DEMOGRAPHIC RESPONSE OF GOLDEN-WINGED WARBLER TO HABITAT AND MANAGEMENT ACROSS A CLIMATE CHANGE GRADIENT IN THE CORE OF THE SPECIES' RANGE[1]:

2013 SUMMARY REPORT

31 December 2013

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[1] Research Work Order No. 87, Minnesota Cooperative Fish and Wildlife Research Unit

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2013 SUMMARY REPORT

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Abstract: No new data were collected for this project during 2013 but the RWO was extended into 2014 to support graduate student Sean Peterson during thesis completion and manuscript preparation. That thesis was successfully defended in November 2013, and the final thesis will be submitted to the University of Minnesota in early 2014 and disseminated to all cooperators as a Final Report for this project in 2014 along with all other published products. This 2013 annual report summarizes completed products and plans for additional data analysis, manuscript preparation, and publication in refereed outlets. So far we have produced 11 manuscripts from this project, of which 4 are published, 1 is in press, 4 are in review or revision, and 2 will be submitted for review in January 2014. We are organizing data and conducting analysis for 5 additional manuscripts. A second graduate student, Gunnar Kramer (supported on a separate RWO) will produce 2 of those manuscripts as part of his thesis. During 2013, we presented results from this project in 8 presentations; 5 at professional conferences, 2 at public venues, and 1 at a university. We have scheduled 2 additional professional presentations for 2014.

Data collection for this project was completed as scheduled in 2012. During 2013 we continued data analysis and preparation of manuscripts for publication. This report summarizes the 2013 progress and products for this project for which the original Study Plan is in Appendix I. In November 2013, Sean Peterson successfully defended his thesis "Landscape productivity and the ecology of brood division in golden-winged warblers of the western Great Lakes region," and the final thesis will be submitted to the University of Minnesota in early 2014.

Including Sean's thesis manuscripts, we have produced 11 manuscripts from this project describing how opposing evolutionary selection pressures influence nest-site choice in songbirds (Streby et al. 2014, *Proceedings of the Royal Society B*), testing the effects of accidental force-fledging on survival of fledgling songbirds (Streby et al. 2013, *Ibis*), testing the effects of radio transmitters on GWWA full-season productivity (Streby et al. 2013, *Journal of Field Ornithology*), testing common assumptions in studies of songbird nesting success (Streby and Andersen 2013, *Ibis*), questioning the consensus that nestling mass is a reliable predictor of fledgling survival in songbirds (in press, *Wildlife Society Bulletin*), developing a tool for modeling full-season landscape productivity in songbirds (in revision, *Studies in Avian Biology*), describing post-fledging movements and habitat selection in GWWA (in revision, *Studies in Avian Biology*), describing the management implications of post-fledging brood division in GWWA (in revision, *Studies in Avian Biology*), describing the ecology of fledgling GWWA after independence from adult care (in review), describing the behavior of post-fledging brood division in GWWA (to be submitted January 2014), and demonstrating the bias associated with standard nest-searching methods (to be submitted January 2014). Published manuscripts are presented in Appendix II. In 2013, we also produced a Final Report for the Minnesota Department of Natural Resources for portions of this project supported by State Wildlife Grant T-38-R-1 / F12AF00329 (Appendix III).

We are organizing data and conducting analysis for 5 additional manuscripts from this project. Gunnar Kramer joined the Andersen lab as a graduate student fall semester 2013 supported on separate funding. Gunnar will produce 2 of the remaining manuscripts for this project as part of his M.S. thesis. One of those manuscripts will use our habitat and productivity data in conjunction with projected climate data to investigate the potential for GWWA distribution and density to move farther north in Minnesota and Manitoba. The second of those manuscripts will expand our full-season productivity surface mapping methods to include multiple species and investigate the co-management potential for GWWA and American Woodcock (*Scolopax minor*). The other 3 manuscripts in preparation include a latitudinal model of GWWA productivity in the western Great Lakes region, a multi-species landscape productivity surface model with GWWA and Ovenbird (*Seiurus aurocapilla*), and an invited perspectives paper describing how our results challenge the nest success paradigm in songbird reproductive ecology (editorially invited for Auk: Ornithological Advances).

2013 PROFESSIONAL AND PUBLIC PRESENTATIONS

Peterson, S.M., H.M. Streby, and D.E. Andersen. 2003. Influence of landscape composition on golden-winged warbler full-season productivity. Annual Meeting of The Wildlife Society. Milwaukee, Wisconsin.

Streby, H.M. 2013. Redefining fitness in songbirds: a challenge to the nest success paradigm. Organismal Biology and Ecology Seminar Series, University of Montana, Missoula.

Streby, H.M. 2013. Measuring productivity in songbirds: tradeoffs between nest success and fledgling survival mean we need to study both stages" Invited Plenary for COS Young Professional Award – Cooper Ornithological Society - American Ornithologists' Union joint meeting, Chicago, Illinois.

Streby, H.M., S.M. Peterson, and D.E. Andersen. 2013 Golden-winged warbler post-fledging habitat use and survival in the western Great Lakes region. Golden-winged

Warbler Symposium, Cooper Ornithological Society - American Ornithologists' Union joint meeting, Chicago, Illinois.

Peterson, S.M., H.M. Streby, and D.E. Andersen. 2013. Influence of landscape composition on golden-winged warbler full-season productivity. Golden-winged Warbler Symposium, Cooper Ornithological Society - American Ornithologists' Union joint meeting, Chicago, Illinois.

Peterson, S.M., H.M. Streby, and D.E. Andersen. 2013. Sex-based differences in strategies of post-fledging parental care in golden-winged warblers. Golden-winged Warbler Symposium, Cooper Ornithological Society - American Ornithologists' Union joint meeting, Chicago, Illinois.

Streby, H.M. 2013. Full-season productivity in songbirds: why managing for nest success is not the best plan. Friday seminar series, PRBO Palomarin Field Station, Point Reyes National Seashore, California.

Peterson, S.M., H.M. Streby, T.C. Will, T.R. Cooper, and D.E. Andersen. 2013. Golden-winged warblers and the importance of diverse forest landscapes. Zumbro Valley Audubon Society. Rochester, Minnesota.

Peterson, S.M., H.M. Streby, T.C. Will, and D.E. Andersen. 2013. Golden-winged warblers and the importance of diverse forest landscapes. Minneapolis Audubon Society. Minneapolis, Minnesota.

PLANNED PRESENTATIONS FOR 2014

Kramer, G.R., H.M. Streby, S.M. Peterson, and D.E. Andersen. 2014. What do we know about golden-winged warblers in the western Great Lakes region? Annual meeting of the Minnesota Chapter of The Wildlife Society, Bemidji, Minnesota.

Kramer, G.R., H.M. Streby, S.M. Peterson, and D.E. Andersen. 2014. Post-independence fledgling ecology in golden-winged warblers: implications for breeding grounds conservation and management. Midwest Fish and Wildlife Conference, Kansas City, Missouri.

Appendix I. Peer-reviewed study plan for project on Golden-winged Warbler demography in the core of the species' range.

Demographic Response of Golden-Winged Warbler to Habitat and Management across a Climate Change Gradient in the Core of the Species Range

Proposed Study Plan

20 January 2010

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Introduction

Golden-winged Warbler (*Vermivora chrysoptera*) populations have been declining across their distribution for at least 40 years (Sauer et al. 2005). This Nearctic-Neotropical migratory species is listed as "threatened," "endangered," or "of management concern" in 10 states, and is described by the U.S. Fish and Wildlife Service as a "species of management concern" (Buehler et al. 2007). The cause of range-wide declines, and some local extinctions, is a complex combination of habitat loss, Blue-winged Warbler (*Vermivora pinus*) hybridization and competition, brood-parasitism by Brown-headed Cowbirds (*Moluthrus ater*), and likely global climate change (Buehler et al. 2007). Although Golden-winged Warbler range is contracting from the south, it is expanding to a lesser degree to the west and north. However, in areas of recent range expansion, populations have been declining over the past 15 years, and range expansion will soon be limited by lack of suitable habitat to the north and west.

