmidt et al. 2008, Streby et al. 2014) compensated for declining nest success in the Poconos but not the Pennsylvania Wilds, where fledgling survival was seasonally constant (Fig. 5.3). Though the drivers of low late-season fledgling mortality in the Poconos remain unclear, possible explanations include predator swamping (Sundell et al. 2008) and increased prey availability (Yackel-Adams et al. 2006).

That nest survival within timber harvests varied independently of structural vegetation suggests that Golden-winged Warbler habitat BMPs may mitigate the effects of vegetation structure on nest survival (McNeil et al. 2017). Constant nest success among managed habitats is likely the result of species-specific habitat BMPs aimed at minimizing variation in nest survival rates (Roth et al. 2012, Terhune et al. 2016). In contrast, current BMPs for Golden-winged Warblers do not explicitly address the needs of fledglings, due to limited data at the time they were developed (Rohrbaugh et al. 2016, Streby et al. 2016). Our results suggest that both micro- and stand-scale habitat features should be considered when creating habitat for Golden-winged Warblers. With this in mind, conservation efforts for other species (*e.g.*, Cerulean Warbler, *Setophaga cerulea*; Wood Thrush, *Hylocichla mustelina*) should explicitly consider post-fledging habitat needs to maximize conservation efficacy (Rosenberg et al. 2003, Wood et al. 2013). Our study provides new insights into demographic contributors to songbird productivity, but research is still needed to understand how stage-specific survival varies with habitat and landscape attributes. In particular, additional research on factors influencing juvenile survival during the post-breeding period are needed, as this period remains a largely undescribed component of Golden-winged Warbler lifecycle (Marra et al. 2015, Rohrbaugh et al. 2016).

Acknowledgments

This project would not have been possible without funding through the Pennsylvania Game Commission and the U.S. Department of Agriculture (USDA) - Natural Resource Conservation Service (NRCS). We are grateful for the exceptional nest-searching and radio telemetry efforts of many our field technicians: R. Veasley, J. Smithmyer, A. Mengle, L. Boodoo, A. Marmo, B. Eddinger, C. Campbell-Shall, K. Rogers, F. Rodruigez, J. Geisel, T. Barbee, S. Toner, C. Sayers, and E. Moser. We also thank the Pennsylvania Bureau of Forestry and the Pennsylvania Game

Commission for access to Delaware State Forest, Sproul State Forest and State Game Lands 100. All warblers were handled and banded under USGS banding permit # 23277. This study was conducted in accordance with the guidelines of the Institutional Animal Care and Use Committees of both Cornell University (#2013-029) and Indiana University of Pennsylvania (#14-1314).

Works Cited

Aldinger, K. R., T. Terhune, P. B. Wood, D. A. Buehler, M. H. Bakermans, J. L. Confer, … and A. Roth (2015). Variables associated with nest survival of Golden-winged Warblers (*Vermivora chrysoptera*) among vegetation communities commonly used for nesting. Avian Conservation and Ecology 10:1.

Borgmann, K. L., C. J. Conway and M. L. Morrison (2013). Breeding phenology of birds: mechanisms underlying seasonal declines in the risk of nest predation. PLoS One 8:e65909.

Bridge, E. S., K. Thorup, M. S. Bowlin, P. B. Chilson, R. H. Diehl, R. W. Fléron, … and M. Wikelski (2011). Technology on the move: recent and forthcoming innovations for tracking migratory birds. BioScience 61:689-698.

Ciuzio, E., W. L. Hohman, B. Martin, M. D. Smith, S. Stephens, A. M. Strong, and T. Vercauteren (2013). Opportunities and challenges to implementing bird conservation on private lands. Wildlife Society Bulletin 37:267-277.

Clark, M. E. and T. E. Martin (2007). Modeling tradeoffs in avian life history traits and consequences for population growth. Ecological Modelling 209:110-120.

Clutton-Brock, T. and B. C. Sheldon (2010). Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends in Ecology and Evolution 25:562-573.

Confer, J. L., K. W. Barnes and E. C. Alvey (2010). Golden-and Blue-winged warblers: Distribution, nesting success, and genetic differences in two habitats.

The Wilson Journal of Ornithology 122:273-278.

Cox, W. A., F. R. Thompson, A. S. Cox and J. Faaborg (2014). Post-fledging survival in passerine birds and the value of post-fledging studies to conservation. Journal of Wildlife Management 78:183-193.

Cuff, D. J. (1989). The atlas of Pennsylvania. Temple University Press, Philadelphia, Pennsylvania, USA.

Dinsmore, S. J. and J. J. Dinsmore (2007). Modeling avian nest survival in program MARK. Studies in Avian Biology (34) 73.

Elmberg, J., Folkesson, K., Guillemain, M., & Gunnarsson, G. (2009). Putting density dependence in perspective: nest density, nesting phenology, and biome, all matter to survival of simulated mallard Anas platyrhynchos nests. Journal of Avian Biology 40:317-326.

Environmental Systems Research Institute (2011). ArcGIS Desktop: Release 10. Redlands, California, USA.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, ... and S. C. Latta (2010). Conserving migratory land birds in the New World: Do we know enough?. Ecological Applications 20:398-418.

Fair, J., E. Paul, and J. Jones, Eds. 2010. Guidelines to the Use of Wild Birds in Research. Ornithological Council. Washington, D.C., USA.

Fiss, C. J. (2018). Multiscale Habitat Selection and Movement of Fledgling Golden-Winged Warblers (*Vermivora chrysoptera*) in Two Managed Mixed-Oak Forest Communities of Northern Pennsylvania (Unpublished Master’s Thesis). Indiana University of Pennsylvania, Indiana, Pennsylvania, USA.

Fiss, C. J., D. J. McNeil, F. Rodruigez, A. D. Rodewald, and J. L. Larkin. (2019). Hail-induced Nest Failure and Adult Mortality in a Declining Ground-nesting Forest Songbird. The Wilson Journal of Ornithology 131:165-170.

Fry, J., G. Xian, S. Jin, J. Dewitz, C. Homer, L. Yang, C. Barnes, N. Herold, and J. Wickham (2011). Completion of the 2006 National Land Cover Database for the conterminous United States. Photogrammetric Engineering and Remove Sensing 77:858-864.

Godfray, H. C. J. and R. A. Johnstone (2000). Begging and bleating: the evolution of parent–offspring signalling. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 355:1581-1591.

Govindarajulu, P., R. Altwegg, and B. R. Anholt (2005). Matrix model investigation of invasive species control: bullfrogs on Vancouver Island. Ecological Applications 15:2161-2170.

Greenberg, R., and P. P. Marra (2005). Birds of two worlds: the ecology and evolution of migration. John Hopkins University Press, Baltimore Maryland, USA.

Hanski, I. and M. Gilpin (1991). Metapopulation dynamics: brief history and conceptual domain. Biological journal of the Linnean Society 42:3-16.

Heppell, S. S., H. Caswell L. B. Crowder (2000). Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology 81:654-665.

Hinde, C. A. and H. C. J. Godfray (2011). Quality, need, or hunger; begging the question. Behavioral Ecology 22:1147-1148.

Hochachka W. (1990) Seasonal Decline in Reproductive-Performance of Song

Sparrows. Ecology 71:1279–1288.

James, F. C. and H. H. Shugart Jr. (1970). A quantitative method of habitat description. Audubon Field Notes 24:727-736.

Johnson, D. H. (1979). Estimating nest success: the Mayfield method and an alternative. The Auk 96:651-661.

Kays, R., M. Crofoot, W. Jetz and M. Wikelski (2015). Terrestrial animal tracking as an eye on life and planet. Science 348:aaa2478.

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.

Knutson, C., M. Hayes and T. Phillips. (1998). How to Reduce Drought Risk. A guide prepared by the Preparedness and Mitigation Working Group of the Western Drought Coordination Council. National Drought Mitigation Center, Lincoln, Nebraska, USA.

Lehman, J. A. (2017). Survival and habitat selection of Golden-winged Warblers (*Vermivora chrysoptera*) during nesting and post-fledging periods at North Cumberland Wildlife Management Area, Tennessee (Unpublished Master's Thesis). University of Tennessee, Knoxville. Knoxville, Tennessee, USA.

Lorenz, D. J., J. A. Otkin, M. Svoboda, C. R. Hain, M. C. Anderson and Y. Zhong (2017). Predicting US Drought Monitor states using precipitation, soil moisture, and evapotranspiration anomalies. Part I: Development of a nondiscrete USDM index. Journal of Hydrometeorology 18:1943-1962.

Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter and C. M. Tonra. (2015). A call for full annual cycle research in animal ecology. Biology Letters 11:20150552.

Martin, T. E. and G. R. Geupel (1993). Nest-Monitoring Plots: Methods for Locating Nests and Monitoring Success. Journal of field Ornithology 64:507-519.

Mayfield, H. F. (1975). Suggestions for calculating nest success. The Wilson Bulletin 87:456-466.

McCaskill, G. L., W. H. McWilliams, C. A. Alerich, B. J. Butler, S. J. Crocker, G. M. Domke … and J. A. Westfall (2009). Pennsylvania's Forests 2009. U.S. Department of Agriculture, Forest Service, Northern Research Station. Newtown Square, Pennsylvania, USA.

McDermott, M. E. and P. B. Wood (2010). Influence of cover and food resource variation on post-breeding bird use of timber harvests with residual canopy trees. Wilson Journal of Ornithology 122:545-555.

McNeil, D. J., K. R. Aldinger, M. H. Bakermans, J. A. Lehman, A. C. Tisdale, J. A. Jones, ... and J. L. Larkin (2017). An evaluation and comparison of conservation guidelines for an at-risk migratory songbird. Global Ecology and Conservation 9:90-103.

McNeil, D. J., C. J. Fiss, E. Wood, J. Duchamp, M. H. Bakermans, and J. L. Larkin (2018). Using a natural reference system to evaluate songbird habitat restoration. Avian Conservation and Ecology 13:1

Meier, S., H. C. Morton, G. Nyhammer, B. E. Grøsvik, V. Makhotin, A. Geffen ... and A. Folkvord (2010). Development of Atlantic cod (*Gadus morhua*) exposed to produced water during early life stages: Effects on embryos, larvae, and juvenile fish. Marine Environmental Research 70:383-394.

Menges, E. S. (1992). Stochastic modeling of extinction in plant populations. Pp. 253-275 In Conservation Biology. Springer, Boston, Massachusetts, USA.

Millspaugh, J. J. and J. M. Marzluff (2001). Radio-tracking and animal populations: past trends and future needs. Pp. 383-393 In Radio Tracking and Animal Populations. J. J. Millspaugh and J. M. Marzluff (Eds.). Academic Press, Cambridge, Massachusetts, USA.

Naef-Daenzer, B. and M. U. Grüebler (2016). Post-fledging survival of altricial birds: Ecological determinants and adaptation. Journal of Field Ornithology 87:227-250.

Newton, I. (1998). Population limitation in birds. Academic Press, Cambridge, Massachusetts, USA.

Nichols, J. D., W. L. Kendall, J. E. Hines and J. A. Spendelow (2004). Estimation of sex-specific survival from capture–recapture data when sex is not always known. Ecology 85:3192-3201.

Norris, R. D. and P. P. Marra, (2015). Seasonal interactions, habitat quality, and population dynamics in migratory birds. The Condor 109:535-547.

Nudds, T. D. (1977). Quantifying the vegetative structure of wildlife cover. Wildlife Society Bulletin 5:113-117.

Peterson, S. M., H. M. Streby, and D. E. Andersen. (2016). Spatially explicit models of full-season productivity and implications for landscape management of Golden-winged Warblers in the western Great Lakes region. Pp. 141–160 in H. M. Streby, D. E. Andersen, and D. A. Buehler (Eds.). Golden-winged Warbler ecology, conservation, and habitat management. Studies in Avian Biology (no.

49), CRC Press, Boca Raton, Florida, USA.

Pulliam, H. R. (1988). Sources, sinks, and population regulation. The American Naturalist 132:652-661.

Radchuk, V., C. Turlure and N. Schtickzelle (2013). Each life stage matters: the importance of assessing the response to climate change over the complete life cycle in butterflies. Journal of Animal Ecology 82:275-285.

Rappole, J. H. and A. R. Tipton (1991). New harness design for attachment of radio transmitters to small passerines. Journal of field Ornithology 62:335-337.

Rohrbaugh, R. W., D. A. Buehler, S. B. Swarthout, D. I. King, J. L. Larkin, K. V. Rosenberg, A. M. Roth, R. Vallender, and T. Will. (2016). Conservation perspectives: Review of new science and primary threats to Golden-winged Warblers. Pp. 207–215 in H. M. Streby, D. E. Andersen, and D. A. Buehler (Eds.). Golden-winged Warbler ecology, conservation, and habitat management. Studies in Avian Biology (no. 49), CRC Press, Boca Raton, Florida, USA.

Robinson, R. A., R. E. Green, S. R. Baillie, W. J. Peach, and D. L. Thomson. (2004). Demographic mechanisms of the population decline of the Song Thrush *Turdus philomelos* in Britian. Journal of Animal Ecology 73:670–682.

Rosenberg, K. V., R. S. Hames, R. W. Rohrbaugh, Jr., S. Barker Swarthout, J. D. Lowe, and A. A. Dhondt. (2003). A Land Manager’s Guide to Improving Habitat for Forest Thrushes. The Cornell Lab of Ornithology. Ithaca, New York, USA.

Rotella, J. J., S. J. Dinsmore and T. L. Shaffer (2004). Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. Animal biodiversity and Conservation 27:187-205.

Roth, A. M., R. W. Rohrbaugh, T. Will, and D. A. Buehler, editors. (2012). Golden-winged Warbler Status Review and Conservation Plan. www.gwwa.org/

Rush, S. A. and B. J. Stutchbury (2008). Survival of Fledgling Hooded Warblers (*Wilsonia Citrina*) in Small and Large Forest Fragments. The Auk 125:183-191.

Sæther, B. E. and Ø. Bakke (2000). Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642-653.

Sauer, J. R., D. K. Niven, J. E. Hines, D. J. Ziolkowski, Jr, K. L. Pardieck, J. E. Fallon, and W. A. Link. (2017). The North American Breeding Bird Survey, Results and Analysis 1966 - 2015. Version 2.07.2017 USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Schmidt, K. A., S. A. Rush and R. S. Ostfeld (2008). Wood thrush nest success and post-fledging survival across a temporal pulse of small mammal abundance in an oak forest. Journal of Animal Ecology 77:830-837.

Shultz, C. H. (1999). The Geology of Pennsylvania. Pennsylvania Geological Survey, Harrisburg, Pennsylvania, USA.

Silvertown, J., M. Franco, I. Pisanty and A. Mendoza (1993). Comparative plant demography--relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. Journal of Ecology 81:465-476.

Sokal, R. R., and F. J. Rohlf. (1969). The principles and practice of statistics in biological research. W.H. Freeman and Company, San Francisco, California, USA.

Stahl, J. T., & Oli, M. K. (2006). Relative importance of avian life-history variables to population growth rate. Ecological modelling, 198(1-2), 23-39.

Streby, H. M., & Andersen, D. E. (2013). Testing common assumptions in studies of songbird nest success. Ibis, 155(2), 327-337.

Streby, H. M., J. M. Refsnider, S. M. Peterson and D. E. Andersen. (2014). Retirement investment theory explains patterns in songbird nest-site choice. Proceedings of the Royal Society B: Biological Sciences 281:20131834.

Streby, H. M., S. M. Peterson, and D. E. Andersen. 2016. Survival and habitat use of fledgling Golden-winged Warblers in the western Great Lakes region. Pp. 127–140 in H. M. Streby, D. E. Andersen, and D. A. Buehler (Eds.). Golden-winged Warbler ecology, conservation, and habitat management. Studies in Avian Biology (no. 49), CRC Press, Boca Raton, Florida, USA.

Sundell, J., J. A. Eccard, R. Tiilikainen, and H. Ylönen (2003). Predation rate, prey preference and predator switching: experiments on voles and weasels. Oikos 101:615–623.

Sykes, P. W., J. W. Carpenter, S. Holzman, and P. H. Geissler. (1990). Evaluation of three miniature radio transmitter attachment methods for small passerines. Wildlife Society Bulletin 18:41-48.

Terhune II, T. M., K. R. Aldinger, D. A. Buehler, D. J. Flaspohler, J. L. Larkin, J. P. Loegering, K. L. Percy, A. M. Roth, C. Smalling, and P. B. Wood. (2016). Golden-winged Warbler nest-site habitat selection. Pp. 109–125 in H. M. Streby, D. E. Andersen, and D. A. Buehler (Eds.). Golden-winged Warbler

Ecology, Conservation, and Habitat Management. Studies in Avian Biology (no. 49), CRC Press, Boca Raton, Florida, USA.

Thomson, D. L., S. R. Baillie and W. J. Peach (1997). The demography and age-specific annual survival of song thrushes during periods of population stability and decline. Journal of Animal Ecology 66:414-424.

Trivers, R. L. (1985). Social Evolution. Benjamin Cummings Publishing Company. Menlo Park, California, USA.

Vega Rivera, J. H., W. J. McShea, J. H. Rappole and C. A. Haas (1999). Postbreeding movements and habitat use of adult Wood Thrushes in northern Virginia. The Auk 116:458-466.

Verhulst S., J. H. Vanbalen and J. M. Tinbergen (1995) Seasonal Decline in Reproductive Success of the Great Tit - Variation in Time or Quality. Ecology 76:2392–2403.

Vitz, A. C. and A. D. Rodewald (2007). Vegetative and fruit resources as determinants of habitat use by mature-forest birds during the postbreeding period. The Auk 124:494-507.

Vitz, A. C. and A. D. Rodewald (2010). Movements of fledgling Ovenbirds (*Seiurus aurocapilla*) and Worm-eating Warblers (*Helmitheros vermivorum*) within and beyond the natal home range. The Auk 127:364-371.

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.

Vonesh, J. R. and O. De la Cruz (2002). Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. Oecologia, 133:325-333.

White, G. C. and K. P. Burnham (1999). Program MARK: survival estimation from populations of marked animals. Bird Study 46:120-139.

White, I. C., and Chance, H. M. (1882). The geology of Pike and Monroe counties. Published by the Board of Commissioners for the Second Geological Survey.

Wilson, A. D., D. W. Brauning, R. D. Mulvhill. (2012). Second Atlas of Breeding Birds in Pennsylvania. Pennsylvania State University Press. State College, Pennsylvania, USA.

Wood, P.B., J. Sheehan, P. Keyser, D. Buehler, J. Larkin, A. Rodewald, S. Stoleson, T.B., Wigley, J. Mizel, T. Boves, G. George, M. Bakermans, T. Beachy, A. Evans, M. McDermott, F. Newell, K. Perkins, and M. White (2013). Management guidelines for enhancing Cerulean Warbler breeding habitat in Appalachian hardwood forests. American Bird Conservancy. The Plains, Virginia, USA.

Yackel Adams, A. A., S. K. Skagen and J. A. Savidge (2006). Modeling post-fledging survival of lark buntings in response to ecological and biological factors. Ecology 87:178-188.

Tables and Figures

Table 5.1. Models explaining survival of Golden-winged Warbler (Vermivora chrysoptera) fledglings in the Pocono Mountains (top) and Pennsylvania Wilds (bottom). We report number of model parameters (k), ΔAICc, AICc weight (w) model likelihood (mod lik), and deviance (dev). The 'date' and 'date2' component of the model are shorthand for 'β0 + β1(date)' and 'β0 + β1(date) + β2(date2)', respectively. The top ten models are shown for each candidate set.

Pocono Mountains					
model	k	ΔAICc	w	mod lik	dev
date + % woody (1 m^2)	3	0.00	0.06	1.00	180.26
date + % *Rubus* spp. (1 m^2)	3	0.08	0.05	0.96	180.34
date + sapling density (5 m radius)	3	0.17	0.05	0.92	180.44
date	2	0.39	0.05	0.82	182.66
date + % leaf litter (1 m^2)	3	0.73	0.04	0.69	181.00
date + basal area	3	0.97	0.03	0.62	181.23
date + >2 m shrub density (5 m radius)	3	1.19	0.03	0.55	181.45
date + sapling height (11.3 m radius)	3	1.31	0.03	0.52	181.57
date + # snags (11.3 m radius)	3	1.38	0.03	0.50	181.64
date^2 + % *Rubus* spp. (1 m^2)	4	1.62	0.03	0.45	179.86
Pennsylvania Wilds					
date + % forbs (11.3 m radius)	3	0.00	0.09	1.00	222.72
date	2	0.73	0.06	0.69	225.46
date + basal area	3	0.9	0.05	0.64	223.62
date + % *Rubus* spp. (1 m^2)	3	0.99	0.05	0.61	223.71
date + % bare ground (1 m^2)	3	1.30	0.04	0.52	224.02
date + % vines (1 m^2)	3	1.79	0.03	0.41	224.51
date + % forbs (1 m^2)	3	1.82	0.03	0.40	224.53
date^2 + % forbs (11.3 m radius)	4	1.86	0.03	0.39	222.56
date + % *Rubus* spp. (11.3 m radius)	3	2.13	0.03	0.34	224.85
date + shrub height (11.3 m radius)	3	2.15	0.03	0.34	224.86

Table 5.2. Models explaining survival of Golden-winged Warbler (*Vermivora chrysoptera*) fledglings in the Pocono Mountains (top) and Pennsylvania Wilds (bottom). We report number of model parameters (k), ΔAICc, AICc weight (*w*) model likelihood (mod lik), and deviance (dev). The 'age^2' component of the model is shorthand for '$\beta_0 + \beta_1(\text{age}_{1\text{-}11}) + \beta_2(\text{age}^2_{1\text{-}11}) + \beta_3(\text{constant}_{12\text{-}30})$' in the Pocono Mountains and '$\beta_0 + \beta_1(\text{age}) + \beta_2(\text{age}^2)$' in the Pennsylvania Wilds. Likewise, the 'age' component represents '$\beta_0 + \beta_1(\text{age})$' (Pennsylvania Wilds only). 'Distance-to-nearest…' is abbreviated as 'DTN'. The top ten models are shown for each candidate set.

Pocono Mountains					
model	k	ΔAICc	w	mod lik	dev
age^2 + % unvegetated + fledge date	6	0.00	0.32	1.00	116.45
age^2 + DTN swamp + % unvegetated + fledge date	7	0.24	0.28	0.89	114.67
age^2 + DTN swamp + fledge date	6	0.33	0.27	0.85	116.78
age^2 + fledge date	5	3.71	0.05	0.16	122.18
age^2 + DTN swamp + % unvegetated	6	4.62	0.03	0.10	121.07
age^2 + DTN swamp	5	5.95	0.02	0.05	124.42
age^2 + % unvegetated	5	6.33	0.01	0.04	124.80
age^2 + DTN shrubland	5	8.83	0.00	0.01	127.30
age^2 + % non-herbaceous	5	11.00	0.00	0.00	129.46
age^2 + % mature forest	5	11.05	0.00	0.00	129.52

Pennsylvania Wilds					
age + begging effort + vertical vegetation density	4	0.00	0.53	1.00	209.97
age^2 + begging effort + vertical vegetation density	5	2.02	0.19	0.36	209.97
age + vertical vegetation density	3	2.21	0.17	0.33	214.20
age^2 + vertical vegetation density	4	4.20	0.06	0.12	214.16
vertical vegetation density	2	5.04	0.04	0.08	219.04
age + lateral vegetation density	3	16.82	0.00	0.00	228.80
age^2 + lateral vegetation density	4	18.46	0.00	0.00	228.43
lateral vegetation density	2	26.62	0.00	0.00	240.62
age + % herbaceous	3	32.40	0.00	0.00	244.39
age^2 + % herbaceous	4	33.92	0.00	0.00	243.89

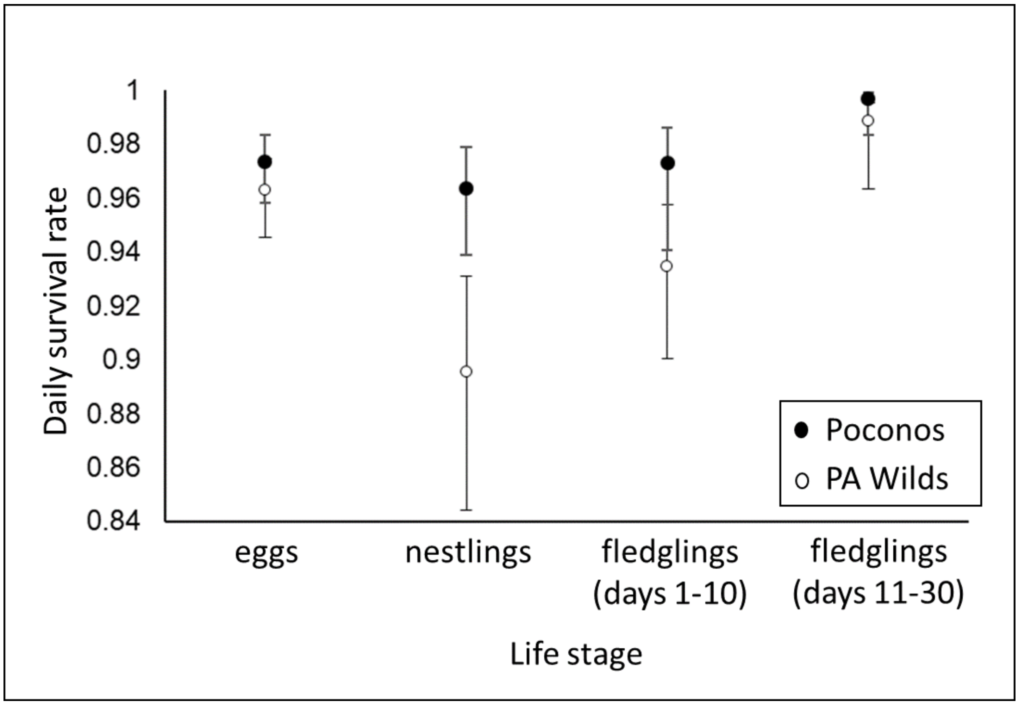

Figure 5.1. Daily survival rates for Golden-winged Warbler life stages from eggs, nestlings, young fledglings (1-10 days post-fledging) and older fledglings (11-30 days post-fledging). We modeled our two landscapes, the Pocono Mountains (solid circles) and Pennsylvania Wilds (open circles) separately. Point estimates are shown along with 95% confidence intervals (error bars).

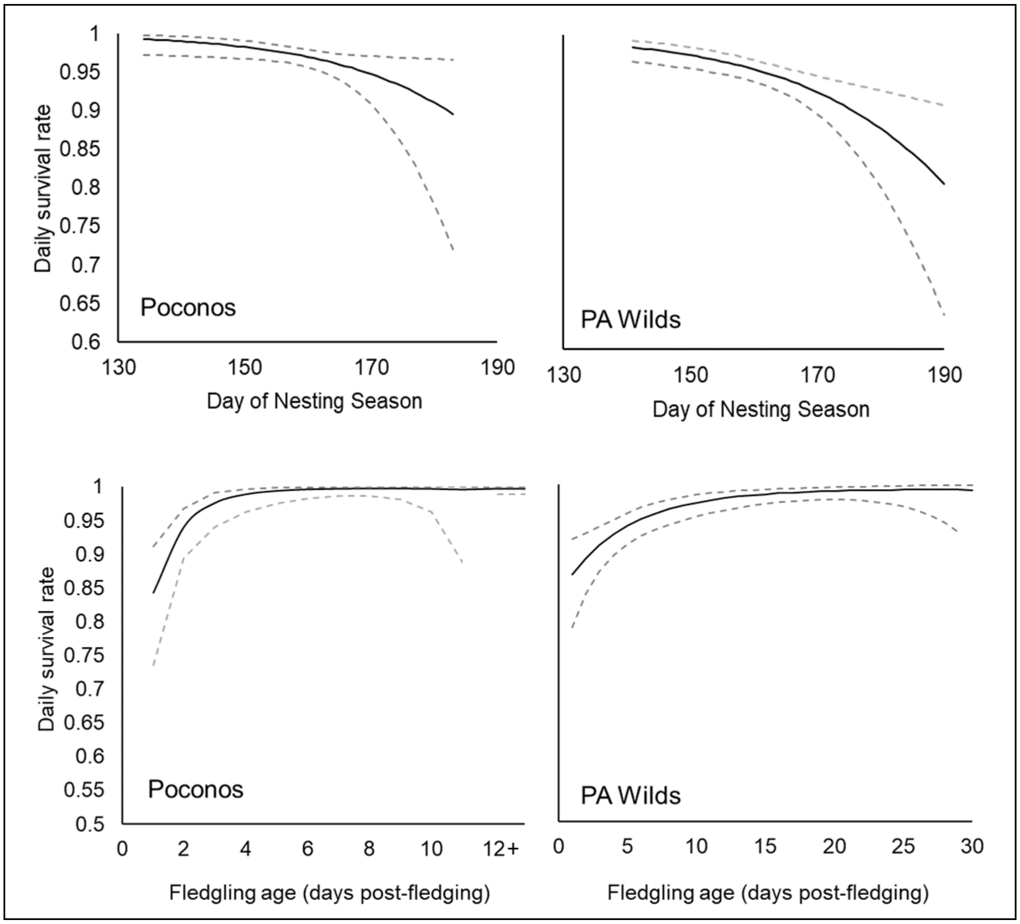

Figure 5.2. Model predictions for survival of Golden-winged Warbler (Vermivora chrysoptera) nests (top) and fledglings (bottom) in the Pocono Mountains (left) and Pennsylvania Wilds (right). Models show nest daily survival rate (DSR) as a function of Julian date, and fledgling DSR as a function of fledgling age (days post-fledging). Solid lines represent model estimates while dashed lines represent 95% confidence intervals.

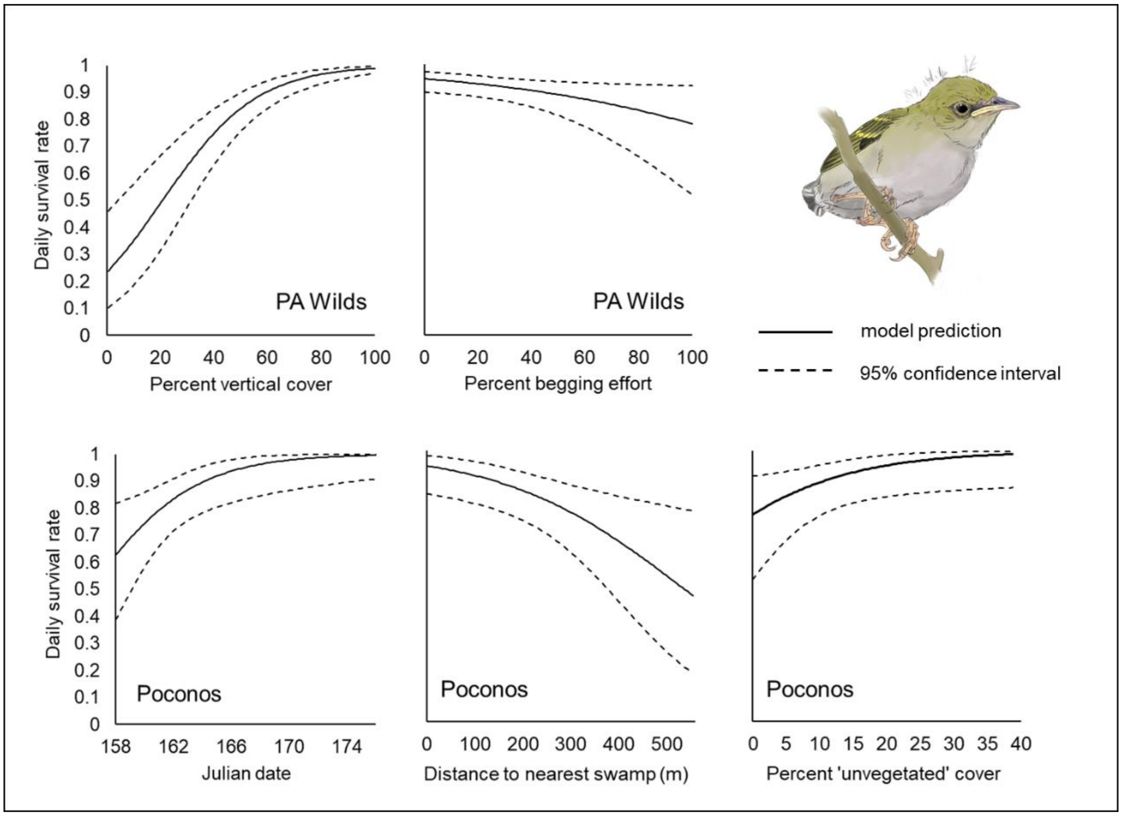

Figure 5.3. Model predictions for supported models explaining variation in fledgling survival (Known Fate, Program MARK) from the Pennsylvania Wilds (top) and Pocono Mountains (bottom). Solid lines represent model estimates while dashed lines represent 95% confidence intervals.

CHAPTER 6

RAPID PRE-FORMATIVE MOLT IN A WOOD-WARBLER: AN OVERLOOKED CHALLENGE DURING THE POST-FLEDGING PERIOD

Abstract

The post-fledging period is a brief but critical component of the avian lifecycle. Although some major stressors on juvenile songbirds have been examined in detail (*e.g.*, shifting habitat needs), one has been largely overlooked: pre-formative molt. Despite the great energetic requirements of growing feathers, the period of greatest energy demand in molting fledglings remains unknown. We expected molt to occur during the period of parental care in a long-distance migratory songbird and hypothesized that the greatest period of energetic demand would not overlap the period of greatest fledgling mortality (the first week post-fledging). We used a combination of radio tracking and visual plumage assessment to document formative plumage development and relative energy demands for fledgling Golden-winged Warblers (*Vermivora chrysoptera*) in Pennsylvania during Spring 2017. We tracked each fledgling once daily and recorded plumage characteristics using digital video and detailed field sketches. Most fledglings completed development of flight feathers (remiges + rectrices) between days 17-18 post-fledging. This period overlapped with the pre-formative molt by an average five days, during which time birds were developing two generations of plumage simultaneously. The overlap between growth periods for different plumage generations, combined with the short duration of molt, resulted in concentrated plumage demand, peaking between days 13-17 post-fledging, approximately 10 days after the period of greatest fledgling mortality. This finding suggests the pre-formative molt likely imposes energetic demands that extend beyond what has been widely regarded as the most vulnerable window of the post-fledging period – the first few days. Plumage demands may thus be an under-appreciated challenge faced by young birds in an otherwise already-challenging life stage. Our study demonstrates that visual observations can be reliably used to assess plumage development, and such assessments may reveal novel aspects of avian life history.

Introduction

The post-fledging period is a critical component of the avian lifecycle (Sæther and Bakke 2000, Robinson et al. 2004, Cox et al. 2014). This period is typically defined as the period between leaving the nest and independence from adults (Faaborg et al. 2010, Vitz and Rodewald 2010, Naef-Daenzer and Grüebler 2016). Although post-fledging ecology for many North American passerines remains poorly known, increasing scientific interest in this period has yielded novel insights for a handful of species (Faaborg et al. 2010, Chandler et al. 2012, Cox et al. 2014, Fiss 2018). For example, several studies have demonstrated that young songbirds have shifting habitat requirements between the nesting and post-fledging periods (Anders et al. 1998, Pagan et al. 2000, King et al. 2006, McDermott and Wood 2010, Chandler et al. 2012). Moreover, the low survival experienced by young fledglings during this period, particularly the first few days post-fledging, makes the post-fledging period a limiting demographic component of avian population growth (Robbins et al. 2003, Yackel Adams et al. 2006, Schmidt et al. 2008, Vitz and Rodewald 2011, Cox et al. 2014). On top of the major stressors that influence survival (*e.g.*, shifting habitat needs, predation), juvenile songbirds also must acquire their first complete set of adult feathers through the pre-formative molt (Pyle 1997, Howell et al. 2003, Howell et al. 2010) — yet the timing and energetic demands of this added stressor have been almost entirely overlooked.

All North American passerines begin development of the juvenal plumage while in the nest and exhibit a pre-formative molt some time thereafter (Howell et al. 2003, Howell 2010). This pre-formative molt facilitates the transition between two distinct plumages in the avian lifecycle, the 'juvenal plumage' and the 'formative plumage' (Howell et al. 2003). Juvenal plumage in songbirds represents the first generation of feathers produced by each of a bird's feather follicles (Howell et al. 2010) and is typically characterized by a loose, downy texture with drab coloration in body feathers (Howell et al. 2003, Newton 2009, Jenni and Winkler 2011) along with the first complete set of remiges and rectrices (flight feathers). Although juvenal plumage is undoubtedly important for surviving early life, most migratory passerines molt into "formative" plumage before their first migration (via the "pre-formative molt"), replacing almost all juvenal feathers in the process (Humphrey and Parkes 1959, Redfern and Alker 1996, Howell 2010). The formative plumage, formerly known as the "first basic plumage", is worn by a bird over its first winter (or longer; Amadon 1966, Howell et al. 2003, Pyle 1997). Most passerine formative plumages consist of a second generation of feathers across the entire body save for the remiges, rectrices, and some wing coverts which are retained from the first generation. These retained juvenal feathers provide a key method to age a bird throughout its first full year of life, including through the first spring and breeding season (Pyle 1997).

The pre-formative molt therefore constitutes an important stage in the development of young passerines. Plumage replacement from juvenal to formative feathers is necessary because many juvenal feathers are of relatively poor quality and presumably inadequate to support the bird's first year of life (Ricklefs 1968, Redfern and Alker 1996, Hera er al. 2009, Leloutre et al. 2014, Podlaszczuk et al. 2016). In small passerines, molt has been shown to be challenging due to increased metabolic rate (Blackmore 1969, Murphy and Taruscio 1995, Cyr et al. 2008), thermoregulatory stress (Lindström et al. 1993, Rohwer et al. 2005), and social costs (VanderWerf and Freed 2003, Tringali and Bowman 2012). In long-distance migratory species, these challenges are exacerbated by the need to undertake lengthy migration within weeks of independence from parental care, imposing extreme time constraints on the post-fledging period (Bennett et al. 2017, Heckscher et al. 2017, Mumme 2018). Although pre-formative molt may take up to two months in some migratory species (Foster 1967), it is also likely that young songbirds undertake portions of the pre-formative molt while still dependent on parental care to maximize the extent to which parental provisioning contributes to energy required for molt. If such overlap occurs, other developmental behaviors such as begging, parental provisioning, and ontogeny of independent foraging may be affected, increasing potential conflict between parent and young during the weaning preiod (Trivers 1985). For most species, however, the physiological demands of this critical developmental stage are unknown, and timing, potential overalp in juvenal and pre-formative molt, and overlap with parental provisioning have not been documented. Until recently, in-depth study of post-fledging molt ecology in wild birds has remained difficult due to technological limitations (Cox et al. 2014) and because most molt studies required repeated recapture of individual birds (Rimmer 1988).

In this study, we used a combination of radio tracking and visual plumage assessment to document, for the first time, chronology and relative energy demands or formative plumage development in a Nearctic-Neotropical migratory passerine the Golden-winged Warbler (*Vermivora chrysoptera*). This species is especially interesting in this regard because it is single-brooded, has a short post-fledging period (Langen1996, Russell et al. 2004, Confer et al. 2011, Peterson et al. 2016), develops specialized foraging behaviors before reaching independence, and attains adult-like plumage via the pre-formative molt prior to their first fall migration (Pyle 1997). Specifically, we test the hypothesis that pre-formative molt occurs during the period of parental care in by answering the following questions: (1) to what extent does pre-formative molt (growth of the second feather generation) overlap with juvenal feather development (growth of the first feather generation)?; (2) is the rate of pre-formative molt (% plumage grown/day) constant during post-fledging care?; and (3) to what extent is the pre-formative molt completed prior to fledgling independence? In addressing these questions, we also provide the first estimates of relative physiological demands for plumage development and molt during this critical avian life stage.

Methods

Study Species

Golden-winged Warblers are long distance Nearctic-Neotropical migrants that breed across portions of the Appalachian Mountains and the Western Great Lakes regions of North America and winters across portions of Central America and northwestern South America (Confer et al. 2011, Rosenberg et al. 2016). These warblers are single brooded and construct open-cup nests on the ground within early-successional communities including natural wetlands, old fields, burned forestlands, and regenerating clearcuts (Bakermans et al. 2011, Roth et al. 2012). Like many open cup nesters, Golden-winged Warblers have relatively rapid nesting cycles with 11 days for incubation and only eight days between hatching and fledging (Martin and Li 1992, Confer et al. 2003, 2011). Upon fledging, broods are divided between parents, which provide care until independence, 25-30 days later (Peterson et al. 2016). During this post-fledging period, Golden-winged Warblers complete the development of their first plumage (juvenal; initiated in the nest) and undergo the pre-formative molt soon thereafter, just prior to fall migration.

Study Area

We studied Golden-winged Warbler post-fledging ecology in central Pennsylvania during the 2017 breeding season. This region hosts one of the few remnant viable populations of Golden-winged Warblers in the Appalchian Region (Larkin and Bakermans 2012, Rosenberg et al. 2016). Our focal habitat patches (n=7) were located within the Sproul State Forest and State Game Lands 100 of Centre and Clinton Counties (Lat: 41.154, Long: -77.898, NAD83). This region is a high-elevation part of the Allegheny Plateau, a portion of the Appalachian Mountains dominated by mature deciduous forest (McCaskill et al. 2009). Our sites were generally large (mean size: 84

ha; SD: 85) and at a mean elevation of 477 m (SD: 43 m). Sites were a mean distance of 4.59 km (SD: 4.42) from their nearest neighboring site. Deciduous forest communities in our study area are dominated by dry heath, oak, and species frequently found in mixed-hardwood forests. Within Sproul State Forest and State Game Lands 100, early-successional forests have been created through wildfire and silviculture. We studied Golden-winged Warblers in five regenerating clearcutscomprised of scattered, residual canopy trees (< 9.18 m^2/ha basal area) which were primarily oaks (*e.g.*, *Quercus alba*, *Q. rubra*), maples (*e.g.*, *Acer rubrum*), and hickories (*e.g.*, *Carya* spp.) and understory vegetation of diverse shrubs (*e.g.*, *Gaylussacia baccata*, *Kalmia latifolia*), regenerating saplings, *Rubus* spp., ferns (*e.g.*, *Pteridium aquilinum*), and sedges (*e.g.*, *Carex pennsylvanica*).

Nest searching and Fledgling Telemetry

We surveyed each of the five regenerating clearcuts every 2-3 days. Surveys consisted of three trained surveyors systematically hiking through Golden-winged Warbler habitat, searching for either adult female or male warblers engaging in reproductive behaviors (*e.g.*, nest construction, provisioning of nestlings/mates, chipping, quiet songs). Females and males were followed until nests were discovered. Upon discovery, nests were monitored every three days with increasing frequency as fledging was anticipated (Martin and Geupel 1993).