Golden-winged Warblers depend on early successional forest stands, open forested wetlands, and lowland shrubby areas for nesting (Confer 1992). The northern hardwood-coniferous forests of northern Minnesota, Wisconsin, Michigan, and south-central Canada host the highest remaining densities of breeding Golden-winged Warblers (Sauer et al. 2005). Predicted to be a bioregion among the earliest and most dramatically affected by global climate change (Frelich and Reich 2009), there is currently considerable debate about the desired future composition and juxtaposition of habitats within these forests. Considerations for wildlife, including species associated with early successional forests, are an important part of this conversation (e.g., Jaakko Pöyry Consulting, Inc. 1992). Golden-winged Warbler nesting habitat is in decline as abandoned farmlands regenerate to mature forest, timber harvest declines, and wetlands are drained for development. Assessing the demographic response of Golden-winged Warbler populations to land management and other habitat alterations is critical for this species to be included in future management planning (Buehler et al. 2007). Detailed knowledge of habitat-specific demographic parameters is necessary to predict Golden-winged Warbler population responses to climate change.

Little is known about Golden-winged Warbler survival and habitat use throughout the nesting period in this region, and less is known about these parameters during the post-fledging period anywhere in the species' range (Buehler et al. 2007). To our knowledge, survival and reproductive success have not been compared among breeding habitat types, and fledgling survival has not been directly estimated for this species.

To address these information needs, we propose to investigate Golden-winged Warbler adult survival and annual productivity between the species' main breeding habitat types: early successional forests and forested wetlands. The objectives of this work are to:

1) Compare Golden-winged Warbler (GWWA) density and annual productivity (nest productivity and juvenile survival) between two main breeding habitat types.
2) Compare adult GWWA survival and habitat use during the nesting and post-fledging period between two main breeding habitat types.
3) Use habitat characteristics to build a predictive model of GWWA reproductive success to provide management recommendations for maximizing high quality GWWA habitat.
4) Replicate the study at 3 locations across a climate change gradient over 2 years to include critical spatial and temporal variation in analyses, maximizing the inference of results and applicability of management recommendations.
5) Combine demographic data with models of predicted climate change for the western Great Lakes region to predict climate-change effects on Golden-winged Warbler population viability.

Study Area

We will conduct this research in the core of Golden-winged Warbler range, at 3 sites that span a 450-km northwest to southeast global climate change gradient, and a gradient of Blue-winged Warbler genetic introgression. Specific study plots have not yet been selected, but will be located within Tamarac National Wildlife Refuge (north-west Minnesota), Rice Lake National Wildlife Refuge (east-central Minnesota), and Chequamegon National Forest (north-west Wisconsin). Tamarac NWR, and Rice Lake NWR have offered in-kind support (e.g., housing) for the duration of the project. These 3 study sites have relatively high GWWA abundance, and are located outside areas of Blue-winged Warbler (BWWA) sympatry, but along a gradient of BWWA genetic introgression in northern Wisconsin and northern Minnesota. Levels of genetic introgression generally decrease with distance from areas of sympatry. Therefore, these sites have been chosen to cover a range of relatively high to low genetic introgression from southeast (Chequamegon National Forest, WI) to northwest (Tamarac National Wildlife Refuge, MN).

Methods

The objectives will be addressed through a combination of field methods including nest searching, nest monitoring, radio telemetry, vegetation sampling, and invertebrate sampling. In addition, we will use GIS software to further assess habitat, and statistical software to model population growth and habitat relationships.

Nest Searching

We will establish nest searching plots in known Golden-winged Warbler nesting areas at each study site. We will use an all-inclusive approach to ensure an adequate sample of nests (GWWA nest on the ground in dense vegetation);

1) We will have 4 fulltime field technicians and 1 project leader at each site, with 3 additional assistants at each site for 3 weeks of peak nest searching. These workers will search for nests following procedures described by Martin and Geupel (1993) and Martin et al. (1997), and used on previous studies of forest-nesting birds in north-central Minnesota (Perry 1998, Manolis 1999).
2) We will capture adult female birds with mist nets to radio track them to nests, and we will capture and track females from known nests to enable monitoring of subsequent nesting attempts in cases of initial nest failure.
3) We will have 1-2 dog handlers train pointer hunting dogs to identify and locate songbird nests.
4) We will use sensitive thermal imaging cameras to locate well hidden nests using temperature differences between nests and surrounding vegetation.

We will evaluate the utility of nest-searching methods 3 and 4 during the first season, and increase or exclude their use during years 2 and 3 of the project accordingly.

Nest Monitoring

We will record the location of each nest using a handheld GPS unit (100 points averaged). We will monitor each discovered nest following procedures described by Martin and Geupel (1993) and Martin et al. (1997), and used on previous studies of forest-nesting birds in north-central Minnesota (Perry 1998, Manolis 1999). We will visit nests at 4-day intervals, and more often when transitional events (i.e. hatching and fledging) are expected. That schedule will result in nests being visited at intervals averaging 2 – 3 days as suggested by Golden-winged Warbler Working Group protocols. During each visit, we will record adult activity and nest contents (i.e. number of eggs, number of nestlings) and the condition of those contents (i.e. age of nestlings). We will band nestlings 3 days prior to the expected fledge date following methods we used in previous work (Streby and Andersen 2007). We will use radio telemetry to monitor adults and fledglings and thereby determine the fate of each nest found empty on or near the expected fledge date. We will use the Logistic Exposure method (Shaffer 2004) to estimate nest productivity, and to model the effects of habitat parameters on nest productivity.

Radio Telemetry

We will monitor birds using radio telemetry methods described by Anders et al. (1998), Vega Rivera et al. (1998, 2003), Lang et al. (2002), Fink (2003), and Cohen and Lindell (2004) that we used in a previous study (Streby and Andersen 2007). We have confirmed the availability of 0.4g (<5% of average body mass) transmitters with ≥30-day battery life. We will attach transmitters to birds using a figure-eight harness design for passerines (Rapolle and Tipton 1991). We will capture female birds from monitored nests by setting mist nets near nests and flushing the female into the net. We will capture and handle females only after the onset of incubation to reduce the probability of nest abandonment. We will indirectly monitor fledgling survival by monitoring radio-marked adult birds during the first week after young leave the nest. After that week, we expect that fledglings will be large enough to carry transmitters. We will relocate fledglings by tracking adults that are regularly feeding young. Once fledglings are located, we will set mist nets and flush fledglings into those nets, a method that has been used successfully in previous studies of Golden-winged Warblers (Rachel Vallender personal communication). We will monitor the adult female from each nest and ≥1 fledgling from each successful nest using radio telemetry to monitor survival, habitat use, and parental care. During the first year of the study, we will also monitor adult male habitat use and survival. Males will be captured using mist nets and call playback within active territories. We will relocate each bird ≥1 time daily, using radio telemetry to triangulate its position, and then approaching to confirm specific microhabitat use and survival. We will record locations of monitored birds using handheld GPS units (100 points averaged). When birds move beyond the range of our ground-tracking capabilities, we will relocate them from the air using standard aerial telemetry techniques (Mech, 1983). We will use the Logistic Exposure method to estimate adult and fledgling survival, and to model the effects of habitat parameters on survival.