To monitor the plumage development of individual Golden-winged Warbler fledglings, we attached radio transmitters to juvenile warblers using the figure-eight harness method (Rappole and Tipton 1991). Harnesses were constructed with < 1 mm black elastic thread. Transmitters were purchased from Blackburn Transmitters (Blackburn Transmitters Inc., Nacogdoches, TX) and weighed 0.39 g which is <5% of the mean mass of a fledgling Golden-winged Warbler (Fair et al. 2010, Peterson et al. 2016). Transmitters had a battery life of ~30 days, which is approximately the same length as the post-fledging period for the Golden-winged Warbler (Fiss 2018). We attached radio transmitters either i) just prior to fledging (7-8 days old) or ii) on the day of fledging (9 days old; "day 1" post-fledging). At the time of radio transmitter attachment, we also fitted each chick with a USGS aluminum band and a single plastic colored leg band to assist with daily re-sightings. Each day after deployment of radio transmitters, fledglings were tracked using a two-element "H-type" Yagi antenna and a hand-held radio receiver once/day between sunrise and 6-hours post-sunrise. To locate fledglings, we used the 'homing' method and attempted to vary time-of-day for each individual's observations to ensure that each bird was sampled at a random time within the sampling period each day.

Plumage Assessment of Fledglings

Upon successfully locating each fledgling daily, we attempted to capture photo/video (digital media) or make sketches of each juvenile from approximately 5-10 m away. A concurrent fledgling behavioral study required us to visually observe each fledgling for five 5 minutes/day. These observations gave us ample opportunity to also record each fledgling's feather status from a variety of angles and light conditions. Plumage data were collected by two observers (DJM, CJF) with a compact digital video camera (Nikon model COOLPIX P530; 42x zoom) or, when digital media could not be collected, with field sketches. Each sketch included standardized notes on plumage development and detailed the condition of as many feather tracts as could be observed.

Golden-winged Warblers fledge their nest with most "juvenal" (*i.e*., first generation) body/head plumage developed, juvenal wing coverts, partially-grown remiges, and very short rectrices (<10% final length; Figure 6.1A). In Parulid warblers, the first -generation of flight feathers (remiges/rectrices) is retained through the first breeding season while most other body plumage is molted 1-2 more times before the first breeding season: pre-formative molt only or pre-formative molt followed by pre-alternate molt (Humphrey and Parkes 1959, Howell 2010). Using our sketches, photos and videos, we assessed the plumage development of recently fledged warblers across three discrete plumage areas: i) flight feathers (remiges/rectrices), ii) formative plumage across the under/upperparts of the body, and iii) formative head plumage. The completion of these three feather groups constitutes all plumage worn by Golden-winged Warblers over the first nonbreeding period (Howell 2010, Pyle 1997).

To quantify growth of flight feathers without taking in-hand measurements, we estimated rectrix length visually and used tail growth as a proxy for remex growth because i) estimating wing cord proved to be highly subjective in the field and ii) remex and tail growth appeared to be correlated (Fig. 6.1) and shown to be grown simultaneously in other small passerines (Redfern and Alker 1996). To estimate daily juvenal tail length (% of final length), we visually compared the juvenile's tail length to that of the regularly provisioning adult that was assumed to have a full-length tail (Fig. 6.2). We expect that tail length estimates made in this way were relatively unbiased because we could readily make side-by-side comparisons between the developing fledgling and a breeding adult, sometimes several times/fledgling/day. To quantify molt of body plumage, we estimated the extent of pre-formative molt as a percentage of the body area covered by new formative plumage (Fig. 6.2). This was accomplished by paying close attention to color contrast between feather generations with the brightest feathers constituting a new plumage generation. We used extent of molt on the underparts as a proxy for overall body molt, because molt in upperparts (*e.g.*, back and rump) was often difficult to observe due to the bird's posture, and because body molt across underpart and upperpart regions is understood to occur in synchrony in similar species (Rimmer 1988). Similarly, pre-formative facial molt was quantified by estimating the extent of the face area covered by newly grown formative plumage. Because facial plumage could be quantified independently among five distinct feather tracts (crown, supercillium, auricular, malar, and throat; Fig. 6.2C), we did so and then calculated the total head molt as the mean of all five tracts. Like body molt, facial molt was easy to discern in the field via sharp contrast between dull juvenal plumage and brightly-colored formative plumage.

Demand of Parulid plumage growth

In passerine birds, the demand of plumage growth is a function of both the mass of plumage developed and the duration feathers are grown (Lindström et al. 1993). Estimating the relative energetic demand of plumage development over the post-fledging period required us to estimate the mass associated with different feather tracts and regions. Because this information is not published for wood-warblers, we measured feather tracks on recently salvaged carcasses of a comparable species - Yellow Warbler (*Setophaga petechia*). Three Yellow Warblers (obtained from the Cornell University Museum of Vertebrates) were a hatch-year female in formative plumage, an after-hatch-year female in basic plumage, and an after-hatch-year male in alternate plumage (determined by plumage pattern, brightness, and molt limits; Pyle 1997). We plucked all feathers from each bird and organized them into individual envelopes for each feather tract. Feathers from each tract were then weighed to the nearest 0.01 mg using an electronic balance (Shimadzu AUW120D, Shimadzu, Kyoto, Japan; readability: ± 0.1 - 0.2 mg). Feather masses from each Yellow Warbler specimen were used as a mean proportion (plumage group mass / total plumage mass) ± SE for feather growth demand analyses. We recognize that Yellow Warblers are larger than Golden-winged Warblers, however, because all mass estimates of feather groups are analyzed as proportions, Yellow Warblers serve as a suitable surrogate species for this analysis.

Statistical Analyses

To model plumage development of Golden-winged Warbler fledglings over the post-fledging period, we created simple linear regression models in R (R Core Team 2018). Linear models were created using individual daily plumage development progress estimates for flight feathers, body molt, and head molt as fledgling plumage developed over time. Because plumage development was deterministically bounded by periods of ‘0% development’ and ‘100% development’, we used only data from the periods of active molt for modeling. For each feather group, we created two models that allowed molt to vary as a function of age: linear and quadratic and compared these models against a null (intercept-only) model. We also tested for potential biases due to sampling method (sketch, versus photo/video) by comparing the top molt model in each group to an additive model including all parameters from the top model + observation type. The relative informative value of these models was assessed using Akaike's Information Criterion adjusted for small sample size (AIC_c). We also assessed the model fit using R^2 for the top-ranked model in each feather group.

To estimate the daily energetic demand of new feather growth, we used the three best-ranked plumage group models to calculate the percentage of each plumage group developed over each day of the post-fledging period. We then applied the masses of Yellow Warbler plumage (±SE) in each of the same feather groups to calculate the percentage of total plumage mass developed on each day of the post-fledging period. For head and body plumage, we scaled model estimates (±SE) directly by plumage masses of Yellow Warbler feathers (±SE). For flight feather development, we did not use a simple summed mass of all flight feathers because Golden-winged Warblers fledge from their nest with flight feathers approximately 50% developed (Fig. 6.1). Fledglings appeared to be lacking many under-wing feathers and all rectrices at the time of fledging. As such, our models of post-fledging molt demands scaled 'flight feather' growth by i) relative rectrix mass, ii) relative underwing plumage mass, and iii) 50% flight feather mass. Upperwing feathers (*e.g.*, secondary coverts) were not included in our models as they were grown prior to fledging and appeared to finish molt post-independence. The combined daily energetic demands therefore summed to < 100%, because the metric does not include the mass of the upper wing coverts (molted partially outside the post-fledging period) and only 50% of the mass of the flight feathers (grown partially before fledging).

Results

From 6 June through 22 July 2017 we observed 34 fledglings originating from n=17 nests (mean = 2.0 fledglings/nest; SD: 0.94. Of these, we obtained plumage assessments for n=24 fledglings of known age and quantified i) tail length, ii) pre-formative body molt, and iii) pre-formative head molt across five feather tracts. Between two observers, 123 of 276 observations (45%) resulted in metrics describing plumage, including 69 field sketches and 54 digital media recordings. Among observations for which at least one plumage metric was recorded, we were able to quantify an average of 6.49 of 7 plumage tracts per observation. Assessments of formative body molt (n=15, 12% of observations), throat molt (n=10, 8%), and tail length (n=10, 8%) were missed most frequently due to visual obstructions in dense vegetation.

Plumage Development Chronology

Linear models including the 'age' covariate were more informative in describing plumage development than quadratic models or the null model, which was expected given that plumage changes with age. Difference in AICc between null models and the highest-ranked linear 'age' models were ΔAIC_c= 165.57, 35.60, and 43.70 for flight feather development (R^2=0.89), linear formative body molt (R^2=0.60), and linear formative head molt (R^2=0.58), respectively. 'Age' and 'age^2' covariates within all models had β 95% confidence intervals that did not overlap zero. Models with the ‘observation type’ covariate never ranked above models lacking this covariate and the β 95% confidence intervals for this parameter always overlapped zero. Our age-dependent flight feather development model corroborated our field data, suggesting that the majority of fledglings would complete development of flight plumage by day 17 post-fledging (Fig. 6.3). Our results indicate that many dependent Golden-winged Warbler fledglings of unknown age could be reliably aged (within 1-2 days precision) using these feather groups (Table 1).

The pre-formative molt began on day 13 (±1 day) post-fledging and began with body plumage followed by head plumage two days later (15 days post-fledging (±1 day); Fig. 6.3). Pre-formative molt occurred over a mean duration of 10 days and overlapped with the continued growth of juvenal flight feathers by five days. The pre-formative molt appeared to occur in a consistent manner for most birds, always beginning with a bright, cream-colored “inverted U” across the breast which gradually spread across the underparts (Fig. 6.3). The yellowish breast color faded significantly as pinfeathers opened but a yellow ‘blush’ remained on the breasts of almost all fledglings. Head molt was almost always initiated at the base of the bill for feather tracts associated with the crown/nape, supercillium, auricular, and malar regions. Some birds deviated from this pattern by initiating crown molt at the apex of the head and then spreading outward. Many birds developed auricular molt at the ear opening and lore simultaneously, and molt progressed bi-directionally toward the bill and back of the head. Throat molt usually began in the center of the throat and spread outward until the entire tract was complete. The pre-formative molt was completely finished by 22-23 days post-fledging (Fig. 6.3), with the exception of the greater and median coverts that began actively molting on day 25 post-fledging and frequently continued post-independence. Greater and median covert replacement was therefore the only molt ongoing after juveniles achieved independence from their parents.

Plumage Masses

Yellow Warbler specimens had 2,108-2,799 total body feathers (mean: 2,410; SD: 381; Table 2). Total feather masses across all body regions for single Yellow Warblers ranged from 539.24 to 747.30 mg (0.54 – 0.75 g). Although the remiges (n=36/bird) and rectrices (n=12/bird) were the most massive feathers on the Yellow Warblers (3.54 – 4.13 mg each; 27% of total plumage), the relatively small body feathers (0.25-0.47 mg each) were more numerous and constituted much greater total mass (n=894 – 1,136/bird; 50% of total plumage). Head feathers varied in mass but were mostly small (0.025 – 0.039 mg each) and constituted only 9% of total plumage mass. Although we did not weigh small feather groups individually, combined non-remex upper-wing plumage (including the greater and median coverts) constituted 10% of warbler feather mass.

Plumage demands over the post-fledging period

Plumage development models indicated the relative demands of daily plumage production, based on feather mass, varied greatly over the post-fledging period (Fig. 6.4). Because upper-wing plumage was still in molt during the conclusion of study for most birds, we exclude upper wing plumage mass from our plumage demand model (~10% of feather mass). Additionally, because remiges were about half grown at the time of fledging, only half of the primary flight feather mass (20% total) was modeled within the flight feather growth period (~10% of feather mass). The removal of these plumage components meant that our models of plumage growth during the post-fledging period represented roughly 80% of total pre-formative plumage development.

The first 10 days out of the nest were characterized by *only* incremental tail and wing plumage growth which occurred slowly. The daily plumage demand over this early 10-day period was relative low (1.4% of total plumage mass/day ±0.1); recall that the total mass of flight feathers is relatively small compared to body feathers. The initiation of the pre-formative molt (*i.e*., replacement of body and head feathers) marked a major increase in daily plumage demand for fledglings, with the peak occurring between days 13-22 post-fledging. During this time, resources were being allocated to all three feather groups simultaneously (wings/tail, body plumage, and head plumage), resulting in plumage development demands more than 6 times greater (9.72% of total plumage mass/day ±3.4 at peak on day 15) than those estimated during the first 12 days out of the nest when only flight feathers are growing (1.4%, above). This period of high plumage demand continued through day 22 post-fledging, after which the daily plumage development demand remained below 1%/day as pre-formative body molt reached completion.

Discussion

Our results demonstrate that Golden-winged Warblers start and nearly finish pre-formative molt while under parental care. Further, we identified a 7-day period (13-19 days post-fledging) of previously under-appreciated high plumage demand, during which all major feather groups—body, flight, and head—developed simultaneously. Most studies of post-fledging ecology (*e.g*., Cox et al. 2014, Naef-Daenzer and

Grüebler 2016) emphasized that the most stressful and dangerous period for young birds is the first few days out of the nest (*e.g.*, Rush and Stutchbury 2008, Vitz and Rodewald 2010). Our results highlight the pre-formative molt as an additional period of potentially high stress for young birds that extends well beyond the first few days, particularly when overlapping with flight-feather development, such that fledglings grow two plumage generations simultaneously: first generation rectrices/remiges and second-generation formative plumage in the head and body. During the pre-basic molt, songbirds may increase energy expenditure from 32 – 60 % (Bonier et al. 2007, Cyr et al. 2008). Although we did not directly measure energy expenditure, our molt models suggest that plumage demands to the pre-formative molt in fledglings peaks at days 13-20 when face, body, and flight feathers grow simultaneously. Thus, in addition to experiencing low rates of survival (Peterson et al. 2016) and shifting habitat needs (Streby et al. 2016, Fiss 2018), at least some Nearctic-Neotropical migratory birds face the added physiological demands of rapid pre-formative molt during the post-fledging period.

While the pre-formative molt clearly involves an important set of physiological functions (*e.g.*, thermoregulation), it also likely serves a social function as a means of communication (Howell 2010). Golden-winged Warbler are unusual among songbirds in that hatch-year birds resemble breeding adults upon the completion of the pre-formative molt (Pyle 1997). Because the formative plumage is worn over the first winter, this ‘adult-like’ plumage may be important for signaling and promoting sexual segregation on the non-breeding grounds (Confer et al. 2011, Bennett 2012). These findings contrast with other Nearctic-Neotropical migratory species, such as the

American Redstart (*Setophaga ruticilla*), that wears a juvenile-like plumage through the first winter and even through the first breeding season (Sherry et al. 2016). The chronology and associated physiological demands of pre-formative molt are therefore highly variable, even within Parulidae. In addition, because Golden-winged Warblers are not known to undertake a pre-alternate molt in spring (Pyle 1997), the rapid pre-formative molt we documented in dependent fledglings is especially critical, as the formative plumage is also used during the first breeding season to establish a territory and attract a mate. Many first-time breeders (“second-year” birds) will therefore have worn this formative plumage for an entire year, only losing their formative plumage during their first pre-basic molt after rearing their own fledglings the following summer. Formative plumage may therefore be profoundly important in this species, even beyond the season of pre-formative molt.

Our results also clarify two poorly understood aspects of post fledging ecology in small altricial birds. First is the duration that juvenal plumages are retained after leaving the nest. High rates of nest predation favor rapid development (Bosques and Bosques 1995, Remeš and Martin 2002), but rapidly-developed young usually produce loosely textured, low quality juvenal plumage (Butler et al. 2008). Juvenal plumage is inferred to be low quality because fledglings of many species replace this plumage shortly after leaving the nest, suggesting that it is poorly suited to events later in life, such as migration, thermoregulation, or social signaling (Rohwer et al. 2005, Howell et al. 2003, Newton 2009, Jenni and Winkler 2001). No previous studies have focused on when species replace juvenal plumage after they fledge the nest. Our finding that Golden-winged Warblers initiated pre-formative molt only 11 days out of the nest demonstrates how quickly these warblers begin replacing this plumage. The second important finding is that fledglings appear to rely on parental provisioning throughout the pre-formative molt. Although we were unable to evaluate the extent to which fledglings rely on parents to meet their energetic needs, recent fledglings are weak fliers and inexperienced foragers that likely cannot meet the energetic demands of this molt without parental provisioning (Naef-Daenzer and Grüebler 2016). The extra energy allotted to the fledgling by the parents may facilitate an increased rate of feather growth. For parents, supporting fledglings up to 30 days and throughout their molt may prolong the period of post-fledging care and delay the onset of adult pre-basic molt (Ogden and Stutchbury 1996, Svensson and Nilsen 1997, Vega Rivera et al. 1998, Vega Rivera et al. 2003). Taken together, these findings suggest that the quality of the juvenal plumage may be linked to the duration of post-fledgling care, and that costs associated with rapid development and the need to subsequently replace low quality-nestling plumage may be shared by both fledglings and their parents.

Our visual assessment of the pre-formative molt provides the first estimate for how long nest-grown juvenal feathers are carried after leaving the nest. We hope that the non-invasive methodology and results presented here prompt other researchers to explicitly quantify plumage development and other important aspects of the post-fledging period. Future studies testing the correlation between visual- and in-hand methods would improve the reliability of both. We note that our method of molt quantification likely underestimates the duration of the pre-formative molt, as newly emerging pinfeathers and near full-length feathers would be difficult to discern from freshly replaced feathers using field observations alone. Further, quantifying absolute energy expenditure before, during, and after the pre-formative molt would aid our understanding of energetic demands during the post-fledgling period. Additional research on other species would allow for comparisons of early-life molt strategies during the post fledging period and provide a more complete picture regarding the importance of pre-formative molt among avian life histories. Golden-winged Warblers may be unusual in their rapid rate of pre-formative molt. In fact, pre-formative molt is estimated to require 40-60 days in other Parulids, suggesting different life history strategies (Foster 1967, Nolan 1978).

Our work provides one of the most detailed examinations of the pre-formative molt in a North American passerine. We show that demands of plumage production vary over the post-fledging period and overlap considerably with other developmental demands, as well as the period of parental care. Pre-formative molt is therefore a previously under-appreciated constraint on the full annual lifecycle in this species. An examination of how the added constraint of rapid plumage development may influence fledgling signaling (*e.g.*, begging, posturing) and associated adult provisioning would provide insight into how Golden-winged Warblers meet energy needs during the critical post-fledging period. Understanding the chronology and physiological demands of pre-formative molt across a larger suite of species will fill an important gap in knowledge of the full avian lifecycle and provide insights regarding the evolution of avian life history strategies.

Acknowledgments

We are very grateful to the Cornell University Museum of Vertebrates for access to

Yellow Warbler carcasses for plumage mass quantification, as well as the Cornell Lab of Ornithology for field funding. We are also grateful to K. Sparks and the Cornell 'Ecology, Evolution, and Behavior' Department for use of laboratory equipment. We appreciate the useful insight regarding molt of Parulid warblers offered by P. Pyle. We are grateful for the exceptional nest-searching and radio telemetry efforts of our field technicians: F. Rodriguez, B. Ramer, N. Christensen, K. Glanville, E. Moser, S. Toner, C. Sayers, and T. Barbee. We also thank the Pennsylvania Bureau of Forestry and the Pennsylvania Game Commission for access to Sproul State Forest and State Game Lands 100. We appreciate the comments of three anonymous reviewers who improved this manuscript. We have no conflicts of interest to report. his project was funded by the Pennsylvania Game Commission and the U.S. Department of Agriculture (USDA) - Natural Resource Conservation Service (NRCS) Conservation Effects Assessment Project (CEAP) award (# 68-7482-12-502) grants awarded to J.L.L. D.J.M. was supported by award # 68-7482-12-502 as well as additional funding provided through the Cornell Laboratory of Ornithology. All birds were handled and banded under USGS banding permit # 23277. This study was conducted in accordance with the guidelines of the Institutional Animal Care and Use Committees of both Cornell University (#2013-029) and Indiana University of Pennsylvania (#14-1314).

Works Cited

Amadon, D. (1966). Avian plumages and molts. Condor 68:263-278.

Anders, A. D., J. Faaborg and F. R. Thompson III (1998). Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. Auk 115:349-358.

Bakermans, M. H., J. L. Larkin, B.W. Smith, T. M. Fearer and B. C. Jones (2011). Golden-winged Warbler habitat best management practices in forestlands in Maryland and Pennsylvania. American Bird Conservancy, the Plains, Virginia, USA.

Bennett, R. E. (2012). Habitat associations of the Golden-winged Warbler in Honduras (Unpublished Master's Thesis). Michigan Technological University. Houghton, Michigan. USA.

Bennett, R. E., S. Barker Swarthout, J. S. Bolsinger, A. D. Rodewald, K. V. Rosenberg and R. W. Rohrbaugh (2017). Extreme genetic similarity does not predict non-breeding distribution of two closely related warblers. Journal of Field Ornithology 88:156-168.

Blackmore, F. H. (1969). The effect of temperature, photoperiod and molt on the energy requirements of the House Sparrow, *Passer domesticus*. Comparative Biochemistry and Physiology 30:433-444.

Bonier, F., P. R. Martin, J. P. Jensen, L. K. Butler, M. Ramenofsky and J. C. Wingfield (2007). Pre-migratory life history stages of juvenile arctic birds: Costs, constraints, and trade-offs. Ecology 88:2729-2735.

Butler, L. K., S. Rohwer and M. G. Speidel (2008). Quantifying structural variation in contour feathers to address functional variation and life history trade-offs. Journal of Avian Biology 39:629-639.

Chandler, C. C., D. I. King and R. B. Chandler (2012). Do mature forest birds prefer early-successional habitat during the post-fledging period?. Forest Ecology and Management 264:1-9.

Confer, J. L., J. L. Larkin, P. E. Allen and F. Moore. (2003). Effects of vegetation, interspecific competition, and brood parasitism on Golden-winged Warbler (*Vermivora chrysoptera*) nesting success. Auk 120:138-144.

Confer, J. L., P. Hartman and A. Roth (2011). Golden-winged Warbler (*Vermivora chrysoptera*). The Birds of North America. Number 20. In P. G. Rodewald (Ed). The birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA.

Cox, W. A., F. R. Thompson, A. S. Cox and J. Faaborg (2014). Post-fledging survival in passerine birds and the value of post-fledging studies to conservation. Journal of Wildlife Management 78:183-193.

Cyr, N. E., M. Wikelski and L. M. Romero. (2008). Increased energy expenditure but decreased stress responsiveness during molt. Physiological and Biochemical Zoology 81:452-462.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson and S. C. Latta. (2010). Conserving migratory land birds in the New World: Do we know enough?. Ecological Applications 20:398-418.

Fair, J., E. Paul and J. Jones (2010). Guidelines to the use of wild birds in research. Ornithological Council. Washington D.C., USA.

Fiss, C. J. (2018). Multiscale Habitat Selection and Movement of Fledgling Golden-Winged Warblers (*Vermivora chrysoptera*) in Two Managed Mixed-Oak Forest Communities of Northern Pennsylvania (Unpublished Master's Thesis). Indiana University of Pennsylvania, Indiana, Pennsylvania, USA.

Foster, M. S. (1967). Molt cycles of the Orange-crowned Warbler. The Condor 69:169-200.

Heckscher, C. M., M. Gutierrez Ramirez and A. H. Kneidel (2017). Reproductive outcomes determine the timing of arrival and settlement of a single-brooded Nearctic–Neotropical migrant songbird (*Catharus fuscescens*) in South America. The Auk 134:842-856.

Hera, I. D. L., J. Perez-Tris and J. L. Telleria (2009). Migratory behaviour affects the trade-off between feather growth rate and feather quality in a passerine bird. Biological Journal of the Linnean Society 97:98-105.

Howell, S. N., C. Corben, P. Pyle and D. I. Rogers (2003). The first basic problem: a review of molt and plumage homologies. Condor 105:635-653.

Howell, S. N. G. (2010). Molt in North American birds. Houghton Mifflin Harcourt, Boston, Massechusetts, USA.

Humphrey, P. S., and K. C. Parkes (1959). An approach to the study of molts and plumages. Auk 76:1-31.

Jenni, L. and R. Winkler (2011). Moult and ageing of European passerines. A and C Black. London, UK.

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.

Langen, T. A. (1996). Skill acquisition and the timing of natal dispersal in the White-throated Magpie-Jay, *Calocitta formosa*. Animal Behaviour 51:575-588.

Larkin, J.L. and M. H. Bakermans. (2012). Golden-winged Warbler. Pp. 50-51 in Wilson, A. M. R., R. Mulvihill, and D. Brauning (Eds). The 2nd Pennsylvania Breeding Bird Atlas. The Penn State University Press. State College, Pennsylvania, USA.

Lindström, Å., G. Henk-Visser and D. Serge (1993). The energetic cost of feather synthesis is proportional to basal metabolic rate. Physiological Zoology 66:490-510.

Leloutre, C., A. Gouzerh and F. Angelier (2014). Hard to fly the nest: A study of body condition and plumage quality in house sparrow fledglings. Current Zoology 60:449-459.

Martin, T. E. and P. Li (1992). Life history traits of open-vs. Cavity-nesting birds. Ecology 73:579-592.

Martin, T. E. and G. R. Geupel (1993). Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64:507-519.

McCaskill, G. L., W. H. McWilliams, C. A. Alerich, B. J. Butler, S. J. Crocker, G. M. Domke … and J. A. Westfall (2009). Pennsylvania’s Forests 2009. U.S. Department of Agriculture, Forest Service, Northern Research Station. Newtown Square, Pennsylvania, USA.

Mcdermott, M. E. and P. B. Wood. (2010). Influence of cover and food resource variation on post-breeding bird use of timber harvests with residual canopy trees. Wilson Journal of Ornithology 122:545-555.

Mumme, R. L. (2018). The trade-off between molt and parental care in Hooded Warblers: Simultaneous rectrix molt and uniparental desertion of late-season young. Auk 135:427-438.

Murphy, M. E. and T. G. Taruscio (1995). Sparrows increase their rates of tissue and whole-body protein synthesis during the annual molt. Comparative Biochemistry and Physiology 111:385-396.

Naef-Daenzer, B. and M. U. Grüebler (2016). Post-fledging survival of altricial birds: Ecological determinants and adaptation. Journal of Field Ornithology 87:227-250.

Newton, I. (2009). Moult and plumage. Ringing and Migration 24:220-226.

Nolan Jr, V. (1978). The ecology and behavior of the prairie warbler, *Dendroica discolor*. Ornithological monographs 31:1-595

Ogden, L. J. E. and B. J. Stutchbury (1996). Constraints on double brooding in a Neotropical migrant, the Hooded Warbler. Condor 98:736-744.

Pagen, R. W., F. R. Thompson III and D. E. Burhans (2000). Breeding and post-breeding habitat use by forest migrant songbirds in the Missouri Ozarks. Condor 102:738-747.

Peterson, S. M., H. M. Streby, and D. E. Andersen. (2016). Spatially explicit models of full-season productivity and implications for landscape management of Golden-winged Warblers in the western Great Lakes region. Pp. 141–160 in H.

M. Streby, D. E. Andersen, and D. A. Buehler (Eds.). Golden-winged Warbler ecology, conservation, and habitat management. Studies in Avian Biology (no. 49), CRC Press, Boca Raton, Florida, USA.

Podlaszczuk, P., M. Kamiński, R. Włodarczyk, K. Kaczmarek, T. Janiszewski, and P. Minias (2016). Plumage quality mediates a life-history trade-off in a migratory bird. Frontiers in Zoology 13:47.

Pyle, P., and S. N. Howell. (1997). Identification guide to North American birds. Slate Creek Press. Bolinas, California, USA.

R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rappole, J. H. and A. R. Tipton. (1991). New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology. 62:335–337.

Redfern, C. P., and P. J. Alker (1996). Plumage development and post-juvenile moult in the Sedge Warbler *Acrocephalus schoenobaenus*. Journal of Avian Biology 27:157-163.

Ricklefs, R. E. (1968). Patterns of growth in birds. Ibis 110:419-451.

Rimmer, C. C. (1988). Timing of the definitive prebasic molt in Yellow Warblers at James Bay, Ontario. Condor 90:141-156.

Robinson, R. A., R. E. Green, S. R. Baillie, W. J. Peach, and D. L. Thomson (2004). Demographic mechanisms of the population decline of the Song Thrush *Turdus philomelo* in Britain. Joural of Animal Ecology 73:670-682.

Roth, A. M., R. W. Rohrbaugh, T. Will, and D. A. Buehler (2012). Golden-winged

Warbler status review and conservation plan. <http://www.gwwa.org/plan>

Rosenberg, K. V., T. Will, D. A. Buehler, S. Barker-Swarthout, W. E. Thogmartin, R. E. Bennett, and R. B. Chandler. 2016. Dynamic distributions and population declines of Golden-winged Warblers. Pp. 3–28 in Streby, H. M., D. E. Andersen, and D. A. Buehler. 2016. Golden-winged Warbler ecology, conservation, and habitat management. Studies in Avian Biology (49). CRC Press, Boca Raton, Florida, USA.

Rohwer, S., L. K. Butler, & D. R. Froehlich. 2005. Ecology and demography of east-west differences in molt scheduling of Neotropical migrant passerines. Pp. 87-105 in Greenberg, R., P. P. Marra. 2005. Birds of two worlds: the ecology and evolution of migration. Johns Hopkins University Press, Baltimore, Maryland, USA.

Rush, S. A., and B. J. Stutchbury. 2008. Survival of fledgling Hooded Warblers (*Wilsonia citrina*) in small and large forest fragments. Auk 125:183-191.

Russell, E. M., Y, Yom-Tov, and E. Geffen. 2004. Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. Behavioral Ecology 15:831-838.

Sæther, B.-E., and Ø. Bakke 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642–653

Schmidt, K. A., S. A. Rush, and R. S. Ostfeld. 2008. Wood Thrush nest success and post-fledging survival across a temporal pulse of small mammal abundance in an oak forest. Journal of Animal Ecology 77:830-837.

Sherry, T. W., R. T. Holmes, P. Pyle, and M. A. Patten. 2016. American Redstart

(*Setophaga ruticilla*), version 3.0. In P. G. Rodewald (Ed). The birds of North America (Cornell Lab of Ornithology, Ithaca, New York, USA.

Streby, H. M., S. M. Peterson, and D. E. Andersen. 2016. Survival and habitat use of fledgling Golden-winged Warblers in the western Great Lakes region. Pp. 127–140 in H. M. Streby, D. E. Andersen, and D. A. Buehler (eds). Golden-winged Warbler ecology, conservation, and habitat management. Studies in Avian Biology (no. 49). CRC Press, Boca Raton, Florida, USA.

Svensson, E., and J. Å. Nilsen. 1997. The trade-off between molt and parental care: a sexual conflict in the Blue Tit?. Behavioral Ecology 8: 92-98.

Tringali, A., and R. Bowman. 2012. Plumage reflectance signals dominance in Florida Scrub-Jay, *Aphelocoma coerulescens*, juveniles. Animal Behavior 84:1517-1522.

Trivers, R. L. (1985). Social Evolution. Benjamin Cummings Publishing Company. Menlo Park, California, USA.

Vanderwerf, E. A., and L. A. Freed. 2003. Elepaio subadult plumages reduce aggression through graded status-signaling, not mimicry. Journal of Field Ornithology 74:406-415.

Vega Rivera, J. H., W. J. Mcshea, J. H. Rappole, and C. A. Haas. 1998. Pattern and chronology of prebasic molt for the Wood Thrush and its relation to reproduction and migration departure. Wilson Journal of Ornithology 110:384-392.

Vega Rivera, J. H., W. J. Mcshea, and J. H. Rappole. 2003. Comparison of breeding and postbreeding movements and habitat requirements for the Scarlet Tanager

(*Piranga olivacea*) in Virginia. Auk 120:632-644.

Vitz, A. C., and A. D. Rodewald. 2010. Movements of fledgling Ovenbirds (*Seiurus aurocapilla*) and Worm-eating Warblers (*Helmitheros vermivorum*) within and beyond the natal home range. Auk 127:364-371.

Vitz, A. C., and A. D. Rodewald. 2011. Influence of condition and habitat use on survival of post-fledging songbirds. Condor 113:400-411.

Yackel Adams, A. A., S. K. Skagen and J. A. Savidge. 2006. Modeling post-fledging survival of Lark Buntings in response to ecological and biological factors. Ecology 87:178-188.

Tables and Figures

Table 6.1. A tool for aging Golden-winged Warbler (*Vermivora chrysoptera*) based on fitted models of observational field data for known-age fledglings. Age is reported as 'day off nest' with the first day = "day 1". Juvenile Golden-winged Warblers began showing noticeable tail growth on day 2 post-fledging. We scaled % tail growth by our mean measurement of adult tail length (n=208; Larkin unpub. data): 46.9 mm. Formative molt extent on breast and head provide additional features for aging through day 22 after which time birds can be aged more broadly based on secondary covert molt which appears to last 1-2 weeks beginning ~ 25 days post-fledging. We note again that these values were generated using visual observation only and in-hand quantification of molt would likely yield slightly different results.

age (days)	tail length (mm)	tail 95% CI (mm)	breast molt (% formative)	breast 95% CI (% formative)	face/head molt (% formative)	face/head 95% CI (% formative)
1	0	-	juvenal	-	juvenal	-
2	1	0 - 1	juvenal	-	juvenal	-
3	3	2 - 5	juvenal	-	juvenal	-
4	7	5 - 8	juvenal	-	juvenal	-
5	10	8 - 11	juvenal	-	juvenal	-
6	13	12 - 15	juvenal	-	juvenal	-
7	16	15 - 18	juvenal	-	juvenal	-
8	20	18 - 21	juvenal	-	juvenal	-
9	23	22 - 24	juvenal	-	juvenal	-
10	26	25 - 27	juvenal	-	juvenal	-
11	29	28 - 30	juvenal	-	juvenal	-
12	32	31 - 34	juvenal	-	juvenal	-
13	35	34 - 37	4	0 - 8	juvenal	-
14	38	37 - 40	16	9 - 23	juvenal	-
15	42	40 - 43	31	24 - 38	3	0 - 5
16	45	43 - 46	46	39 - 53	13	6 - 19
17	46.9	46 – 46.9	61	54 - 68	27	20 - 33
18	complete	-	76	69 - 83	40	34 - 46
19	complete	-	91	84 - 98	54	47 - 60
20	complete	-	99.5	99 - 100	68	61 - 74
21	complete	-	formative	-	81	75 - 87
22	complete	-	formative	-	94	88 - 100
≥23	complete	-	formative	-	formative	-

Table 6.2. Feather counts (means) and masses (expressed as mean percent of total) for three Yellow Warblers (*Setophaga petechia*) salvaged from window strikes. All feathers were individually plucked and weighed together by each plumage region. Values shown in parentheses represent standard deviations (SD).

plumage region	feather count (SD)	feather % mass (SD)
rectrices	12 (SD: 0)	7.09 (SD: 0.63)
remiges	36 (SD: 0)	21.96 (SD: 1.90)
under wing	181 (SD: 13)	3.17 (SD: 0.32)
upper wing	283 (SD: 36)	9.8 (SD: 9.80)
underparts	758 (SD: 137)	32.8 (SD: 5.52)
back/rump	275 (SD: 110)	16.34 (SD: 3.88)
throat	95 (SD: 3)	1.17 (SD: 0.23)
malar	84 (SD: 16)	0.60 (SD: 0.04)
auriculars	286 (SD: 78)	1.61 (SD: 0.17)
supercillium	118 (SD: 90)	0.94 (SD: 0.19)
crown/nape	284 (SD: 74)	4.52 (SD: 0.21)
head	867 (SD: 215)	8.84 (SD: 0.17)
wings + tail	512 (SD: 41)	42.04 (SD: 0.76)
body	1,033 (SD: 125)	49.12 (SD: 4.70)
total	2,412 (SD: 381)	100

Figure 6.1. Photos of plumage development for fledgling Golden-winged Warblers over the post-fledging (dependency) period: 1-30 days post-fledging (labelled on each photo). Each individual shown was either a focal bird of know age (*i.e.*, wearing a transmitter) or a focal bird's brood mate (*i.e.*, also of known age). The first third of the post-fledging period was characterized by rectrix and remige growth but no apparent pre-formative molt (top row). The middle of the post-fledging period was characterized by both rectrix/remige growth and rapid pre-formative molt (middle row). The final third of the post-fledging period was characterized by the conclusion of pre-formative molt, save for the greater coverts which continued developing post-independence (bottom row).

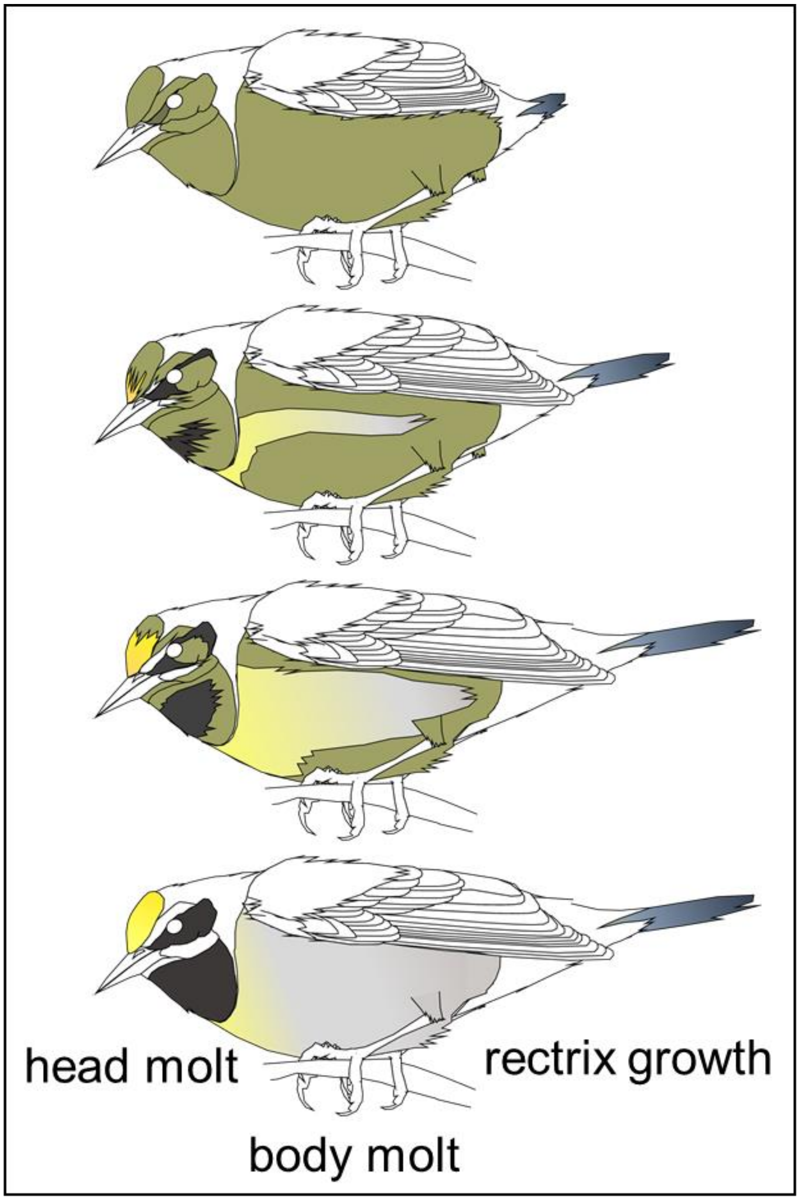

Figure 6.2. A visual molt assessment method employed on juvenile Golden-winged Warblers (*Vermivora chrysoptera*). We assessed pre-formative head molt (left), by estimating the extent of formative plumage occurring across five feather tracts (crown, auriculars, supercillia, malars, and throat) that were then averaged for a total "head molt" extent. To evaluate progress of pre-formative body molt (center), we estimated the extent of formative plumage occurring on the flanks, belly, and breast. To evaluate progress of rectrix development (right), we compared the juvenile tail length to that of the attending parent. To evaluate progress of Across all three plumage patches, we show a gradient in plumage production from nearly 0% (immediately after fledging; top) to 100% formative (bottom).

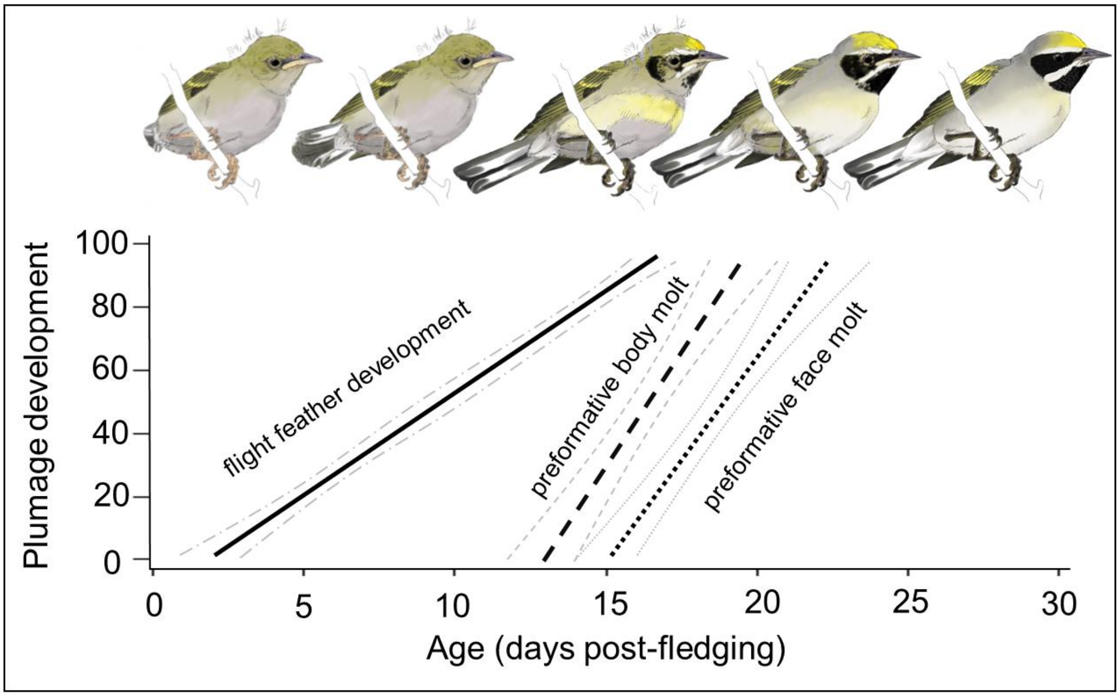

Figure 6.3. Modeled plumage development of fledgling Golden-winged Warblers (*Vermivora chrysoptera*) over the post-fledging period (~30 days). 'Day 0 post-fledging' represents 8 days of age. Relationships represent linear models for flight feathers (remiges/rectrices; solid lines), formative body molt (upper- and underparts; long-dashed lines) and formative head molt (averaged across five feather tracts; short-dashed lines). Dark lines represent model estimates with gray lines representing 95% confidence intervals. Note that, although flight feather development is bounded by 0 – 100%, we accounted for partial remex growth at the time of fledging (~50%) in subsequent models.