Sample Sizes

During the pilot season at Tamarac NWR, we plan to monitor 25 – 50 nests, and monitor with radio telemetry >20 male, >20 female, and >20 fledgling GWWA.
During the full study at all 3 sites during 2011 and 2012 we plan to monitor 200 – 400 nests, and monitor with radio telemetry 150 – 200 adult females, and 150 – 200 fledgling GWWA. We will determine after the pilot year whether we will continue to monitor adult males with radio telemetry.

Habitat Assessment

Two main breeding habitat types will be investigated at each site; (1) Lowland (e.g., tamarack bogs, alder thickets, and other shrubby wetlands) and (2) Upland successional (e.g., regenerating clearcuts and open shrubby managed areas).

We will survey sites using vegetation sampling protocols established by the Golden-winged Warbler Working Group. In addition, we will sample food availability throughout the season for comparison between habitats and study sites following procedures we have used during previous research (Streby and Andersen 2007). Food availability will be compared with stomach samples from recovered mortalities during telemetry to investigate food-type preferences. Vegetation structure and food availability variables will be used to model habitat quality for GWWA across the geographic range of the study.

Population Modeling

We will build stochastic models of GWWA population growth including habitat variables across the geographic range of the study. These models will be used with predicted future habitat changes to predict the effects of climate change on GWWA populations.

Climate Change

In years 2 and 3 of this study, we will investigate population dynamics of GWWA across a gradient from southeast to northwest. This gradient represents a range of climatic conditions and corresponds with the perceived northwest range expansion of GWWA. We will evaluate reproduction and influences of habitat on population dynamics across this gradient. We will combine these data with models of future climate change for the western Great Lakes region to predict climate-change effects on Golden-winged Warbler population viability.

Timeline

Spring 2010 – Select graduate student and hire research associate
May – August 2010 – Pilot study at Tamarac National Wildlife Refuge
May – August 2011 – Full study at all 3 sites
May – August 2012 – Full study at all 3 sites

Expected Products

Products will include annual project reports, a final project report, a graduate student thesis, and primary literature publications presenting project results.

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Appendix II: Final Report to MN Department of Natural Resources for State Wildlife Grant Program funding

Golden-winged Warbler Demography and Habitat Associations in Minnesota

Final Report

MN State Wildlife Grants Program

T-38-R-1 / F12AF00329

November 14, 2013

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Abstract

In 2012 we studied demography of Golden-winged Warblers (*Vermivora chrysoptera*) at Tamarac National Wildlife Refuge (NWR) in northwest Minnesota. We found and monitored 90 nesting attempts, and we radio-marked and monitored survival of 44 adult females and 68 fledglings from 40 broods. We estimated that 58% of females successfully nested, producing an average of 4.4 fledglings per successful nest, and that 53% of fledglings survived to independence from adult care. These parameter estimates yielded an estimate of strong population growth for the third consecutive year at Tamarac NWR. Adults nested most densely in upland shrublands and in the mature forest adjacent to upland shrublands and shrubby wetlands, and nested less densely within shrubby wetlands. Comparing seasonal productivity among habitat types was confounded by the use of multiple habitat types by most individuals for first and second nesting attempts and for post-fledging habitat. Fledglings were divided approximately evenly between adult males and females upon leaving the nest. Post fledging habitat use was similar (although distances moved differed) for male- and female-reared fledglings, with the use of shrublands decreasing early in the post-fledging period and the use of mature forest increasing to >50% of daily fledgling locations before fledglings became independent from adult care. Analysis of landscape habitat associations with population productivity of Golden-winged Warblers at Tamarac NWR and 2 other study sites in Minnesota and Manitoba, Canada, indicate an importance of a diverse forest landscape in which upland shrublands and dense mid-successional forest stands are interspersed within a matrix of primarily mature forest. In addition, high seasonal productivity was most strongly associated with moderate amounts of edge (i.e., complex stand shapes rather than simple shapes such as circles or squares) and a locally diverse landscape (i.e., many small- to medium-sized shrublands and midsuccessional stands as opposed to fewer large stands). Detailed study results will be disseminated in a graduate student thesis (Fall 2013), 3 chapters of an edited volume of Studies in Avian Biology (Fall 2014), and additional peer-reviewed scientific publications.

Introduction

Many migratory songbirds that breed in North America are experiencing long-term population declines (Dettmers 2003). These declines are thought to be largely associated with alteration and loss of habitat in North American breeding grounds. Loss of early-successional forest and shrub-scrub habitat is particularly dramatic, and conservation of those habitats and the birds that use them is critical (Hunter et al. 2001, Dettmers 2003). There is currently considerable discussion and debate about how to best develop and implement conservation and management strategies to reverse songbird population declines. A pervasive limitation of songbird conservation planning is the lack of sufficient demographic information about most species to make informed management and conservation decisions. Although there is a large body of literature about presence/absence of singing males and nesting ecology of many migratory songbirds, there is far less information about adult breeding survival, and very little information about fledgling survival and habitat use. Recent studies have demonstrated the importance of the post-fledging period (the time between nesting and migration) to songbird population productivity (e.g., Streby 2010). Large-scale studies of breeding habitat associations, adult breeding survival, and seasonal productivity (i.e., nest productivity and fledgling survival) are necessary to make informed decisions about the management and conservation of migratory songbirds.

One species declining at such dramatic rates that informed conservation initiatives are imperative is the Golden-winged Warbler (*Vermivora chrysoptera*), which is listed as a Species in Greatest Need of Conservation (SGCN) in Minnesota's State Wildlife Action Plan (SWAP) (MNDNR 2006). The purpose of Minnesota's SWAP is to maintain the state's native fauna and ensure that no additional species are lost (MNDNR 2006:35). Golden-winged Warbler populations have been declining precipitously across their distribution for >45 years (Sauer et al. 2005, Will 2011), and the species is listed as Threatened, Endangered, or of high management concern in 10 states (Buehler et al. 2007) and as Threatened under Canada's Species at Risk Act. The cause of range-wide declines, and some local extinctions, appears to be a complex combination of habitat loss, hybridization and competition with Blue-winged Warblers (*Vermivora pinus*), brood-parasitism by Brown-headed Cowbirds (*Moluthrus ater*), and likely global climate change (Buehler et al. 2007). Although Golden-winged Warbler range is contracting from the south, it is expanding to a lesser degree to the north and west. However, range expansion will soon be limited by lack of suitable habitat to the north and west, and also potentially by breeding-season weather at more northerly locations. Demographic research on Golden-winged Warblers in the upper Midwest has been identified as a pressing conservation need by the Minnesota Department of Natural Resources, the Golden-winged Warbler Working Group, the U.S. Fish and Wildlife Service, the Great Lakes Region Joint Venture, Audubon Minnesota, the National Fish and Wildlife Foundation, and the Wildlife Management Institute. Recently, the U.S. Fish and Wildlife Service was petitioned to consider the Golden-winged Warbler for listing under the Endangered Species Act, accelerating the urgent need for this demographic information.

At least 40% of the global population of Golden-winged Warblers nests in Minnesota (Table 1). No other bird species has such a large concentration of its global population breeding in Minnesota. Furthermore, Minnesota is the only state in which Golden-winged Warbler populations have been experiencing a positive growth trend over the past decade (Table 2), presenting a strong stewardship responsibility for the state. Although we have found Golden-winged Warblers use more mature forest than previously known (Streby et al. 2012), they depend on relatively open cover types such as early-successional forest stands, open forested wetlands, and lowland shrubby areas within a mature forest matrix as primary nesting areas (Confer 1992). Golden-winged Warbler nesting habitat is in decline, particularly in eastern portions of the species' range (Appalachian Mountains), as abandoned farmlands regenerate to mature forest, timber harvest declines, and wetlands are drained for development. There is currently considerable debate about the desired future composition and juxtaposition of habitats within the northern hardwood-coniferous forests of Minnesota and nearby states, a bioregion predicted to be among the earliest and most dramatically affected by global climate change (Frelich and Reich 2009). Considerations for wildlife, including songbirds of conservation concern, are an important part of this conversation. Information about Golden-winged Warbler survival and habitat use throughout the nesting period is limited, and almost nothing is known about these parameters during the post-fledging period (Buehler et al. 2007). Assessing the demographic response of

Golden-winged Warbler populations to land management and other habitat alterations is critical for the conservation of this species (Buehler et al. 2007).