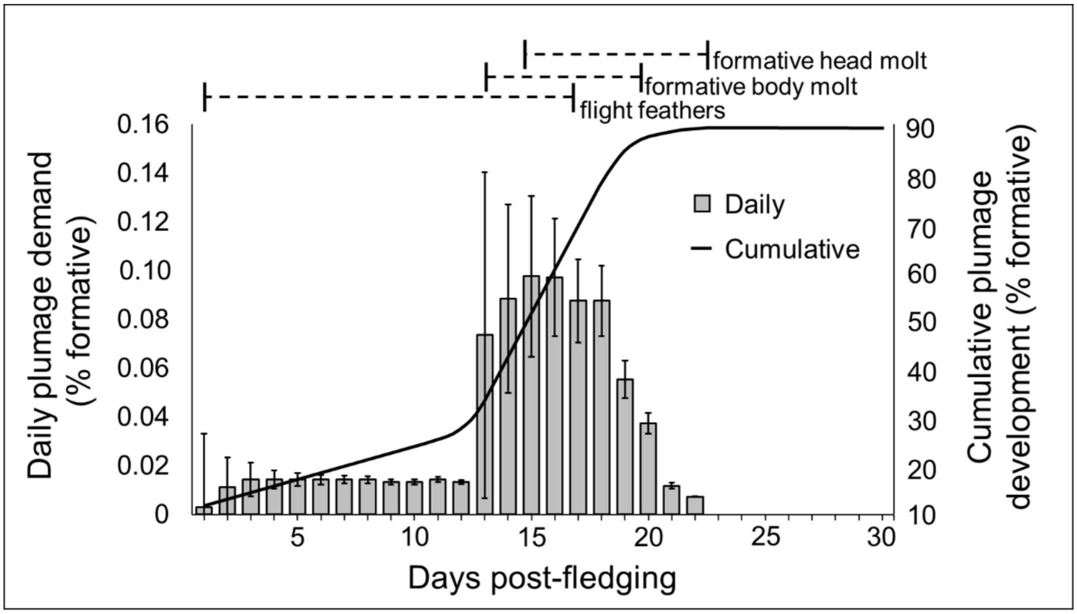

Figure 6.4. Estimates of daily relative plumage demand (% of total mass/day) incurred as fledglings complete juvenal develop growth and molt their formative plumage. Daily plumage demand estimates are shown as gray bars with error bars representing 95% confidence intervals. Additionally shown is the cumulative development of the formative plumage (black line). Formative plumage consists of i) flight feathers (first generation), ii) body plumage (second generation), and head plumage (second generation). Combined estimates are the result of the best-supported linear models for each of the three feather groups. Cumulative plumage development is bounded by 10% and 90% because 10% of formative plumage is already grown at the time of fledging (partial remiges) and the wing coverts began molting at the end of the post-fledging period and continue for some unknown period of time.

CHAPTER 7

WEANING CONFLICT IN A LONG-DISTANCE MIGRATORY SONGBIRD: BALANCING PARENTAL PROVISIONING AND THE ONTOGENY OF INDEPENDENT FORAGING

Abstract

Although parental care is a critical component of many animal lifecycles, conflict between parents and offspring is common. Parent-offspring conflict, often most pronounced during weaning (*i.e.*, weaning conflict), occurs because the motivations of adults and their young do not perfectly align. In passerine birds, weaning conflict may occur during the post-fledging period but few studies have examined this in long-distance migratory species. This is important because many migratory songbirds have highly truncated periods of parental care which may preclude extensive parent-offspring interaction. Patterns of parent-offspring conflict may be more challenging yet in migratory species that exhibit specialized foraging behaviors. Consequently, patterns of parent-offspring interaction in long-distance migratory songbirds differ from those of non-migratory species or those with lengthy parental care periods. In this paper, we investigate parent-offspring conflict and the development of specialized foraging behavior in a Nearctic-Neotropical migratory songbird, the Golden-winged Warbler (*Vermivora chrysoptera*). We specifically asked: 1) How does the ontogeny of independent foraging affect begging and provisioning behavior of fledglings and adults?; (2) Do fledglings develop specialized foraging (probe-and-gape) before cessation of parental care?; and (3) Do foraging behaviors provide evidence of parent-offspring conflict in this rapidly-developing migratory bird? From 2016-17, we radio tracked 63 fledglings from northern Pennsylvania that yielded 887 fledgling observations. Begging effort was lowest among the youngest fledglings but increased until independence (~30 days post-fledging), whereas adults provisioned food most during the middle of the post-fledging period (day 15-20). Fledglings began foraging almost immediately after leaving the nest and rapidly specialized on probe-and-gape maneuvers. The disconnect between peak begging and probability of provisioning suggests that the brevity of parental care in many long-distance migratory songbirds does not preclude conspicuous parent-offspring conflict. Moreover, our foraging observations suggest that Golden-winged Warblers begin foraging earlier than most songbirds (≤ 3 days post-fledging) highlighting the importance of rapid behavioral development in this species. Our study provides one of the few descriptions of early foraging behaviors among passerines and thus offers new insights into ways that parent-offspring interactions may shape behavioral development.

Introduction

Behavioral interactions between parent and offspring profoundly shape behavioral, physiological, and anatomical development (Clutton-Brock 1991, Royal et al. 2012). Although most interactions between parent and offspring are mutually beneficial, their respective needs do not always align perfectly and, in some cases, may conflict sharply (Hamilton 1964, Godfray 1995, Royle et al. 2012). In general, parent-offspring conflict will arise when the costs of investing in current reproduction are higher than the expected benefits of future reproduction (Trivers 1974, Royle et al.

2012). As young near independence, conflict may become especially pronounced as the gap between costs and benefits to parents of additional care widen ("weaning conflict"; Leonard et al. 1991, Godfray and Johnstone 2000). The weaning period can involve raucous solicitation from young (Godfray and Johnstone 2000, Thompson et al. 2013) and aggressive reprimand from parents (Trivers 1974, Leonard et al. 1991).

In passerine birds, weaning occurs during the post-fledging period (Royle et al. 2012, Cox et al. 2014). Early on, young rely entirely upon parents to meet their nutritional requirements (Heinsohn 1991, Anders et al. 1997). Because the energetic demands of growth (Russell et al. 2004), pre-formative molt (Howell et al. 2003), and behavioral development (Greenberg 1987, Weathers and Sullivan 1991) are substantial, young birds may not reach independence for several weeks (McGowan and Woolfenden 1990), months (Heinsohn 1991, Stotz and Balda 1995), or even beyond a year (Langen1996, Russell et al. 2004). As young transition to independent foraging, they require less provisioning by parents (Trivers 1985). However, to the extent that young birds disproportionately benefit from additional provisioning relative to parental fitness, a weaning conflict can result (Hamilton 1964, Heinsohn 1991, Thompson et al. 2003) (Royle et al. 2012). As young are weaned, adults respond less to begging (Middleton et al. 2007), provision less frequently (Heinsohn 1991), and may be aggressive towards young (Leonard et al. 1991). With less parental care, young may resort to elaborate and often dangerous begging displays (Trivers 1974, Godfray and Johnstone 2000). For example, fledgling Pied Babblers (*Turdoides bicolor*) coerce adults into provisioning by shifting their perched begging locations from the safety of trees to the open ground when solicitation is not otherwise rewarded

(Thompson et al. 2013).

Migratory species provide an interesting case to examine weaning conflicts because most rarely extend post-fledging care beyond a few weeks (Naef Daenzer and Grüebler 2016) in contrast to non-migratory species or those with extended parental care (Langen1996, Russell et al. 2004). The short period of parental care for most migratory songbirds might reflect constraints imposed by a short breeding season and the need to prepare for migration (*e.g.*, molt, mass gain; Greenberg and Marra 2005, Hecksecher et al. 2017). In some cases, adults may be forced to abandon late-hatched young to ensure sufficient time to molt and prepare for migration (Hecksecher et al. 2017, Mumme 2018). Juveniles also may need to prospect for their first breeding territory (Bennett et al. 2017, Kramer et al. 2018, Witynski and Bonter 2018) in addition to improving foraging skills before their first fall migration (Sullivan 1988, Baker and Ferree 2016). Despite the critical importance of the post-fledging period, interactions between parents and fledglings remain poorly described and understood (Sykes et al. 1990, Cox et al. 2014). In this paper, we investigate parent-offspring conflict and the development of specialized foraging behavior in a Nearctic-Neotropical migratory songbird, the Golden-winged Warbler (*Vermivora chrysoptera*). The unusual coupling of a short post-fledging period (~30 days; Fiss 2018) with the need to develop specialized foraging behavior (*i.e.*, probe-and-gape inside damaged leaves; Confer et al. 2011, Bellush et al. 2016, Chandler et al. 2016) make the species of special interest. In this study, we specifically asked: 1) How does the ontogeny of independent foraging affect begging and provisioning behavior of fledglings and adults?; (2) Do fledglings develop specialized foraging skills before cessation of parental care?; and (3) Do these behaviors provide evidence for parent-offspring conflict in this time-constrained migratory bird? Populations of Golden-winged Warbler have been steadily declining for > 50 years, but a poor understanding of post-fledging ecology still limits conservation efforts (Rohrbaugh et al. 2016, Sauer et al. 2017). We therefore consider these questions in the context of both behavioral ecology and conservation, and ultimately provide the first evidence of weaning conflict in a long-distance migratory songbird with a highly constrained post-fledging period.

Methods

Study Species

Golden-winged Warblers are obligates of early-successional/shrubland communities (Hunter et al. 2001, Confer et al. 2011). Breeding pairs construct nests on the ground at the base of woody vegetation where eggs are incubated for 11 days, and young fledge eight days later (Bent 1953, Murray and Gill 1976). Upon fledging, broods are split between parents, and are nutritionally dependent for approximately 30 days (Peterson et al. 2016, Fiss 2018). Adult Golden-winged Warblers, are foraging specialists that employ probe-and-gape to extract prey from concealing substrates (Confer et al. 2011, Chandler et al. 2016).

Study Area

We studied Golden-winged Warblers from 2016-17 in the heavily forested portion of north-central Pennsylvania, the Pennsylvania Wilds. This region occurs within the Appalachian Plateau of the northcentral Appalachian Mountains and is characterized by a series of high-elevation ridges (500-750 m.a.s.l.) along the Allegheny Front

(Shultz 1999). The Pennsylvania Wilds region is dominated by mixed-deciduous forest with oak (*Quercus* spp.), maple (*Acer* spp.), and other hardwoods among the most abundant species (Davis 1993, Shultz 1999, McCaskill et al. 2009). We sampled 11 timber harvests where Golden-winged Warblers are known to nest at relatively high densities (Fiss 2018) in Sproul State Forest and Pennsylvania State Game Lands 100 (Centre and Clinton Counties).

Nest searching and Fledgling Telemetry

We searched for nests in each timber harvest every 2-3 days during each nesting season. Our searching regime consisted of three trained surveyors systematically searching each site for nesting cues (*e.g.*, females constructing nests, etc.). We monitored nests every three days increasing frequency as fledging was anticipated (eight days, post-hatch; Martin and Geupel 1993, Confer et al. 2011). We attached radio transmitters to 1-2 randomly-selected nestlings using the figure-eight harness method (Rappole and Tipton 1991) either i) just prior to fledging (7-8 days old) or ii) on the day of fledging (9 days old; "day 1" post-fledging). Transmitter (Blackburn Transmitters Inc., Nacogdoches, TX) batteries lasted 30-35 days and weighed 0.39 g, < 5% the mass of a fledgling (Fair et al. 2010, Peterson et al. 2016; USGS banding permit # 23277).

At the time of transmitter attachment, we banded each warbler with a USGS aluminum band and a single plastic colored leg band. Each day after transmitter deployment, fledglings were tracked on-foot by two trained field technicians between sunrise and 6-hours post-sunrise using a two-element "H-type" Yagi antenna and hand-held receiver. Fledglings were tracked daily until mortality or transmitter failure. Each day we attempted to observe each fledgling for approximately five minutes to collect basic behavioral data: begging effort and parental provisioning. We recorded begging intensity as an estimated percent of time each fledgling spent begging (*i.e.*, 0% represented silence and 100% represented nonstop begging). We trained technicians to round estimates to the nearest 20% as this allowed consistent data collection among observers. Provisioning data consisted of the presence/absence of a provisioning event during the observation period.

Foraging Observations

During 2017, we also conducted foraging observations of all transmittered fledglings. After recording begging and provisioning for each fledgling, we conducted a six-minute foraging observation. We allowed ‘complete’ daily observation to consist of multiple smaller observations, so long as observations were > 20 seconds. We narrated foraging observations into a handheld recorder and compiled them later using the program CowLog (V. 3.0 Pastell 2016). We noted the following behaviors: “glean”, “probe-and-gape”, and “other foraging maneuver”. We defined “glean” as surface contact between the beak and a substrate (Figure 7.1). We defined “probe-and-gape” as probing of the beak into a substrate followed by opening of the bill (Fig. 7.1). Finally, we defined “other” foraging maneuvers as any foraging behavior aside from glean or probe-and-gape.

Statistical Analyses

We modeled behaviors using linear mixed-effects models in R, package *lme4* (R Core Team 2018). Specifically, we created four model sets: linear models to describe fledgling begging as a function of age (i. “begging models”), linear models describing foraging development as a function of fledgling age (ii. “foraging models”), logistic models describing provisioning as a function of fledgling age (iii. “provisioning models”) and finally, logistic models describing provisioning as a function of begging (iv. “behavioral interaction models”). All model sets included a random effect for ‘fledgling ID’ to account for variation among individuals. Although we also attempted to incorporate random effects for sub-brood ID (individually- and nested), these models failed to converge properly, likely because most sub-broods had only a single fledgling (mean = 1.17 fledglings/sub-brood).

Within each model set, we constructed a null (intercept-only) model and compared it against models parameterized with predictor variables. We modeled predictor variables using linear (x), quadratic ($x+x^2$), and cubic relationships ($x+x^2+x^3$) for all model sets. To evaluate the predictive value of our models, we used an information-theoretic approach (Andersen 2007) with model ranking based on Akaike’s Information Criterion adjusted for small sample size (AIC_c; Burnham and Andersen 2003). Foraging models were evaluated using ‘glean’ only, ‘probe-and-gape’ only, and ‘all foraging’.

Results

Over the 2016-17 field seasons, we radio tracked 63 fledglings (25 nests) from the

Pennsylvania Wilds. We collected begging/provisioning data on 887 occasions (days 1 – 30 post-fledging). During the 2017 field season, we collected 243 foraging observations across 24 juveniles that fledged from 13 nests.

Begging, Provisioning, and Behavioral Interactions

Our best-ranked model suggested that begging effort over the post-fledging period was best explained by a cubic model (Table 1). On average, the youngest fledglings begged least (~25% of time) and begging gradually increased until around 25 days post-fledging (~65%) and remained high until independence (Fig. 7.2A). Unlike begging, the probability of adult provisioning over the post-fledging period was best explained by a quadratic model (Table 1) with fledglings ~ day 15-20 post-fledging most likely to be provisioned (probability = 0.5 – 0.6) while the youngest and oldest (> day 25 post-fledging) fledglings were least likely to be provisioned during our observations (Fig. 7.2B). The probability of provisioning increased with begging effort on any given day, except when begging exceeded 60% and provisioning either flattened or declined (Table 1; Fig. 7.2C).

Fledgling foraging development

Models of foraging development suggested linear associations with age for gleaning, probe-and-gaping, and all foraging maneuvers combined (Table 2, Fig. 7.2D). Our models also suggested foraging began almost immediately post-fledging (gleaning first, then probe-and-gaping) though the earliest visual observation of fledgling foraging was three days post-fledging (11 days old; Fig. 7.3A). The first probe-and-gape was observed four days post-fledging. Although both the frequency of foraging maneuvers increased linearly over the post-fledging period, probe-and-gaping increased at a faster rate (Fig. 7.3). After day seven post-fledging, > 50% of all foraging maneuvers were probe-and-gape and this specialized behavior appeared to asymptote at ~ 70% of all maneuvers (Fig 7.3B).

Discussion

Although the period of dependency after fledging is brief for most long-distance migrants (Hecksecher et al. 2017, Mumme 2018), we found evidence of weaning conflict between Golden-winged Warblers during the post-fledgling period. Specifically, we found that the amount of provisioning by parents declined across the second half of the post-fledging period (*i.e.*, weaning) despite increased begging by young, Thus, brevity of parental care in many songbirds (Greenberg and Marra 2005) does not preclude conspicuous parent-offspring conflict.

Though parental care accrues fitness benefits for both adults and their offspring, our observations suggest that benefits become increasingly asymmetric as fledglings approach independence (Godfray and Johnstone 2000, Royle et al. 2012). In particular, as young birds improve foraging skills and become more self-reliant, the benefits of additional parental care decline for parents (Hamilton 1964, Royle et al. 2012), eventually yielding a benefit/cost ratio < 1.0 for parents (Trivers 1974, 1985) driving the weaning conflict in this system, as described in many other animal systems (Trivers 1974, Drummond 1987, Godfray and Johnstone 2000, Royle et al. 2012, Bowers et al. 2019).

Our finding that adults were most likely to provision during the middle of the post-fledging period despite only receiving intermediate begging signals, suggests adults use signals other than begging to gauge fledgling nutritional need. Plumage is often an important cue used by adult birds to allocate care (Ligon and Hill 2010). For example, young American Coots (*Fulica americana*) with bright head plumes were provisioned most because such plumage, counterintuitively, signals nutritional need (Lyon et al. 1994). Golden-winged Warbler fledglings, like young coots, may offer plumage-based cues of nutritional need to parents as the period of maximum provisioning probability (~ day 15, post-fledging) corresponds with the height of pre-formative molt (formative plumage acquired at ~20-25 days post-fledgling; McNeil, unpublished data). Interestingly, the pre-formative molt is understood to proceed more slowly in most species (Howell et al. 2003). Even other migratory Parulids require 1-2 months to complete pre-formative molt after fledgling (*e.g.*, Orange-crowned Warblers [*Oreothlypis celata*], Foster 1967; Prairie Warbler [*Setophaga discolor*], Nolan 1978). During pre-formative molt, fledglings wear a conspicuous, mottled plumage comprised of newly-grown formative feathers and older juvenal feathers. Because molt is energetically expensive, (Blackmore 1969, Cyr et al. 2008), plumage may represent a more useful (*i.e.*, honest) indicator of nutritional need than begging alone (Godfray 1991, 1995, Bowers et al. 2019). As such, other species molt without parental care during the pre-migration period of habitat prospecting (Brown and Taylor 2015). Golden-winged Warbler may therefore be unique among passerines in this pattern of provisioning maximized on a period of molt.

Our study showed that young birds improved foraging skills throughout the post-fledging period, and initiated foraging more rapidly than expected (first observation: 2 days post-fledging, 11 days old). Based on these observations, Golden-winged Warblers initiate foraging earlier than most other passerine species reported to date (Horwich 1969, Davies 1976, Haftorn 1992), highlighting the importance of rapid development in this species. Such rapid foraging development is surprising because Golden-winged Warbler fledglings are largely flightless at this age (Naef Daenzer and Grüebler 2016, Peterson et al. 2016). Still, gleaning behavior was subtle, usually involving only small movements of the head and neck and did not require strong locomotion skills (Fig. 7.1). Such stationary foraging contrasts with species like dippers (*Cinclus* spp.) which must develop strong locomotive skills before foraging initiation (Yoerg 1998, Middleton et al. 2007). Indeed, it is likely that beginning with simple foraging maneuvers like gleaning facilitated the transition to specialized probe-and-gape shortly thereafter. Although we did not quantify prey capture rates, we expect early foraging attempts were largely unsuccessful (Davies 1976). While early foraging attempts likely contributed little to nutritional intake, practice is a critical precursor to self-feeding (Davies 1976, Haftorn 1992, Baker and Ferree 2016).

The rapid shift from predominantly generalized to specialized foraging represents a major milestone for young birds. Though foraging development in migratory songbirds has been seldom studied in the wild, aviary experiments by Greenberg (1987a, b) demonstrated that a similar species, the Worm-eating Warbler (*Helmitheros vermivorum*), also used specialized foraging maneuvers within the first few weeks of fledging. The shift from 100% gleaning to 70% probe-and-gape in

Golden-winged Warblers matches almost exactly the maneuver rates used by foraging adults (71% probe-and-gape; Chandler et al. 2016). Delaying probe-and-gape maneuvers until late in the post-fledging period may partly reflect the inherent riskiness of the behavior, which is noisy and requires compromised vigilance as birds insert the head into a substrate (Remsen and Parker 1984, Rosenberg 1997, Chandler et al. 2016). Indeed, reliance upon probe-and-gape maneuvers may explain why *Vermivora* spp. are obligate members of mixed-species flocks during the non-breeding season (Ficken and Ficken 1974, Chandler et al. 2016). Fledglings, which already are vulnerable to predation (Cox et al. 2014), should be at even greater risk than adults due to their limited mobility. Our observations are consistent with the idea that both food subsidies and cultural transmission (*i.e.*, learning) from parents remain critically important to fledglings as they develop their abilities to forage and evade predators. Indeed, on numerous occasions, we observed fledglings mimicking parental behavior when foraging in close proximity (<0.5 m) to adults.

Despite reducing the proportion of foraging time spent gleaning, gleaning rates (maneuvers/min) increased over time among Golden-winged Warbler fledglings. Young birds, therefore, do not replace generalist foraging behaviors (*i.e.*, glean) with specialized maneuvers, but rather expand their repertoire- presumably to optimize nutritional intake (Charnov 1976, Greenberg 1987a, b). Our observations of increased use of 'rare' foraging maneuvers like fly-catching and hover-gleaning as fledglings grew older and better coordinated further supported this idea (Table 1; Chandler et al. 2016). A diverse repertoire of foraging skills may be especially important for young birds during migration or non-breeding periods within novel habitat types (Greenberg

1987b, Bellush et al. 2016, Chandler et al. 2016). In fact, all wood-warblers become generalist foragers during migration (Martin and Karr 1990) as specialized resources become less predictable.

In recent years, scientists have increasingly recognized the need to understand the full annual cycle in migratory birds (Faaborg et al. 2010, Naef Daenzer and Grüebler 2016). The post-fledging period is important because fledglings incur high mortality (Cox et al. 2014) that disproportionately impacts avian population dynamics (Thomson et al. 1997, Robinson et al. 2004). Understanding post-fledging ecology is especially critical for imperiled species like the Golden-winged Warbler (Rohrbaugh et al. 2016). Our study marks a first exploration into the behavioral ontogeny in a long-distance migratory songbird, and suggests that parent-offspring interactions resemble those of non-migratory species and those with lengthy parental care (Langen1996, Russell et al. 2004). To expand upon our work, future researchers should attempt to quantify prey intake/foraging maneuver to allow quantification of foraging efficiency, a more informative metric of foraging development (Davies et al. 1976). Moreover, we only assessed development within the Appalachian Mountains, a region characterized by chronic population declines, thought to be driven, in part, by reproductive failure (Confer et al. 2011, Rohrbaugh et al. 2016). A comparison of fledgling ontogeny between the Appalachians and the Great Lakes, where the species is somewhat more secure, may provide additional insights into the developmental factors associated with species decline (Rosenberg et al. 2016).

Acknowledgments

This project would not have been possible without funding through the Pennsylvania Game Commission and the U.S. Department of Agriculture (USDA) - Natural Resource Conservation Service (NRCS). We are grateful for the exceptional nest-searching and radio telemetry efforts of many our field technicians. We are very grateful to the efforts of Hayley Hall for transcribing audio recorded fledgling observations. We also thank the Pennsylvania Bureau of Forestry and the Pennsylvania Game Commission for access to Delaware State Forest, Sproul State Forest and State Game Lands 100. All warblers were handled and banded under USGS banding permit # 23277. This study was conducted in accordance with the guidelines of the Institutional Animal Care and Use Committees of both Cornell University (#2013-029) and Indiana University of Pennsylvania (#14-1314).

Works Cited

Anderson, D. R. (2007). Model based inference in the life sciences: a primer on evidence. Springer Science & Business Media.

Anders, A. D., D. C. Dearborn, J. Faaborg and F. R. T. Iii (1997). Juvenile survival in a population of Neotropical migrant birds. Conservation Biology 11:698-707.

Baker, J. and E. D. Ferree (2016) Foraging ontogeny in a suburban population of Black Phoebes (*Sayornis nigricans*). The Wilson Journal of Ornithology 128:368-377.

Barg, J. J. and R. L. Mumme (1994). Parental recognition of juvenile begging calls in the Florida scrub jay. The Auk 111:459-464.

Bellush, E. C., J. Duchamp, J. L. Confer, and J. L. Larkin. (2016). Influence of plant species composition on Golden-winged Warbler foraging ecology in north-central Pennsylvania. Pp. 95–108 in H. M. Streby, D. E. Andersen, and D. A. Buehler (Eds.). Golden-winged Warbler ecology, conservation, and habitat management. Studies in Avian Biology (no. 49). CRC Press, Boca Raton, Florida, USA.

Bennett, R. E., Barker Swarthout, S., Bolsinger, J. S., Rodewald, A. D., Rosenberg, K. V., & Rohrbaugh, R. W. (2017). Extreme genetic similarity does not predict non-breeding distribution of two closely related warblers. Journal of Field Ornithology 88:156-168.

Blackmore, F. H. (1969). The effect of temperature, photoperiod and molt on the energy requirements of the House Sparrow, *Passer domesticus*. Comparative Biochemistry and Physiology 30:433-444.

Bowers, K. E., J. B. Jenkins, A. J. Mueller, K. D. Miller, C. F. Thompson, and S. K. Sakaluk. (2019). Condition-Dependent Begging Elicits Increased Parental Investment in a Wild Bird Population. The American Naturalist 193 (5). https://doi.org/10.1086/702848

Brown, J. M. and P. D. Taylor (2015). Adult and hatch-year blackpoll warblers exhibit radically different regional-scale movements during post-fledging dispersal. Biology Letters 11:20150593.

Burnham, K. P. and D. R. Anderson (2003). Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media, Berlin, Germany.

Bent, A. C. (1953). Life Histories of North American wood warblers. Part One. Dover Publications, Inc., New York, New York, USA.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. Theoretical Population Biology 9:129-136.

Chandler, R. B., S. Tolfree, J. Gerwin, C. Smalling, L. Chavarría-Duriaux, G. Duriaux, and D. I. King (2016). Conservation implications of Golden-winged Warbler social and foraging behaviors during the nonbreeding season. Pp. 175–192 in H. M. Streby, D. E. Andersen, and D. A. Buehler (Eds.). Golden-winged Warbler ecology, conservation, and habitat management. Studies in Avian Biology (no. 49). CRC Press, Boca Raton, Florida, USA.

Clutton-Brock, T. H. (1991). The evolution of parental care. Princeton University Press, Princeton, New Jersey, USA.

Confer, J. L., P. Hartman and A. Roth. (2011). Golden-winged Warbler (*Vermivora chrysoptera*). In A. F. Poole, editor. The birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA.

Cox, W. A., F. R. Thompson, A. S. Cox and J. Faaborg (2014). Post-fledging survival in passerine birds and the value of post-fledging studies to conservation. Journal of Wildlife Management 78:183-193.

Cyr, N. E., M. Wikelski and L. M. Romero (2008). Increased energy expenditure but decreased stress responsiveness during molt. Physiological and Biochemical Zoology 81:452-462.

Davies, N. B. (1976). Parental care and the transition to independent feeding in the young spotted flycatcher (*Muscicapa striata*). Behaviour, 59:280-294.

Davis, A. F. (1993). Rare Wetland Plants and Their Habitats in Pennsylvania. Proceedings of the Academy of Natural Sciences of Philadelphia 144:254-262.

Drummond, H. (1987). A review of parent-offspring conflict and brood reduction in the Pelecaniformes. Colonial Waterbirds 10:1-15.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson and S. C. Latta. (2010). Conserving migratory land birds in the New World: Do we know enough?. Ecological Applications 20:398-418.

Fair, J., E. Paul and J. Jones (2010). Guidelines to the Use of Wild Birds in Research. Ornithological Council. Washington, D.C., USA.

Ficken, M. S. and R. W. Ficken (1974). Is the Golden-winged Warbler a social mimic of the Black-capped Chickadee?. The Wilson Bulletin 86:468-471.

Fiss, C. J. (2018). Multiscale Habitat Selection and Movement of Fledgling Golden-Winged Warblers (*Vermivora chrysoptera*) in Two Managed Mixed-Oak Forest Communities of Northern Pennsylvania (Unpublished Master’s Thesis). Indiana University of Pennsylvania, Indiana, Pennsylvania, USA.

Foster, M. S. (1967). Molt cycles of the Orange-crowned Warbler. The Condor 69:169-200.

Gamero, A. and P. M. Kappeler (2015). Slow development of foraging skills and parental costs of family-living in a semi-precocial, non-cooperatively breeding bird. Behavioral Ecology and Sociobiology 69:1301-1309

Greenberg, R. (1987a). Development of dead leaf foraging in a tropical migrant warbler. Ecology 68:130-141.

Greenberg, R. (1987b). Seasonal foraging specialization in the Worm-eating Warbler. Condor 89:158-168.

Greenberg, R., and P. P. Marra (2005). Birds of two worlds: the ecology and evolution of migration. John Hopkins University Press, Baltimore Maryland, USA.

Godfray, H. C. J. (1991). Signalling of need by offspring to their parents. Nature 352:328.

Godfray, H. C. J. (1995). Signaling of need between parents and young: parent-offspring conflict and sibling rivalry. The American Naturalist 146:1-24.

Haftorn, S. (1992). Ontogeny of food storing in titmice *Parus* spp. The Ibis 134:69-71.

Hamilton, W. D. (1964). The genetical evolution of social behaviour. Journal of Theoretical Biology 7:1-16.

Heckscher, C. M., M. Gutierrez Ramirez and A. H. Kneidel (2017). Reproductive outcomes determine the timing of arrival and settlement of a single-brooded Nearctic–Neotropical migrant songbird (*Catharus fuscescens*) in South America. The Auk 134:842-856.

Heinsohn, R. G. (1991). Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged choughs. The American Naturalist 137:864-881.

Horwich, R. H. (1969). Behavioral ontogeny of the mockingbird. The Wilson Bulletin 81:87-93.

Howell, S. N., C. Corben, P. Pyle and D. I. Rogers (2003). The first basic problem: a review of molt and plumage homologies. Condor 105:635-653.

Hunter, W. C., D. A. Buehler, R. A. Canterbury, J. L. Confer and P. B. Hamel (2001).

Conservation of disturbance-dependent birds in eastern North America. Wildlife Society Bulletin 29:440-455.

Jenni, L. and R. Winkler (2011). Moult and ageing of European passerines. A and C Black. London, UK.

Larkin, J. L. and M. H. Bakermans (2012). Golden-winged Warbler, *Vermivora chrysoptera*. Second Atlas of Breeding Birds in Pennsylvania. Penn State University Press, State College, Pennsylvania, USA.

Katsnelson, E., U. Motro, M. W. Feldman and A. Lotem (2010). Individual-learning ability predicts social-foraging strategy in house sparrows. Proceedings of the Royal Society of London B: Biological Sciences rspb20101151.

Kilner, R. and R. A. Johnstone (1997). Begging the question: are offspring solicitation behaviours signals of need?. Trends in Ecology & Evolution 12:11-15.

Kramer, G. R., H. M. Streby, S. M. Peterson, J. A. Lehman, D. A. Buehler, P. B. Wood ... and D. E. Andersen (2017). Nonbreeding isolation and population-specific migration patterns among three populations of Golden-winged Warblers. The Condor 119:108-121.

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.

Kopachena, J. G. and J. B. Falls (1993). Postfledging parental care in the white-throated sparrow (*Zonotrichia albicollis*). Canadian Journal of Zoology 71:227-232.

Langen, T. A. (1996). Skill acquisition and the timing of natal dispersal in the white-throated magpie-jay, *Calocitta formosa*. Animal Behaviour 51:575-588.

Leonard, M. L., A. G. Horn, and L. M. Ratcliffe (1991). Parental aggression in black-capped chickadees. Behavioral Ecology 2:228-233.

Ligon, R. A. and G. E. Hill (2010). Feeding decisions of eastern bluebirds are situationally influenced by fledgling plumage color. Behavioral Ecology 21:456-464.

Martin, T. E. and G. R. Geupel (1993). Nest-Monitoring Plots: Methods for Locating Nests and Monitoring Success. Journal of field Ornithology 64:507-519.

Martin, T.E. and J. R. Karr (1990). Behavioral plasticity of foraging maneuvers of migratory warblers: multiple selection periods for niches? Studies in Avian Biology 13:353-359.

Martin, T. E. and Li, P. 1992. Life history traits of open-vs. cavity-nesting birds. Ecology 73:579-592.

McCaskill, G. L., W. H. McWilliams, C. A. Alerich, B. J. Butler, S. J. Crocker, G. M. Domke … and J. A. Westfall (2009). Pennsylvania’s Forests 2009. U.S. Department of Agriculture, Forest Service, Northern Research Station. Newtown Square, Pennsylvania, USA.

McCarty, J. P. (1996). The energetic cost of begging in nestling passerines. The Auk 113:178-188.

McGowan, K. J. and G. E. Woolfenden (1990). Contributions to fledgling feeding in the Florida scrub jay. The Journal of Animal Ecology 59:691-707.

McKinnon, E. A. and O. P. Love (2018). Ten years tracking the migrations of small landbirds: Lessons learned in the golden age of bio-logging. The Auk 135:834-

856.

McNeil, D. J, C. J. Fiss, E. M. Wood, J. E. Duchamp, M. J. Bakermans, and J. L. Larkin. (2018). Using a Natural Reference System to Evaluate Songbird Habitat Restoration. Avian Conservation and Ecology 13:22.

McNeil, D. J., K. R. Aldinger, M. H. Bakermans, J. A. Lehman, A. C. Tisdale, J. A. Jones, ... and J. L. Larkin (2017). An evaluation and comparison of conservation guidelines for an at-risk migratory songbird. Global Ecology and Conservation 9:90-103.

Middleton, H. A., D. J. Green and E. A. Krebs (2007). Fledgling begging and parental responsiveness in American dippers (*Cinclus mexicanus*). Behaviour 144:485-501.

Mumme, R. L. (2018). The trade-off between molt and parental care in Hooded Warblers: Simultaneous rectrix molt and uniparental desertion of late-season young. The Auk 135:427-438.

Murray, Jr., B. G. and F. B. Gill (1976). Behavioral interactions of Blue-winged and Golden-winged Warblers. Wilson Bulletin 88:231-254.

Naef Daenzer, B. and M. U. Grüebler (2016). Post-fledging survival of altricial birds: Ecological determinants and adaptation. Journal of Field Ornithology 87:227-250.

Nice, M. M. (1962). Development of behavior in precocial birds. Transcripts of Linnaean Society of New York 8:1-211.

Nolan Jr, V. (1978). The ecology and behavior of the prairie warbler, *Dendroica discolor*. Ornithological monographs; no. 26.

Owens, I. P. and P. M. Bennett (2000). Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. Proceedings of the National Academy of Sciences 97:12144-12148

Pastell, M. (2016). CowLog – Cross-Platform Application for Coding Behaviours from Video. Journal of Open Research Software. 4(1), p.e15. DOI: http://doi.org/10.5334/jors.113

Peterson, S. M. (2014). Landscape productivity and the ecology of brood division in Golden-winged Warblers in the Western Great Lakes Region (Unpublished Masters Thesis). University of Minnesota, Saint Paul, Minnesota, USA.

Peterson, S. M., H. M. Streby, and D. E. Andersen. (2016). Spatially explicit models of full-season productivity and implications for landscape management of Golden-winged Warblers in the western Great Lakes region. Pp. 141–160 in H. M. Streby, D. E. Andersen, and D. A. Buehler (Eds.). Golden-winged Warbler ecology, conservation, and habitat management. Studies in Avian Biology (no. 49), CRC Press, Boca Raton, Florida, USA.

Pond, C. M. (1977). The significance of lactation in the evolution of mammals. Evolution 31:177-199.

R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Remsen Jr, J. V. and T. A. Parker (1984). Arboreal dead-leaf-searching birds of the Neotropics. The Condor 86:36-41.

Rohrbaugh, R. W., D. A. Buehler, S. B. Swarthout, D. I. King, J. L. Larkin, K. V.

Rosenberg, A. M. Roth, R. Vallender, and T. Will. (2016). Conservation perspectives: Review of new science and primary threats to Golden-winged Warblers. Pp. 207–215 in H. M. Streby, D. E. Andersen, and D. A. Buehler (Eds.). Golden-winged Warbler ecology, conservation, and habitat management. Studies in Avian Biology (no. 49), CRC Press, Boca Raton, Florida, USA.

Royle, N. J., P. T. Smiseth and M. Kölliker (2012). The Evolution of Parental Care. Oxford University Press, Oxford, UK.

Recher, H. F. and J. A. Recher (1969). Comparative foraging efficiency of adult and immature Little Blue Herons (*Florida caerulea*). Animal Behaviour 17:320-22.

Robinson, R. A., R. E. Green, S. R. Baillie, W. J. Peach and D. L. Thomson (2004). Demographic mechanisms of the population decline of the Song Thrush *Turdus philomelos* in Britian. Journal of Animal Ecology 73:670–682.

Rosenberg, K. V. (1997). Ecology of dead-leaf foraging specialists and their contribution to Amazonian bird diversity. Ornithological Monographs 48:673-700.

Rosenberg, K. V., T. Will, D. A. Buehler, S. B. Swarthout, W. E. Thogmartin, R. E. Bennett and R. B. Chandler (2016). Dynamic distributions and population declines of Golden-winged Warblers. Pp. 3–28 in H. M. Streby, D. E. Andersen, and D. A. Buehler (Eds.). Golden-winged Warbler ecology, conservation, and habitat management. Studies in Avian Biology (no. 49), CRC Press, Boca Raton, Florida, USA.

Royle, N. J., I. R. Hartley and G. A. Parker (2002). Begging for control: when are offspring solicitation behaviours honest?. Trends in Ecology & Evolution 17:434-440.

Russell, E. M., Y. Yom-Tov and E. Geffen (2004). Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. Behavioral Ecology 15:831-838.

Sauer, J. R., D. K. Niven, J. E. Hines, D. J. Ziolkowski, Jr, K. L. Pardieck, J. E. Fallon, and W. A. Link. (2017). The North American Breeding Bird Survey, Results and Analysis 1966 - 2015. Version 2.07.2017 USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Schekkerman, H. and A. Boele (2009). Foraging in precocial chicks of the black-tailed godwit *Limosa limosa*: vulnerability to weather and prey size. Journal of Avian Biology 40:369-379.

Shultz, C. H. (1999). The Geology of Pennsylvania. Pennsylvania Geological Survey, Harrisburg, Pennsylvania, USA.

Sullivan, K. A. (1988). Ontogeny of Time Budgets in Yellow-eyed Juncos: Adaptation to Ecological Constraints. Ecology 69:118-124.

Soler, M., J. J. Palomino, J. G. Martinez and J. J. Soler (1994). Activity, survival, independence and migration of fledgling great spotted cuckoos. The Condor 96:802-805.

Stotz, N.G. and R.P. Balda (1995). Cache and recovery behavior of wild pinyon jays in northern Arizona. The Southwestern Naturalist 40:180-184

Sykes, P. W., J. W. Carpenter, S. Holzman, and P. H. Geissler. (1990). Evaluation of three miniature radio transmitter attachment methods for small passerines.

Wildlife Society Bulletin 18:41-48.

Trivers, R. L. (1974). Parent-offspring conflict. Integrative and Comparative Biology 14:249-264.

Trivers, R. L. (1985). Social Evolution. Benjamin Cummings Publishing Company. Menlo Park, California, USA.

Thompson, A. M., Raihani, N. J., Hockey, P. A. R., Britton, A., Finch, F. M., & Ridley, A. R. (2013). The influence of fledgling location on adult provisioning: a test of the blackmail hypothesis. Proceedings of the Royal Society B: Biological Sciences 280: 20130558.

Thomson, D. L., S. R. Baillie and W. J. Peach (1997). The demography and age-specific annual survival of song thrushes during periods of population stability and decline. Journal of Animal Ecology 66:414-424.

Vitz, A. C. and A. D. Rodewald. 2010. Movements of fledgling Ovenbirds (*Seiurus aurocapilla*) and Worm-eating Warblers (*Helmitheros vermivorum*) within and beyond the natal home range. Auk 127:364-371.

Vormwald, L. M., M. L. Morrison, H. A. Mathewson, M. C. Cocimano and B. A. Collier (2011). Survival and movements of fledgling Willow and Dusky flycatchers. The Condor 113:834-842.

Weathers, W. W. and K. A. Sullivan (1991). Foraging efficiency of parent juncos and their young. Condor 93:346-353.

Woolfenden, G. E. (1978). Growth and survival of young Florida scrub jays. Wilson Bulletin 90:1-18.

Witynski, M. L. and D. N. Bonter (2018). Crosswise migration by Yellow Warblers, Nearctic-Neotropical passerine migrants. Journal of Field Ornithology 89:37-46.

Yoerg, S. I. (1998). Foraging behavior predicts age at independence in juvenile Eurasian dippers (*Cinclus cinclus*). Behavioral Ecology 9:471-477.