Working with the Minnesota Cooperative Fish and Wildlife Research Unit and the University of Minnesota, in collaboration with the U.S. Fish and Wildlife Service and the Golden-winged Warbler Working Group, we designed a study to begin to address these information needs. This study, which began in 2010, investigates Golden-winged Warbler survival and productivity (both nest productivity and fledgling survival) in their primary breeding habitat types (early-successional forests and shrubby forested wetlands) at Tamarac National Wildlife Refuge (NWR) in northern Minnesota, Rice Lake National Wildlife Refuge in eastern Minnesota, and Sandilands Provincial Forest (PF) in Manitoba. We will use demographic data from this study to build predictive models of seasonal productivity and population growth and provide management recommendations for maximizing habitat characteristics, at multiple spatial scales, associated with increased population growth for Golden-winged Warblers. **This grant and the current report only address the work done on the portion of this study being conducted at the Tamarac National Wildlife Refuge from May 1, 2012 through April 30, 2013.**

Objectives and Results

To address the immediate information needs listed above, we studied Golden-winged Warbler (GWWA) adult survival and seasonal productivity in the species' main breeding habitat types: early successional forests, shrubby forested wetlands, and the mature forest surrounding those stands at Tamarac NWR from 1 May 2012 – 30 April 2013. Sample sizes and parameter estimates are summarized in Table 3.

6) **Objective – Monitor GWWA nest productivity and fledging success for 40 – 50 nests**.
We monitored 90 nesting attempts at Tamarac NWR, which is the largest sample size of GWWA nests ever monitored at one site in one season. We estimated that 58% of females successfully nested producing an average of 4.4 fledglings per successful nest. The percentage of females successfully nesting was lower than in the 2 prior seasons in this population, but the number of fledglings per nest was higher, resulting in a third consecutive year of high fledgling production at Tamarac NWR.

7) **Objective – Using radio-telemetry, monitor the movements of 40 – 50 nesting birds and 40 – 50 fledglings.**
We radio-monitored 44 adult females and recorded 1 mortality, resulting in an estimate of 98% adult survival during the breeding season. When not incubating eggs or brooding nestlings, adult females followed movement patterns similar to those of adult males during nesting (Streby et al. 2012) by using forested edges and open shrublands during early morning hours, and then foraging in the canopy and understory of mature forest later in the day. We monitored survival of 68 radio-marked fledglings from 40 successful nests. We estimated that 53% of fledglings survived to independence from adult care. Fledglings were divided approximately evenly between adult males and females upon leaving the nest. Post-fledging habitat use was similar (although distances moved differed) for male- and female-reared fledglings with the use of shrublands decreasing early in the post-fledging period and the use of mature forest

increasing to >50% of daily fledgling locations before fledglings became independent from adult care.

8) **Objective – Compare GWWA density and seasonal productivity (nest productivity and fledgling survival) between main breeding habitat types within Tamarac NWR and with additional sites studied under separate funding.**
   Golden-winged Warblers nested most densely in upland shrublands and in the mature forest adjacent to upland shrublands and shrubby wetlands, and nested less densely within shrubby wetlands. Nests were distributed approximately normally with respect to forest edge with 60% of nests within 25 m of forest edge, both extending into mature forest and upland shrublands and shrubby wetlands. Comparing seasonal productivity among habitat types was confounded by the use of multiple habitat types by most individuals for first and second nesting attempts and for post-fledging habitat. Nest success was consistently lower in mature forest compared to upland shrublands and shrubby wetlands. However, fledgling survival was consistently higher in mature forest compared to upland shrublands and shrubby wetlands. These results indicate that each habitat type plays an important role in a landscape that maximizes seasonal productivity in this species, and they indicate that long and moderately complex edges between habitat types are also important. Despite similar habitat use among both adults and juveniles, GWWA breeding density was higher at Tamarac NWR than other sites studied under separate funding. Nest productivity and fledgling survival was higher at Tamarac NWR than other sites studied, suggesting that Tamarac NWR is a source population for the region.

9) **Objective: Compare adult female GWWA survival and habitat use during the nesting and post-fledging periods among the main breeding habitat types within Tamarac NWR and with additional sites studied under separate funding.**
   We observed evidence of only 1 (2%) adult female mortality during the 2012 breeding season at Tamarac NWR, and of only 6 (<3%) adult females during the entire study. Coupled with similar observations at sites studied under separate funding, these observations suggest that survival is generally high for breeding females in this region. At least 1 female mortality occurred in each of the 3 primary breeding habitat types, suggesting that adult female breeding survival is generally high across the landscape regardless of habitat-type use. Females used habitat similarly at Tamarac NWR and our other study sites. When they were not incubating eggs, females used habitat similar to that used by their male mates as described by Streby et al. (2012). During morning hours they primarily foraged in shrubs and in the canopy of individual mature trees within upland and wetland shrublands and along mature-forest edge. Later in the day, females almost exclusively foraged in mature forest canopy, often with their mates. Females moved with their young into forested areas during the post-fledging period. Also similar to males, females selected mature forest and midsuccessional regenerating forest stands over all other cover types for raising fledglings. They foraged in the leaves of forest canopy and understory trees and provisioned young that remained primarily in dense shrubs and understory vegetation. Due to transmitter expiration, we could not assess female habitat use after fledglings became independent from adult care.

10) **Objective: Use habitat characteristics and pool with data from other study sites to build a predictive model of GWWA seasonal productivity to provide management recommendations for maximizing GWWA population growth.**
    We developed full-season productivity surfaces to predict mean seasonal productivity of GWWA pairs across Tamarac NWR. Highest predicted full-season productivity occurred where cover types were diverse, and included upland shrublands and dense mid-successional forest stands interspersed within a matrix of primarily mature forest. On our study sites, we identified areas of lower-than-expected productivity (i.e., potential ecological traps) associated with overly complex forest edges. Whereas the amount of forest edge was positively related to productivity at moderate amounts of forest edge, we predicted decreasing productivity as the amount of forest edge increased beyond an apparent threshold. We similarly identified grassland as a cover type associated with low productivity. In both of these scenarios, we were able to increase predicted productivity in simulations by either smoothing some of the most complex edges in our study area or simulating succession from grassland into shrubland or midsuccessional forest. Additionally, when we compared wetland and upland landscapes of identical structure, we found that productivity was higher in upland landscapes. Analyses of potential management scenarios on a mature forest landscape indicated that small- to medium-sized shrublands (~5 ha) would result in higher GWWA productivity than large shrublands (~25 ha). Because fledgling survival and nest success are differentially impacted by landscape, our results suggest that current GWWA management plans based on counts of singing males, and sometimes nest success, may overemphasize the importance of large open shrublands and may be at least partially counterproductive by reducing fledgling survival, which is considerably higher in or near midsuccessional stands or mature forest with dense and patchy understory. Furthermore, our results indicated that seasonal productivity was more strongly correlated with fledgling survival than with nest success, suggesting that management to prioritize fledgling survival rather than nest success would have a larger impact on GWWA productivity.

Minnesota State Wildlife Action Plan Goals and Achievements

This project was intended to help address the following goals and strategies of Minnesota’s State Wildlife Action Plan (MNDNR 2006:37):

Goal I: Stabilize and Increase SGCN populations
Strategy IA: Identify key SGCN habitats
Goal II: Improve knowledge about SGCN
Strategy IIA: Survey SGCN populations and habitats
Strategy IIB: Research populations and habitats.

Stabilize and Increase SGCN populations:
Our results indicate that the GWWA population at Tamarac NWR is self-sustaining and a consistent annual source population for surrounding areas. Combined with results from our Rice Lake NWR study site, our results suggest much of the Minnesota GWWA population is self-sustaining and generally growing and sourcing surrounding areas.

These results are consistent with the 3.5% annual population increase in Minnesota estimated from the North American Breeding Bird Survey over the past decade.

Identify, survey, and research SGCN habitats:
(Copied from Summary Result for Objective 5) We developed full-season productivity surfaces to predict mean seasonal productivity of GWWA pairs across Tamarac NWR. Highest predicted full-season productivity occurred where cover types were diverse, and included upland shrublands and dense mid-successional forest stands interspersed within a matrix of primarily mature forest. On our study sites, we identified areas of lower-than-expected productivity (i.e., potential ecological traps) associated with overly complex forest edges. Whereas the amount of forest edge was positively related to productivity at moderate amounts of forest edge, we predicted decreasing productivity as the amount of forest edge increased beyond an apparent threshold. We similarly identified grassland as a cover type associated with low productivity. In both of these scenarios, we were able to increase predicted productivity in simulations by either smoothing some of the most complex edges in our study area or simulating succession from grassland into shrubland or midsuccessional forest. Additionally, when we compared wetland and upland landscapes of identical structure, we found that productivity was higher in upland landscapes. Analyses of potential management scenarios on a mature forest landscape indicated that small- to medium-sized shrublands (~5 ha) would result in higher GWWA productivity than large shrublands (~25 ha). Because fledgling survival and nest success are differentially impacted by landscape, our results suggest that current GWWA management plans based on counts of singing males, and sometimes nest success, may overemphasize the importance of large open shrublands and may be at least partially counterproductive by reducing fledgling survival, which is considerably higher in or near midsuccessional stands or mature forest with dense and patchy understory. Furthermore, our results indicated that seasonal productivity was more strongly correlated with fledgling survival than with nest success, suggesting that management to prioritize fledgling survival rather than nest success would have a larger impact on GWWA productivity.

Potential Impacts of Climate Change
During our full study (all years, all sites) we identified 2 consequential issues that may be important in the face of continued climate change. The first is the expected climate-change related increase in the frequency of extreme events, including flooding. In 2012, our study site at Rice Lake NWR experienced a flood in late June during which water reached the highest recorded levels since the establishment of the refuge in 1935. The timing of the flood (late June) spared most nests that had already fledged young and most fledglings that were already old enough to reach higher branches or higher land. However, a similar flooding event occurring in early June would be locally catastrophic for productivity of ground-nesting songbirds. If such flooding events become increasingly common in future years, we expect shrubby wetlands and low areas adjacent to wetlands to host low GWWA productivity in those years. We speculate that regular within-season variation in water levels may contribute to the lower nesting density we observed in shrubby wetlands compared to uplands.

The second issue is the relatively short nesting season and occurrence of cold nights early in the post-fledging period at our Sandilands PF site in Manitoba. Golden-winged Warblers appear to be expanding their range and abundance in Manitoba in recent years. However, our results suggest that the shorter nesting season allows fewer renesting attempts and leads to lower nest productivity, and the regularity of June nighttime temperatures dropping close to freezing causes exposure mortality of young fledglings. In combination, these observations suggest that GWWA productivity at that site ranges from moderate to low, and is not consistently high enough to maintain the population without immigration. Therefore, if climate change is driving the northern range expansion of GWWA, we speculate that the expansion is into areas that are not currently suitable for hosting self-sustaining populations.

Additional Products

Data collected during research activities funded by this grant have contributed to several manuscripts currently in press, in review, or in late stages of preparation in addition to the intended manuscripts about nest productivity, fledgling survival and habitat use, and the effects of landscape composition on full-season productivity. We have produced, or are producing, manuscripts testing the effects of accidental force-fledging on survival of fledgling songbirds (published in *Ibis*), testing the effects of radio transmitters on GWWA seasonal productivity (published in *Journal of Field Ornithology*), testing common assumptions in studies of songbird nesting success (published in *Ibis*), describing how opposing evolutionary selection pressures influence nest-site choice in songbirds (in revision, *Proceedings of the Royal Society of London, B*), testing the assumption that nestling mass is a reliable predictor of fledgling survival (in press, *Wildlife Society Bulletin*), and describing the ecology of post-fledging brood division in GWWA (in preparation).

Professional and Public Presentations

During this grant cycle, we made presentations about the project at many public and professional venues, and we acknowledged this SWG grant, the MN DNR, and the USFWS during each presentation. Henry Streby gave presentations to members of the public at Tamarac NWR, to the Department of Environmental Science Policy and Management at the University of California at Berkeley, to the staff of Point Reyes Bird Observatory, and at the North American Ornithological Conference in Vancouver, British Columbia, Canada. Sean Peterson presented results of this research at the Midwest Fish and Wildlife meeting in Wichita, Kansas, and at the Zumbro Valley Audubon Society meeting in Rochester, Minnesota. Travel costs associated with these presentations were not charged to the SWG grant.

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Table 1. State and province population estimates for Golden-winged Warblers. Estimates are derived from the Partners in Flight Population Estimates Database (Blancher et al. 2007). Table replicated from Will (2011).

Province/State	Country	Population Estimate	% Total Population
Minnesota	**USA**	**90,000**	**42**
Wisconsin	USA	47,000	22
Ontario	Canada	40,000	18
Michigan	USA	11,000	5
West Virginia	USA	8,000	4
Pennsylvania	USA	7,000	3
New York	USA	6,000	3
Tennessee	USA	2,000	1
Virginia	USA	800	0.4
North Carolina	USA	600	0.3
Québec	Canada	40	0.2
Maryland	USA	300	0.2
Vermont	USA	300	0.2
Massachusetts	USA	300	0.2
New Jersey	USA	170	0.1
Illinois	USA	170	0.1
Manitoba	Canada	120	0.1
Ohio	USA	60	0.00

Table 2. Golden-winged Warbler population trends by state. Minnesota is the only state hosting a population likely experiencing positive growth. Table partially replicated from Will (2011). Trends derived from North American Breeding Bird Survey.

State	%/Yr 2000-2009	LCL	UCL
Connecticut	-24.1	-46.9	-3.1
Massachusetts	-8.9	-25.3	8.0
Maryland	-5.8	-11.4	-0.8
Michigan	-5.6	-12.0	0.1
Minnesota	**3.5**	**-0.3**	**8.8**
North Carolina	-10	-17.9	-1.3
New Hampshire	-6.3	-75	177.9
New Jersey	-9.3	-19.2	2.0
New York	-4.0	-8.6	1.6
Pennsylvania	-7.2	-13.4	-0.9
Tennessee	-7.1	-15.7	4.4
Virginia	-8.7	-15.8	-0.7
Wisconsin	-2.9	-6.8	1.0
West Virginia	-7.8	-12.8	0.7

Table 3. Summary of Golden-winged Warbler data collected during the 2012 field season at Tamarac National Wildlife Refuge (NWR), Rice Lake NWR, and Sandilands Provincial Forest (PF). Data collection at Tamarac NWR (in bold) was in part supported by this grant.

	Tamarac NWR	Rice Lake NWR	Sandilands PF	Total or grand mean
No. adults color-banded (M/F)	**80 (35/45)**	98 (51/47)	41 (26/15)	219 (112/107)
No. females radio-marked	**44**	46	21	111
No. nesting attempts monitored[a]	**90**	41	18	149
Successful females (%, with renesting)	**58**	74	79	65
No. fledglings per successful nest	**4.4**	4.0	3.9	4.2
No. nestlings/fledglings banded	**153**	92	66	311
No. fledglings radio-tracked	**68**	54	53	175
No. fledgling locations recorded[b]	**1,006**	562	649	2217
Fledgling survival to independence (%)	**53**	49	48	50

[a] We found an additional 20 GWWA nests (10 at Tamarac NWR) that were apparently abandoned during construction or failed before we found them.