Tables and Figures

Table 7.1. Models of Golden-winged Warbler begging behavior as a function of age (top), adult provisioning as a function of fledgling age (center), and adult provisioning as a function of fledgling begging (bottom). Models were compared against a null model and ranked in descending order of Akaike's Information Criterion adjusted for small sample size (AICc). We considered models within <2.0 ΔAICc to be competing models and statistically equivalent. AICc weight is depicted as "w", cumulative AICc weight is depicted as "cum. wgt.", Log likelihood is depicted as "LL", and the number of model parameters is represented by "k". The "null" model includes a Y-intercept and random effects.

adult provisioning ~ fledgling begging						
Model name	k	AIC_c	ΔAIC_c	w	cum. wgt	LL
age + age^2 + age^3	5	2610.94	0.00	0.70	0.70	-1300.43
age + age^2	4	2612.66	1.72	0.30	1.00	-1302.31
age	3	2625.16	14.22	0.00	1.00	-1309.57
null	2	2692.04	81.10	0.00	1.00	-1344.01
adult provisioning ~ fledgling age						
age + age^2	4	1007.87	0.00	0.72	0.72	-499.91
age + age^2 + age^3	5	1009.73	1.87	0.28	1.00	-499.83
null	2	1037.92	30.06	0.00	1.00	-516.95
age	3	1038.29	30.42	0.00	1.00	-516.13
fledgling begging ~ fledgling age						
age + age^2 + age^3	6	951.10	0.00	0.80	0.80	-469.50
age + age^2	5	953.89	2.79	0.20	1.00	-471.91
age	4	995.71	44.61	0.00	1.00	-493.83
null	3	1038.29	87.19	0.00	1.00	-516.13

Table 7.2. Models of Golden-winged Warbler foraging behavior as a function of age. We modeled glean (top), probe-and-gape (center), and all foraging maneuvers combined (bottom). Models were compared against a null model and ranked in descending order of Akaike's Information Criterion adjusted for small sample size (AIC_c). We considered models within <2.0 ΔAIC_c to be competing models and statistically equivalent. AICc weight is depicted as "w", cumulative AICc weight is depicted as "cum. wgt.", Log likelihood is depicted as "LL", and the number of model parameters is represented by "k". The "null" model includes a Y-intercept and random effects.

glean						
Model name	k	AIC_c	ΔAIC_c	w	cum. wgt	LL
age	4	692.8	0.00	0.99	0.99	-342.31
null	3	703.32	10.52	0.01	1.00	-348.61
age + age^2	5	706.88	14.09	0.00	1.00	-348.31
age + age^2 + age^3	6	723.85	31.06	0.00	1.00	-355.75
probe-and-gape						
age	4	894.51	0.00	1.00	1.00	-443.17
age + age^2	5	908.11	13.60	0.00	1.00	-448.93
age + age^2 + age^3	6	923.87	29.36	0.00	1.00	-455.76
null	3	939.93	45.42	0.00	1.00	-466.91
all foraging combined						
age	4	1008.34	0.00	1.00	1.00	-500.09
age + age^2	5	1021.21	12.87	0.00	1.00	-505.48
age + age^2 + age^3	6	1038.39	30.04	0.00	1.00	-513.01
null	3	1063.96	55.62	0.00	1.00	-528.93

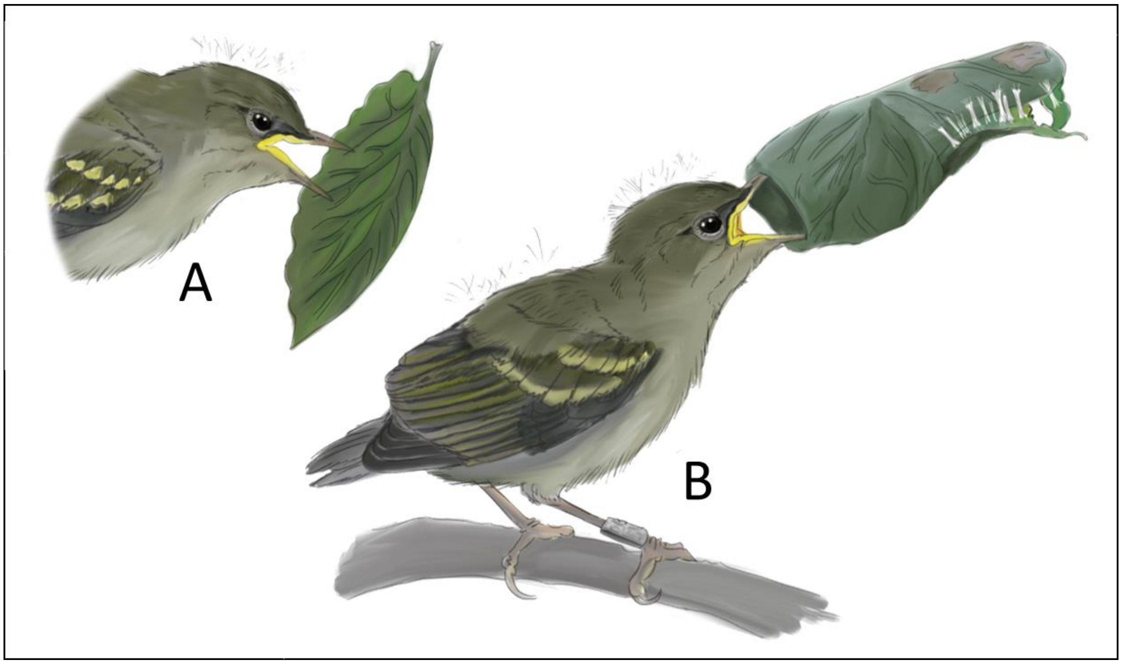

Figure 7.1. Foraging maneuvers used most by fledgling Golden-winged Warblers. The two most commonly-observed were the generalist maneuver “glean” (A) and the specialist maneuver “probe-and-gape” (B). A glean was defined as surface contact between the beak and a substrate (*e.g.*, a flat leaf). A “probe-and-gape” was defined as insertion of the beak into a substrate (*e.g.*, a curled leaf) followed by spreading of the bill.

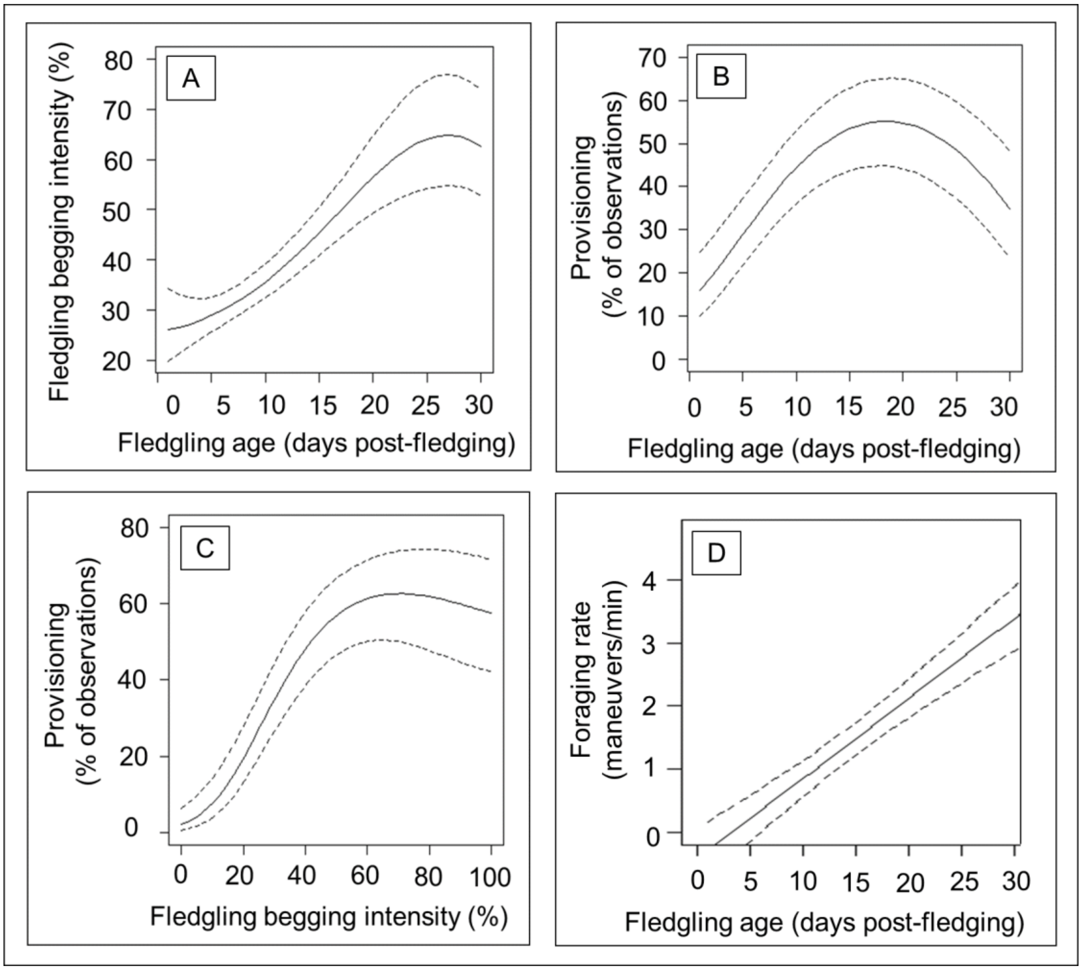

Figure 7.2. Best-ranked linear mixed-effects models of fledgling begging effort as a function of fledgling age (A), adult provisioning as a function of fledgling age (B), adult provisioning as a function of fledgling begging effort (C), and fledgling foraging as a function of fledgling age (D). The top ranked foraging rate (all maneuvers combined) model included a linear term for fledgling age. Solid lines represent model parameter estimates while dashed lines represent 95% confidence intervals.

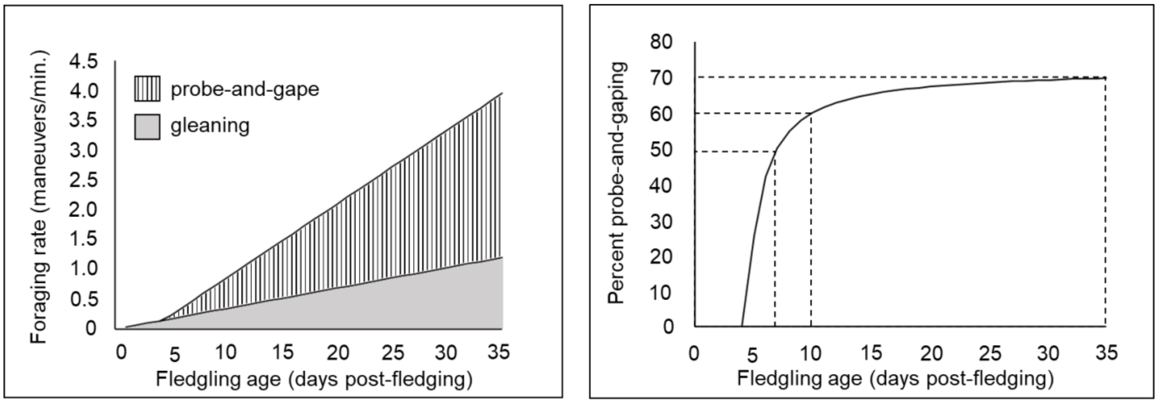

Figure 7.3. Linear models suggested that gleaning and probe-and-gaping both increased over the post-fledging period for fledgling Golden-winged Warblers. Although both increased (left), probe-and-gaping, the specialist foraging behavior, increased at a faster rate and was the dominant foraging type after seven days post-fledging (right). Dashed lines indicate when probe-and-gape reached 50% of all foraging (7 days post-fledging), 60% (10 days post-fledging) and 70% (35 days post-fledging).

CHAPTER 2 APPENDIX

This appendix contains a summary of the data that was analyzed in Chapter 2 with the following elements:

- Table 2A: Models of detection probability for Golden-winged Warblers within restored early-successional forests in the Appalachian Mountains (top) and Great Lakes (bottom). The top ten models are shown in each candidate set. We modeled Golden-winged Warbler use of restored habitats using occupancy in the Appalachian Mountains and hierarchical distance models in the Great Lakes. Shown are models for detection probability (p) with associated detection covariates: Julian date (“date”), minutes since sunrise (“mssr”), Beautfort wind index (“wind”), and percent cloud cover (“cloud”). Also shown are the number of model parameters (k), model weight (w), and Δ Akaike’s Information Criterion adjusted for small sample size (ΔAICc).
- Table 2B: Models of occupancy and density for Golden-winged Warblers within restored early-successional forests in the Appalachian Mountains (top) and Great Lakes (bottom). The top ten models are shown in each candidate set. All models include a detection probability (*p*) with associated detection covariates: Julian date (“date”), minutes since sunrise (“mssr”), Beautfort wind index (“wind”), and percent cloud cover (“cloud”). Additionally, models include components for occupancy (Ψ) and density (λ) with associated covariates: latitude (lat), longitude (long) and elevation (elev). Also shown are

the number of model parameters (k), model weight (w), and Δ Akaike's Information Criterion adjusted for small sample size (ΔAIC_c).

- Table 2C: Models of occupancy and density for Golden-winged Warblers within restored early-successional forests in the Appalachian Mountains (top) and Great Lakes (bottom). The top ten models are shown in each candidate set. All models include a detection probability (*p*) with associated detection covariates: Julian date ("date"), minutes since sunrise ("mssr"), Beautfort wind index ("wind"), and percent cloud cover ("cloud"). Additionally, models include components for occupancy (Ψ) and density (λ) with associated covariates: latitude (lat), longitude (long) and elevation (elev). Also shown are the number of model parameters (k), model weight (w), and Δ Akaike's Information Criterion adjusted for small sample size (ΔAIC_c).
- Figure 2A: Projections of Golden-winged Warbler density in Western Minnesota (A), central Minnesota (B) and the Minnesota/Wisconsin boarder (C).
- Figure 2B: Projections of Golden-winged Warbler occupancy in Eastern Pennsylvania (A), central Pennsylvania (B) and southcentral Pennsylvania (C). Gray lines indicate mean estimates of occupancy

Table 2A. Models of detection probability for Golden-winged Warblers within restored early-successional forests in the Appalachian Mountains (top) and Great Lakes (bottom). The top ten models are shown in each candidate set. We modeled Golden-winged Warbler use of restored habitats using occupancy in the Appalachian Mountains and hierarchical distance models in the Great Lakes. Shown are models for detection probability (*p*) with associated detection covariates: Julian date (“date”), minutes since sunrise (“mssr”), Beaufort wind index (“wind”), and percent cloud cover (“cloud”). Also shown are the number of model parameters (k), model weight (w), and Δ Akaike’s Information Criterion adjusted for small sample size (ΔAIC_c).

Detection models – Occupancy (Appalachian Mountains)			
Model	k	ΔAIC_c	w
p(date + mssr + wind)	5	0.00	0.48
p(date + cloud + mssr + wind)	6	1.51	0.23
p(date + wind)	4	3.17	0.10
p(date + mssr)	4	3.56	0.08
p(date + cloud + wind)	5	4.33	0.06
p(date + cloud + mssr)	5	5.12	0.04
p(mssr + wind)	4	8.17	0.01
p(mssr)	3	9.48	0.00
p(date)	3	9.68	0.00
p(cloud + mssr + wind)	5	10.13	0.00

Detection models – Hierarchical Distance (Great Lakes)			
p(wind)	6	0.00	0.57
p(.)	3	2.17	0.19
p(date)	4	3.51	0.10
p(mssr)	4	4.23	0.07
p(cloud)	4	4.25	0.07

Table 2B. Models of occupancy and density for Golden-winged Warblers within restored early-successional forests in the Appalachian Mountains (top) and Great Lakes (bottom). The top ten models are shown in each candidate set. All models include a detection probability (p) with associated detection covariates: Julian date (“date”), minutes since sunrise (“mssr”), Beaufort wind index (“wind”), and percent cloud cover (“cloud”). Additionally, models include components for occupancy (Ψ) and density (λ) with associated covariates: latitude (lat), longitude (long) and elevation (elev). Also shown are the number of model parameters (k), model weight (w), and Δ Akaike’s Information Criterion adjusted for small sample size (ΔAIC_c).

Detection models – Occupancy (Appalachian Mountains)			
Model	k	ΔAIC_c	w
p(date + mssr + wind), Ψ(elev + long)	7	0.00	0.65
p(date + mssr + wind), Ψ(elev + lat + long)	8	1.26	0.35
p(date + mssr + wind), Ψ(lat + long)	7	13.34	0.00
p(date + mssr + wind), Ψ(long)	6	13.41	0.00
p(date + mssr + wind), Ψ(elev + lat)	7	22.11	0.00
p(date + mssr + wind), Ψ(lat)	6	84.77	0.00
p(date + mssr + wind), Ψ(lat^2)	8	112.10	0.00
p(date + mssr + wind), Ψ(elev + lat^2 + long)	9	114.22	0.00
p(date + mssr + wind), Ψ(.)	5	124.58	0.00
p(date + mssr + wind), Ψ(lat^2)	7	162.14	0.00
Detection models – Hierarchical Distance (Great Lakes)			
p(wind), λ(long + lat^2 + elev)	10	0.00	0.74
p(wind), λ(long^2 + lat^2 + elev)	11	2.09	0.26
p(wind), λ(long^2 + lat^2)	10	13.41	0.00
p(wind), λ(long + lat + elev)	9	14.02	0.00
p(wind), λ(long^2 + lat + elev)	10	14.31	0.00
p(wind), λ(long^2 + lat)	9	23.29	0.00
p(wind), λ(long + lat^2)	9	23.97	0.00
p(wind), λ(lat^2 + elev)	9	27.55	0.00
p(wind), λ(long + elev)	8	38.68	0.00
p(wind), λ(long^2 + elev)	9	40.49	0.00

Table 2C: Models of occupancy and density for Golden-winged Warblers within restored early-successional forests in the Appalachian Mountains (top) and Great Lakes (bottom). The top ten models are shown in each candidate set. All models include a detection probability (p) with associated detection covariates: Julian date (“date”), minutes since sunrise (“mssr”), Beaufort wind index (“wind”), and percent cloud cover (“cloud”). Additionally, models include components for occupancy (Ψ) and density (λ) with associated covariates: latitude (lat), longitude (long) and elevation (elev). Also shown are the number of model parameters (k), model weight (w), and Δ Akaike’s Information Criterion adjusted for small sample size (ΔAIC_c).

Detection models – Occupancy (Appalachian Mountains)

State variable covariates	k	ΔAIC_c	w
long + elev + deciduous + mixed + site age	10	0.00	0.35
long + elev + deciduous + mixed + site age	9	1.54	0.16
lat + long + elev + deciduous + mixed + site age	11	1.76	0.14
long + elev + deciduous + mixed + site age	9	3.20	0.07
lat + long + elev + deciduous + mixed + site age	10	3.57	0.06
long + elev + deciduous + mixed + site age	9	4.00	0.05
long + elev + deciduous + mixed + site age	8	4.93	0.03
long + elev + deciduous + mixed + site age	9	5.63	0.02
lat + long + elev + deciduous + mixed + site age	10	5.84	0.02
long + elev + deciduous + mixed + site age	8	5.85	0.02

Detection models – Hierarchical Distance (Great Lakes)

lat2 + long2 + elev + mixed + siteage	13	0.00	1.00
long2 + lat2 + elev + siteage	12	12.21	0.00
long2 + lat2 + elev + mixed	12	40.45	0.00

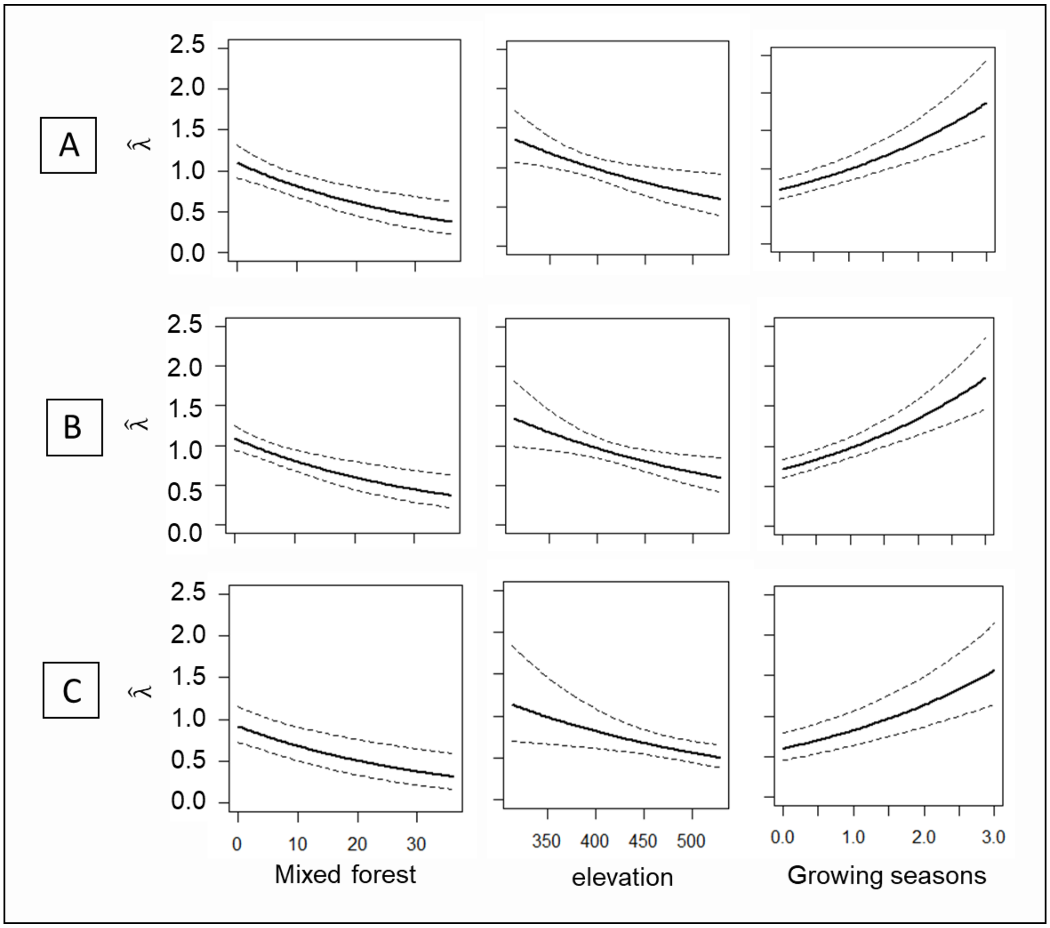

Figure 2A: Projections of Golden-winged Warbler density in Western Minnesota (A), central Minnesota (B) and the Minnesota/Wisconsin boarder (C).