[b] Data collected at each fledgling location included GPS location, occupied cover type, occupied vegetation strata, canopy cover, vegetation density, fledgling and parental activity, other birds present, and other behavioral observations.

Appendix III. Attached are 4 manuscripts from this project published in Ibis (2), Journal of Field Ornithology, and Proceedings of the Royal Society B.

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Short communication

The effects of force-fledging and premature fledging on the survival of nestling songbirds

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Despite the broad consensus that force-fledging of nestling songbirds lowers their probability of survival and therefore should be generally avoided by researchers, that presumption has not been tested. We used radiotelemetry to monitor the survival of fledglings of Ovenbirds *Seiurus aurocapilla* and Golden-winged Warblers *Vermivora chrysoptera* that we unintentionally force-fledged (i.e. nestlings left the nest in response to our research activities at typical fledging age), that fledged prematurely (i.e. nestlings left the nest earlier than typical fledging age), and that fledged independently of our activities. Force-fledged Ovenbirds experienced significantly higher survival than those that fledged independent of our activities, and prematurely fledged Ovenbirds had a similarly high survival to those that force-fledged at typical fledging age. We observed a similar, though not statistically significant, pattern in Golden-winged Warbler fledgling survival. Our results suggest that investigator-induced force-fledging of nestlings, even when deemed premature, does not necessarily result in reduced fledgling survival in these species. Instead, our results suggest that a propensity or ability to fledge in response to disturbance may be a predictor of a higher probability of fledgling survival.

Keywords: breeding ecology, fledgling survival, Golden-winged Warbler, observer effects, Ovenbird, *Seiurus aurocapilla*, *Vermivora chrysoptera*.

Many studies of nesting passerines use different methods late in the nestling stage from those used earlier in the nestling stage to avoid the negative impacts of force-fledging or prematurely fledging young from nests (e.g. Anderson & Anderson 1961, Bjornstad & Lifjeld 1996, Holmes *et al.* 1996, Payne & Payne 1998, Sillet *et al.* 2000, Ferretti *et al.* 2005, Maddox & Weatherhead 2008). Although the terms are often used interchangeably, we use 'force-fledging' to refer to nestlings leaving the nest in response to investigator stimulus, and 'premature fledging' as force-fledging that occurs prior to typical fledging age. Although the term fledge technically refers to the developmental stage at which young birds first fly, it is used ubiquitously in the songbird literature to refer to leaving the nest (i.e. fledging from the nest; Gill 1995), and we maintain the latter common definition here. Anecdotal evidence of detrimental effects of force-fledging and premature fledging dates back more than 100 years, when Cole (1910) reported finding ringed nestlings dead outside nests. Cole (1910) subsequently stated that observing dead nestlings outside nests, regardless of researcher activities, 'is not an uncommon thing', and concluded that no causal relationship could be drawn between nestling handling and mortality in those cases. Cole nevertheless concluded that premature-fledging is 'probably, however, the greatest danger to the birds from our work'. Recently, Pietz *et al.* (2012) reiterated that warning: 'We echo Cole's (1910) advice from a century ago that researchers who handle older nestlings (e.g. to measure or band) need to be aware of their possible impacts.' Yet Pietz *et al.* (2012) conceded that the fates of force-fledged or prematurely fledged birds are rarely known. We are not aware of any empirical studies of the impacts of force-fledging or premature fledging on songbirds despite widespread attempts to avoid it (e.g. Ezaki 1988, Briskie 1995, Brooke & Nakamura 1998, Confer *et al.* 2003, Nagy & Holmes 2005, Ardia 2006) on the assumption that it results in reduced fledgling survival (e.g. Hamilton & Martin 1985, Miller & Leonard 2010, Ball & Bayne 2012).

We examined the impact of force-fledging at typical fledging age and premature fledging on fledgling survival in Ovenbirds *Seiurus aurocapilla* and Golden-winged Warblers *Vermivora chrysoptera* in the western Great Lakes region, USA and Canada. We did not purposefully force any nestlings to fledge, but some broods did not remain in nests after our ringing and transmitter attachment activities, which provided an ideal opportunity to test the assumption that force-fledging and premature fledging caused by investigator activities negatively affect fledgling survival. We compared survival of fledglings that left nests independently of our activities within 3 days of marking, those that force-fledged (nestlings would not stay in nest after handling at typical fledging age) and those that prematurely fledged (nestlings would not stay in nest after handling those younger than typical fledging age).

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METHODS

As part of separate studies of population ecology, we searched for and monitored Ovenbird nests during 2007 and 2008 in the Chippewa National Forest (47°31′N, 94°16′W) in north-central Minnesota, and Golden-winged Warbler nests during 2011 and 2012 in Tamarac National Wildlife Refuge (NWR; 47°2′N, 95°35′W) in northwest Minnesota, Rice Lake NWR (46°31′N, 93°20′W) in east-central Minnesota, and Sandilands Provincial Forest (PF; 49°39′N, 96°15′W) in southeast Manitoba. We located nests of both species using methods modified from Martin and Geupel (1993), including monitoring parental activity and systematic searching. We also located Golden-winged Warbler nests by netting and attaching radio-transmitters to females and radiotracking them through the breeding season. We visited nests every 4 days, or more often when we expected stage transitions (i.e. onset of incubation and hatching) to confirm ages of nestlings and to predict expected fledging dates.

Nestlings in our study populations typically fledge on day 8 (Ovenbirds) and day 8 or 9 (Golden-winged Warblers) of the nestling stage, where hatching day is day 1. However, some Ovenbirds fledge on days 7 or 9, and some Golden-winged Warblers fledge on days 7, 10 and, rarely, 11. On day 7 of the nestling stage for both species in Minnesota, we removed broods from nests (mean brood size was 4.2 for Ovenbirds and 4.4 for Golden-winged Warblers), ringed all nestlings with U.S. Geological Survey aluminium leg rings, and attached radio-transmitters to one to two (Ovenbirds) and one to five (Golden-winged Warblers) nestlings using a figure-eight harness design modified from Rappole and Tipton (1991). Due to logistical constraints, bad weather or finding nests at late stages, we sometimes attached transmitters on days 8–10. In Sandilands PF, we attempted to attach transmitters to Golden-winged Warblers on day 6 in an effort to avoid premature fledging and its presumed negative consequences for this species protected under Canada's Species at Risk Act. However, for the reasons stated above and because birds were sometimes too small to fit with transmitters on day 6, we often marked Manitoba birds on day 7 and sometimes day 8.

We removed nestlings from nests for ringing and transmitter attachment and replaced each brood in its nest within 15 min. When nestlings remained in the nest (84% of broods from 179 nests), we observed them for 3–5 min from a distance of > 5 m, and checked many nests (*c.* 50%) 30–60 min after handling to confirm that nestlings had not fledged. We also monitored some (*c.* 5%) nests with digital video cameras for up to 3 days after handling nestlings. We did not observe evidence of any broods fledging between 1 min and 1 h after handling. Therefore, we considered those broods that fledged within the first minute after handling to have fledged in response to our activities. We considered all other broods to have fledged naturally, although certainly some of those broods could have been force-fledged by other stimuli (e.g. predators). Although some small percentage (< 10% in our study) of Ovenbirds and Golden-winged Warblers fledge on day 7 in the absence of force-fledging, we considered any brood that we force-fledged on day 7 to have fledged prematurely. In the first few cases of force-fledging Ovenbirds in 2007, we attempted to gather the birds and replace them in the nest, but they immediately jumped back out. In all other cases of force-fledging or premature fledging in both species, we immediately left the area and did not attempt to gather and replace fledglings into the nest. At three Golden-winged Warbler nests, we prematurely fledged partial broods (i.e. some nestlings force-fledged on day 7 and others remained in the nest). In each case, the remaining nestlings would have been included as fledging independent of our activities, but they were subsequently depredated before fledging. We used radiotelemetry to monitor the fate (i.e. survival or mortality) of each radiomarked fledgling once a day for 24 days, the approximate age of independence from adult care for each species (Streby & Andersen 2011, H.M. Streby unpubl. data).

Statistical analysis

We compared survival among force-fledged, prematurely fledged and apparently naturally fledged Ovenbird and Golden-winged Warbler fledglings. For each group, we calculated daily survival from coefficients of a logistic exposure model (Shaffer 2004). All models included a random effect for brood, because survival among siblings was unlikely to be independent. In addition, all models included a quadratic term for fledgling age because survival clearly increased non-linearly with fledgling age. We calculated the probability of a fledgling in each group surviving to independence as the product of daily survival probabilities for days 1–24. We used Z-tests to compare survival estimates, and we considered tests significant if $Z > 1.96$, equivalent to $a = 0.05$.

RESULTS

We monitored 90 fledgling Ovenbirds from 83 broods and 227 fledgling Golden-winged Warblers from 96 broods. Of those 317 individuals monitored, six fledglings from four (5%) Ovenbird broods and 18 fledglings from 12 (12%) Golden-winged Warbler broods were force-fledged on day 8 or 9, and nine nestlings from nine (11%) Ovenbird broods and eight nestlings from seven (7%) Golden-winged Warbler broods (four whole broods and three partial broods) fledged on day 7 and were considered to have fledged prematurely. In all three cases in which partial broods prematurely fledged, the fledglings we monitored ($n = 3$) survived to independence from adult care, whereas the remaining radio-marked nestlings ($n = 5$) were predated in their nests within 24 h of handling and marking with rings and transmitters. Nestling mortalities were not included in the comparison of fledgling survival.

Ovenbirds that force-fledged as a result of being handled experienced higher survival than those that fledged independently of our activities, and those that prematurely fledged experienced similar survival to force-fledged birds, but not significantly higher survival than those that fledged independently of our activities (Fig. 1). Fledgling Golden-winged Warbler survival followed a similar pattern, but the differences were not statistically significant (Fig. 1).

None of the birds we force-fledged or prematurely fledged died from exposure, whereas one (2%) Ovenbird and five (3%) Golden-winged Warblers that fledged independently of our activities died from apparent exposure the first or second night after fledging. Exposure mortalities occurred during exceptionally cold and usually wet nights primarily in Sandilands PF, our northernmost study site. All other mortalities were attributed to predation by mammals, hawks and snakes.

DISCUSSION

Force-fledging in response to investigator activities is widely believed to decrease reproductive success through reduced survival of fledglings, and many authors caution against it. However, little or no empirical evidence has been published in the scientific literature to evaluate this assumption. In two species of ground-nesting forest warblers (Ovenbirds and Golden-winged Warblers) in the western Great Lakes region of central North America, we found that force-fledging did not negatively influence fledgling survival. Indeed, nestlings that fledged in response to our research activities experienced survival as high as or higher than those that fledged independently of our activities. We speculate that this somewhat unexpected result is related to the condition of individual nestlings and broods, and we do not suggest that purposely forcing nestlings to fledge would positively influence fledgling survival. It is likely that a propensity or ability to fledge in response to a stimulus reflects nestling condition, with nestlings in better condition than other nestlings of similar age, even brood-mates, more likely to fledge. If the birds that force-fledged were indeed of superior condition to nestlings of similar age, it is possible that their survival would have been higher still if they had fledged later, but that hypothesis is untestable because a bird cannot be both force-fledged and allowed to fledge naturally. Unfortunately, in a separate analysis we found that differences in nestling digestive contents rendered nestling mass useless as an indicator of relative condition (H.M. Streby unpubl. data), so we could not test this hypothesis. It is also possible that force-fledged birds were negatively affected in unseen ways through longer-term energetic compensation for a short-term deficit. However, we observed no differences in daily movements or survival between force-fledged fledglings and other fledglings beyond the first week following fledging (H.M. Streby unpubl. data). Importantly, we found no evidence that nestlings that prematurely fledged experienced reduced survival, suggesting that those birds were likely to have been prepared to fledge when we banded and attached transmitters to nestlings. We suggest that broods and individual nestlings that readily fledge in response to predators or investigator activities should

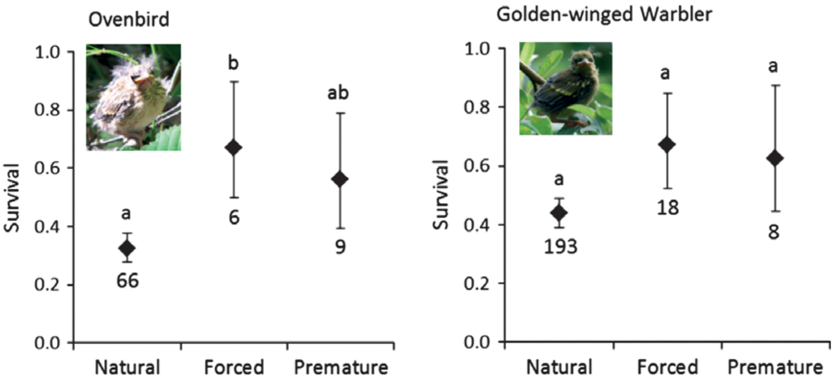

Figure 1. Survival from fledging to independence from adult care for Ovenbirds and Golden-winged Warblers that fledged from nests independent of investigator activity (natural), and those that fledged in response to investigator activity at a typical fledging age (forced) or earlier than typical fledging age (premature). Diamonds and whiskers represent means and se, respectively. Numbers and letters denote number of fledglings and significantly different groups for each species.

not be described as fledging prematurely, a term that implies fledging prior to when a fledgling is capable of surviving at typical rates.

Video surveillance of songbird nests suggests that force-fledging in response to mammalian, avian, reptilian and invertebrate predators is common in songbirds (Pietz *et al.* 2012). Lima (2009) suggested that force-fledging might be beneficial only if nestlings are sufficiently ambulatory to elude predators. Although capable of travelling > 100 m within a day of fledging (Streby & Andersen 2013a), recently fledged Ovenbirds and Golden-winged Warblers are not impressive locomotors compared with their predators. However, having one large prey item (i.e. the entire brood) become multiple separate prey items (i.e. fledglings) is likely to have some fitness benefit. The nestlings we force-fledged usually travelled < 3 m in apparently random directions from the nest and then remained silent and motionless while the adults loudly and actively distracted us, presumably as they would for any other perceived predator. Our results suggest that nestlings need only thermoregulatory, not considerable ambulatory, preparedness for force-fledging to be an adaptive behaviour.