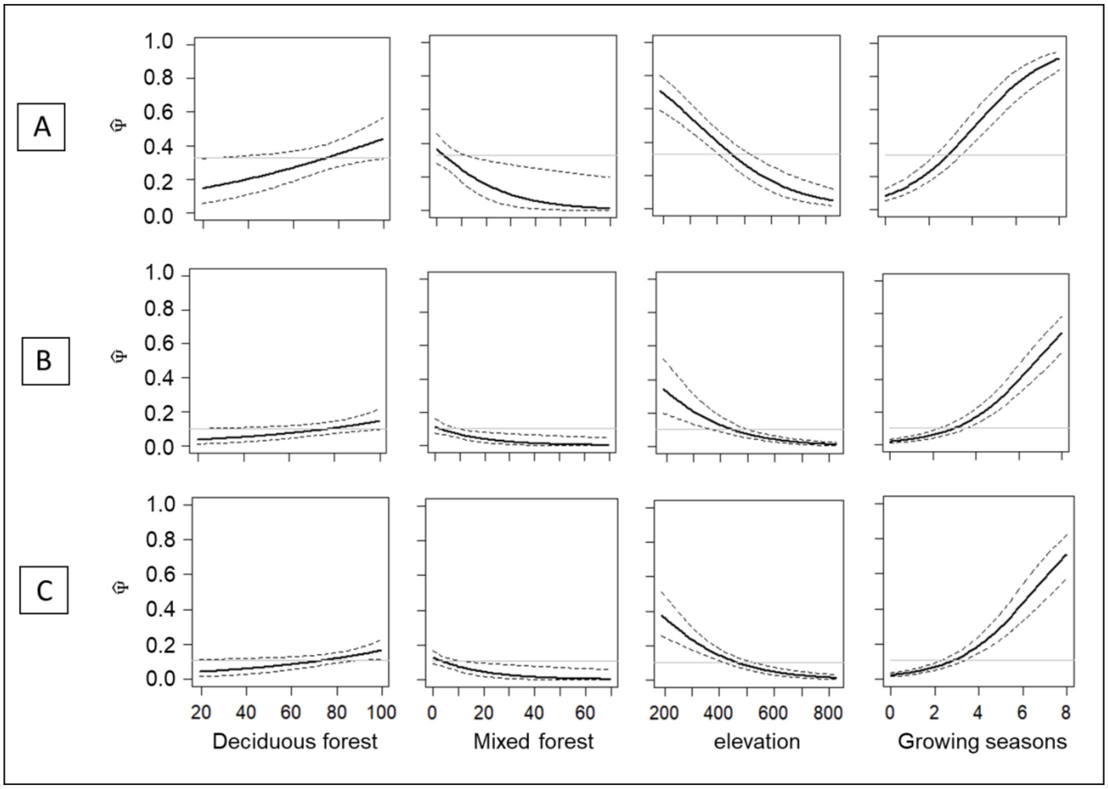

Figure 2B: Projections of Golden-winged Warbler occupancy in Eastern Pennsylvania (A), central Pennsylvania (B) and southcentral Pennsylvania (C). Gray lines indicate mean estimates of occupancy

CHAPTER 3 APPENDIX

This appendix contains a summary of the data that was analyzed in Chapter 3 with the following elements:

- Table 3A: Dynamic occupancy models for Golden-winged Warblers within restored habitats across the Appalachian Mountains (top) and Great Lakes (bottom) Conservation Regions. Models are ranked in descending order of Akaike's Information Criterion adjusted for small sample size (AIC$_c$). All four model components (detection probability [p], initial occupancy [ψ_1], colonization [γ], and extinction [ε]) were modeled using all possible subsets of model parameters. We allowed detection probability to vary as a function of four survey covariates: i) minutes since sunrise ('mssr'), ii) cloud cover ('cloud'), iii) Julian date ('date'), and Beaufort wind index ('wind'). State variables were modeled using covariates for management type ('mgmt', Great Lakes only; shrub management/timber harvest), time since management ('tsm', # growing seasons), and survey year ('year'; 2015-17). We only report detection models < 4.0 ΔAICc. For each model, we report number of model parameters (k), ΔAIC$_c$, and AIC$_c$ weight (w).
- Table 3B: Static occupancy models for Golden-winged Warblers within restored habitats across the four Focal Landscapes: Western Minnesota, Eastern Minnesota, Central Pennsylvania, and Eastern Pennsylvania. Models are ranked in descending order of Akaike's Information Criterion adjusted for

small sample size (AIC$_c$). We considered all possible combinations of survey covariates (Julian date (‘date’), cloud cover (%), minutes since sunrise (‘mssr’), and Beaufort wind index (‘wind’) and three site covariates: management type (‘mgmt’; Great Lakes only), time since management (‘tsm’, # growing seasons), and survey year (‘year’; 2015-18). Shown are only the top-ranked model for each Focal Landscape. We modeled each Focal Landscape separately and assessed two spatial scales for our two Pennsylvania Landscapes (15 and 35 km radius). For each model set, we report number of model parameters (k), ΔAIC$_c$, and AIC$_c$ weight (*w*).

Table 3A: Dynamic occupancy models for Golden-winged Warblers within restored habitats across the Appalachian Mountains (top) and Great Lakes (bottom) Conservation Regions. Models are ranked in descending order of Akaike's Information Criterion adjusted for small sample size (AIC_c). All four model components (detection probability [*p*], initial occupancy [Ψ_1], colonization [γ], and extinction [ε]) were modeled using all possible subsets of model parameters. We allowed detection probability to vary as a function of four survey covariates: i) minutes since sunrise ('mssr'), ii) cloud cover ('cloud'), iii) Julian date ('date'), and Beaufort wind index ('wind'). State variables were modeled using covariates for management type ('mgmt', Great Lakes only; shrub management/timber harvest), time since management ('tsm', # growing seasons), and survey year ('year'; 2015-17). We only report detection models < 4.0 ΔAICc. For each model, we report number of model parameters (k), ΔAIC_c, and AIC_c weight (*w*).

Appalachian Mountains Conservation Region

***p* (detection)**				**Ψ_1 (initial occupancy)**		**γ (local colonization)**			**ε (local extinction)**			**k**	**ΔAIC_c**	**w**
cloud	**date**	**mssr**	**wind**	**mgmt**	**tsm**	**mgmt**	**tsm**	**year**	**mgmt**	**tsm**	**year**			
pos	neg	neg	neg	-	pos	-			-	neg		10	0.00	0.09
	neg	neg	neg	-	pos	-			-	neg		9	0.04	0.09
	neg	neg	neg	-	pos	-	pos		-	neg		10	0.51	0.07
	neg	neg	neg	-	pos	-			-	neg		10	0.52	0.07
pos	neg	neg	neg	-	pos	-			-	neg		11	0.66	0.07
pos	neg	neg	neg	-	pos	-	pos		-	neg		11	0.88	0.06
	neg	neg	neg	-	pos	-	pos		-	neg	yes	11	1.07	0.05
	neg	neg	neg	-	pos	-		yes	-	neg		10	1.27	0.05
pos	neg	neg	neg	-	pos	-		yes	-	neg		11	1.34	0.05
pos	neg	neg	neg	-	pos	-	pos		-	neg	yes	12	1.59	0.04
	neg	neg	neg	-	pos	-		yes	-	neg	yes	11	1.61	0.04
pos	neg	neg	neg	-	pos	-		yes	-	neg	yes	12	1.87	0.04
	neg	neg	neg	-	pos	-	pos	yes	-	neg		11	2.07	0.03
pos	neg	neg	neg	-	pos	-	pos	yes	-	neg		12	2.48	0.03
	neg	neg	neg	-	pos	-	pos	yes	-	neg	yes	12	2.53	0.03
pos	neg	neg	neg	-	pos	-	pos	yes	-	neg	yes	13	3.10	0.02
pos	neg	neg	neg	-	pos	-			-			9	3.44	0.02
	neg	neg	neg	-	pos	-	pos		-			9	3.51	0.02
pos	neg	neg	neg	-	pos	-	pos		-			10	3.73	0.01
	neg	neg	neg	-	pos	-			-			8	3.84	0.01
pos	neg	neg	neg	-	pos	-			-		yes	10	3.91	0.01

Great Lakes Conservation Region														
p **(detection)**				***Ψ*₁ (initial occupancy)**		***γ*** **(local colonization)**			***ε*** **(local extinction)**			**k**	**ΔAIC_c**	**w**
cloud	**date**	**mssr**	**wind**	**mgmt**	**tsm**	**mgmt**	**tsm**	**year**	**mgmt**	**tsm**	**year**			
	neg		neg	yes		yes						8	0.00	0.05
	neg		neg	yes		yes	neg					9	0.85	0.03
	neg		neg	yes								7	1.62	0.02
	neg		neg	yes	pos	yes						9	1.63	0.02
	neg	pos	neg	yes		yes						9	1.93	0.02
	neg		neg	yes		yes					yes	9	2.16	0.02
pos	neg		neg	yes		yes						9	2.16	0.02
	neg		neg	yes		yes				pos		9	2.17	0.02
	neg		neg	yes		yes			yes			9	2.21	0.02
	neg		neg	yes		yes		yes				9	2.24	0.02
	neg		neg	yes	pos	yes	neg					10	2.60	0.01
	neg	pos	neg	yes		yes	neg					10	2.82	0.01
	neg		neg	yes			neg					8	2.84	0.01
	neg		neg	yes		yes	neg				yes	10	3.05	0.01
pos	neg		neg	yes		yes	neg					10	3.05	0.01
	neg		neg	yes		yes	neg			pos		10	3.08	0.01
	neg		neg	yes		yes	neg		yes			10	3.09	0.01
	neg		neg	yes		yes	neg	yes				10	3.14	0.01
	neg		neg	yes	pos							8	3.28	0.01
	neg		neg	yes					yes			8	3.55	0.01
	neg	pos	neg	yes								8	3.57	0.01
	neg	pos	neg	yes	pos	yes						10	3.61	0.01
neg	neg		neg	yes								8	3.69	0.01
	neg		neg	yes						pos		8	3.80	0.01
	neg		neg	yes	pos	yes				pos		10	3.81	0.01
	neg		neg	yes	pos	yes					yes	10	3.81	0.01
	neg		neg	yes							yes	8	3.82	0.01
	neg		neg	yes				yes				8	3.83	0.01
neg	neg		neg	yes	pos	yes						10	3.86	0.01
	neg		neg	yes	pos	yes			yes			10	3.88	0.01
	neg		neg	yes	pos	yes		yes				10	3.90	0.01

Table 3B. Static occupancy models for Golden-winged Warblers within restored habitats across the four Focal Landscapes: Western Minnesota, Eastern Minnesota, Central Pennsylvania, and Eastern Pennsylvania. Models are ranked in descending order of Akaike's Information Criterion adjusted for small sample size (AIC$_c$). We considered all possible combinations of survey covariates (Julian date ('date'), cloud cover (%), minutes since sunrise ('mssr'), and Beaufort wind index ('wind') and three site covariates: management type ('mgmt'; Great Lakes only), time since management ('tsm', # growing seasons), and survey year ('year'; 2015-18). Shown are only the top-ranked model for each Focal Landscape (). We modeled each Focal Landscape separately and assessed two spatial scales for our two Pennsylvania Landscapes (15 and 35 km radius). For each model set, we report number of model parameters (k), ΔAIC$_c$, and AIC$_c$ weight (*w*).

Eastern Pennsylvania, 35 Km Radius									
***p* (detection)**				**Ψ (occupancy)**			**k**	**ΔAICc**	**w**
date	**cloud cover**	**mssr**	**wind**	**mgmt**	**tsm**	**year**			
neg			yes	-	pos	yes	7	0.00	0.190
			yes	-	pos	yes	6	0.30	0.163
neg	neg		yes	-	pos	yes	8	1.16	0.106
	neg		yes	-	pos	yes	7	1.21	0.103
neg		neg	yes	-	pos	yes	8	2.09	0.067
		neg	yes	-	pos	yes	7	2.34	0.059
neg	neg	neg	yes	-	pos	yes	9	3.28	0.037
	neg	neg	yes	-	pos	yes	8	3.29	0.037
neg			yes	-	pos		5	3.43	0.034
			yes	-	pos		4	3.56	0.032
Eastern Pennsylvania, 15 Km Radius									
			yes	-	pos		4	0.00	0.206
neg			yes	-	pos		5	1.16	0.115
			yes	-	pos	yes	6	1.77	0.085
	neg		yes	-	pos		5	1.95	0.078
		neg	yes	-	pos		5	2.06	0.074
neg			yes	-	pos	yes	7	2.84	0.050
				-	pos		3	3.17	0.042
neg	neg		yes	-	pos		6	3.18	0.042
neg		neg	yes	-	pos		6	3.26	0.040
	neg		yes	-	pos	yes	7	3.74	0.032
		neg	yes	-	pos	yes	7	3.85	0.030
Central Pennsylvania, 35 Km Radius									
		neg		-	pos		4	0.00	0.193
				-	pos		3	0.48	0.152
		neg	yes	-	pos		5	2.05	0.069
pos		neg		-	pos		5	2.08	0.068
	neg	neg		-	pos		5	2.09	0.068
			yes	-	pos		4	2.13	0.067
	neg			-	pos		4	2.53	0.054
pos				-	pos		4	2.56	0.054
		neg		-	pos	yes	6	3.94	0.027

Central Pennsylvania, 15 Km Radius									
***p* (detection)**				**Ψ (occupancy)**			**K**	**ΔAICc**	**w**
date	**cloud cover**	**mssr**	**wind**	**mgmt**	**tsm**	**year**			
		neg		-	pos	yes	6	0.00	0.212
	pos	neg		-	pos	yes	7	1.07	0.124
		neg		-	pos		4	1.48	0.101
neg		neg		-	pos	yes	7	2.14	0.073
		neg	yes	-	pos	yes	7	2.24	0.069
neg	pos	neg		-	pos	yes	8	3.23	0.042
		neg	yes	-	pos		5	3.34	0.040
	pos	neg	yes	-	pos	yes	8	3.36	0.040
				-	pos	yes	5	3.51	0.037
	neg	neg		-	pos		5	3.64	0.034
Eastern Minnesota, 35 Km Radius									
neg			yes				4	0	0.181
neg			yes		pos		5	0.94	0.113
neg			yes	yes			5	1.77	0.075
neg		pos	yes				5	2.24	0.059
neg	neg		yes				5	2.27	0.058
neg			yes	yes	pos		6	2.62	0.049
neg	neg		yes		pos		6	3.25	0.036
neg		pos	yes		pos		6	3.26	0.036
Western Minnesota, 35 Km Radius									
		pos	yes	yes	pos		6	0	0.213
			yes	yes	pos		5	0.25	0.188
pos		pos	yes	yes	pos		7	2.1	0.075
	pos	pos	yes	yes	pos		7	2.14	0.073
pos			yes	yes	pos		6	2.39	0.065
	pos		yes	yes	pos		6	2.45	0.063

CHAPTER 5 APPENDIX

This appendix contains a summary of the data that was analyzed in Chapter 5 with the following elements:

- Figure 5A. Periods of drought as defined by the National Drought Mitigation Center (Knutson et al. 1998) from May through July 2014-17 in the Pocono Mountains (black) and Pennsylvania Wilds (red). Drought index shown (% drought) is the mean for Pike + Monroe Counties (Pocono Mountains) and Center + Clinton Counties (Pennsylvania Wilds).
- Figure 5B. Julian dates of nest initiation for nests in in the Pocono Mountains (A) and Pennsylvania Wilds (B), with the mean nest initiation date indicated by an arrow.

•

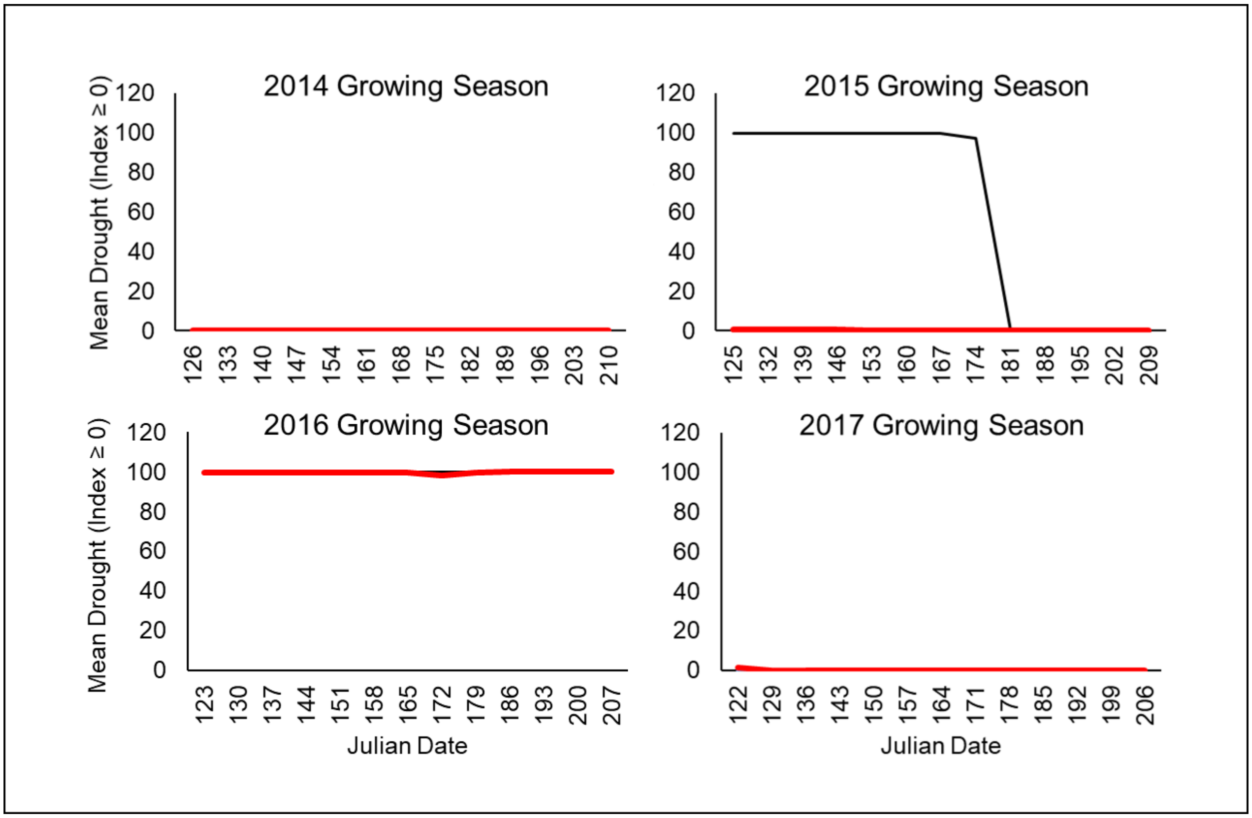

Figure 5A. Periods of drought as defined by the National Drought Mitigation Center (Knutson et al. 1998) from May through July 2014-17 in the Pocono Mountains (black) and Pennsylvania Wilds (red). Drought index shown (% drought) is the mean for Pike + Monroe Counties (Pocono Mountains) and Center + Clinton Counties (Pennsylvania Wilds).

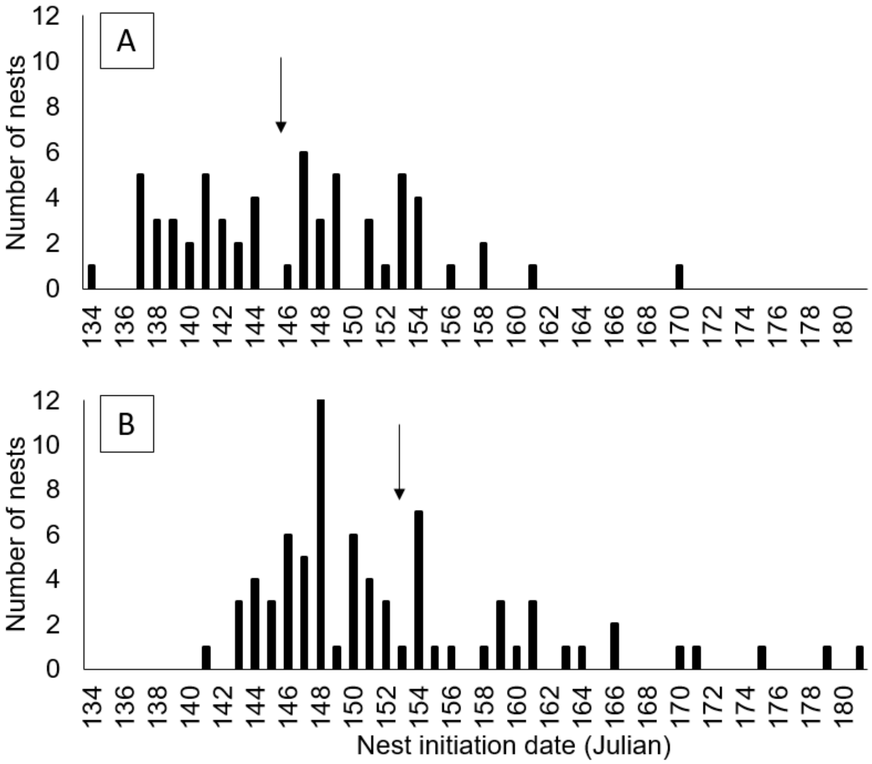

Figure 5B. Julian dates of nest initiation for nests in in the Pocono Mountains (A) and Pennsylvania Wilds (B), with the mean nest initiation date indicated by an arrow.