Clearly, force-fledging prior to when nestlings are capable of surviving outside the nest (e.g. unable to thermoregulate effectively) would decrease survival due to exposure and possibly predation. However, video monitoring of nests suggests that nearly all force-fledging (whether predator- or researcher-induced) occurs after *c.* 80% of the typical nestling stage length (Ball & Bayne 2012, Pietz *et al.* 2012), similar to our observations. We speculate that force-fledging may only occur after a certain threshold (i.e. adequate condition to survive outside the nest) is reached. However, we suggest it is prudent to avoid force-fledging under circumstances that probably would compromise fledgling survival (e.g. nests high in trees, nests over water, or during inclement weather). We further caution that our results should not inspire a new assumption that force-fledging is universally harmless. However, in circumstances where research objectives require handling nestlings near fledging age, the assumption that force-fledging will always negatively influence fledgling survival is not supported by our results. For example, radiotracking fledgling songbirds is becoming increasingly common (e.g. King *et al.* 2006, Berkeley *et al.* 2007, Streby & Andersen 2013c). Attaching transmitters to nestlings too early can result in poorly fitted harnesses falling off in the nest (pers. obs.). However, waiting for birds to fledge before attaching transmitters presents additional challenges because fledglings often leave natal territories shortly after fledging, greatly reducing the probability of capture and increasing the probability of confusing unmarked broods with each other (Streby & Andersen 2013a). Furthermore, marking birds after they fledge potentially excludes fledgling mortalities that occur in the first few hours or days after fledging (Streby & Andersen 2013b). The ideal time for attaching transmitters to nestling songbirds is therefore during the 20% of the nestling stage preceding expected fledging, the period during which force-fledging some birds is likely. Our results suggest that, at least for Ovenbirds and Golden-winged Warblers, concerns about force-fledging should not be a deterrent to handling birds near the expected fledging age. In addition, if birds are inadvertently force-fledged it may be counterproductive to attempt to gather and force them back in the nest, risking disturbance to surrounding vegetation, attraction of predators to the area, injury or mortality of fledglings, and additional stress to fledglings and adults.

Force-fledging may also influence estimates of nest survival, because predation is often highest in the final days and hours of the nestling stage (Martin *et al.* 2000, Streby & Andersen 2013a) and those predation events could be precluded if young fledge early. However, video monitoring and radiotelemetry studies have demonstrated that fates of empty nests are sometimes incorrectly identified by observers anyway (Pietz *et al.* 2012, Streby & Andersen 2013a), and that estimates of productivity based solely on data from nests can be misleading regardless of assumptions about ambiguous nest fates (Streby & Andersen 2011). Our assessment of the impacts of force-fledging further supports the importance of monitoring juvenile songbird survival beyond when fledglings leave the nest. Leaving the nest is merely one occurrence during the highest mortality period for young songbirds, a most inopportune transition during which to cease data collection and make assumptions about fates of birds or the impacts of investigator activities.

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Testing common assumptions in studies of songbird nest success

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We studied Ovenbird *Seiurus aurocapilla* and Golden-winged Warbler *Vermivora chrysoptera* populations in northern Minnesota, USA, to test two common assumptions in studies of songbird nest success: (1) that the condition of an empty nest on or near its expected fledge date is an indicator of nest fate; and (2) that the presence of a fledgling or family group within a territory confirms a successful nest in that territory. We monitored the condition of nests and used radiotelemetry to monitor juveniles through the expected fledging date and early post-fledging period. Of nests that contained nestlings 1–2 days before the expected fledge date, fates were misidentified using nest condition alone for 9.5% of Ovenbird nests, but those misidentifications were made in both directions (succeeded or failed), yielding only a small bias in estimated nest success. However, 20% of Golden-winged Warbler nests were misidentified as successful using nest condition during the final visit interval, biasing the nest success estimate upward by 21–28% depending on the treatment of uncertain nest fates. Fledgling Ovenbirds from 58% of nests travelled beyond their natal territory within 24 h, rising to 98% after 5 days, and those fledglings travelled up to 390 m from nests within 10 days of fledging. Fledgling Golden-winged Warblers from 13% of nests travelled beyond their natal territory within 24 h, rising to 85% after 5 days, and those fledglings travelled up to 510 m from nests within 10 days of fledging. We conclude that nest condition and fledgling presence can be misleading indicators of nest fate, probably commonly biasing nest success estimates upward, and we recommend that these assumptions should be tested in additional species.

Keywords: fledgling, Golden-winged Warbler, Ovenbird, *Seiurus aurocapilla*, telemetry, *Vermivora chrysoptera*.

Estimates of songbird reproductive success, typically limited to nest data, are used to assess habitat quality (e.g. Weinberg & Roth 1998), model population dynamics (e.g. Podolski *et al.* 2007), identify source and sink populations (e.g. Donovan *et al.* 1995), and inform conservation and management plans (e.g. Woodworth 1999). Although songbird population growth may be generally more sensitive to adult annual survival and fledgling survival (Donovan & Thompson 2001, Streby & Andersen 2011), population growth is also sensitive to variation in nest success (Donovan *et al.* 1995), and nest success is the only directly estimated parameter in most studies of songbird reproductive success (Anders *et al.* 1997). Many population models account for re-nesting (birds nesting again after initial failure) and estimates of nest productivity (number of young produced per successful nest). All such studies require accurate field identification of whether each monitored nest succeeded or failed in producing young. However, observational studies of songbird nests often

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depend on several assumptions that potentially bias results. Here we address two such assumptions that are critical because they deal with the determination of whether nesting attempts succeeded or failed when fledging events were not observed.

First, it is often difficult to determine the fate of a nest that is found empty on or near the date young are expected to fledge. Nest-monitoring protocols recommend that nests be checked from a distance daily, starting the day before expected fledging (Ralph *et al.* 1993). However, daily checks are not always possible due to logistical constraints, inclement weather or disturbance risk, and it is difficult to ascertain the fate of an empty nest regardless of how often it was visited.

Excluding nests with uncertain fates from analyses can cause a downward bias in nest success estimates that assume constant daily survival (Manolis *et al.* 2000). Manolis *et al.* (2000) used simulation models to determine the most effective treatment of uncertain nest fates in estimation of nest success. They found the least bias when terminating exposure (number of days a nest is observed active) with the last observation the nest was active for nests with uncertain fates. However, some bias remains if the probability of failure during the final interval differs between nests with known or uncertain fates. If the signs of failure or success are more obvious (i.e. more easily determined), or more likely to be incorrectly identified during observations of empty nests, bias in the direction of the more easily determined fate will increase as a function of the proportion of uncertain fates in a dataset. In addition, if the probability of predation increases with nestling age, as theory and experimental evidence suggest (Haskell 1994, Martin *et al.* 2000, McDonald *et al.* 2009), even proper treatment of uncertain fates during analysis would underestimate failures and bias nest success estimates upward. Some studies exclude the final days of the nestling period altogether and include all nestlings alive within a few days of the expected fledging date as fledged young (e.g. Murphy 2007), which inherently assumes predation does not occur in the final days before fledging. As nestlings age, parental nest-visit frequency increases (Kluyver 1961), nestling vocalization type changes and volume increases (Khayutin 1985), and the reward to predators (i.e. nestling mass) increases, all of which can increase predation risk (Haskell 1994, Martin *et al.* 2000, McDonald *et al.* 2009). The common assumption that predation risk remains unchanged or is absent during the days immediately preceding fledging therefore contradicts the evidence. Datasets that exclude the final days of the nestling stage or those that include many uncertain fates may produce estimates of nest success biased upward.

Manolis *et al.* (2000) used the Mayfield (1961) method for estimating nest daily survival. This method requires the commonly unrealistic assumption that the exact day of nest failure is known (Heisey *et al.* 2007). Recently developed methods, including those in program MARK (Dinsmore *et al.* 2002) and generalized linear models (Shaffer 2004), incorporate the appropriate likelihood estimator for interval data. However, even the most robust statistical techniques are limited by the quality of the raw data, and all nest survival analyses share the assumption that nest fates are correctly determined (Johnson 2007). Many studies limit the number of nest fates classified as uncertain by examining nest condition for signs of success or failure as suggested by the BBIRD protocol (Martin *et al.* 1997). This 'Nest Condition' method uses a series of rules to make an educated guess about the fate of a nest that is empty on or near the expected fledging date. The rules differ among studies, but a typical summary follows. If a nest is empty prior to the expected fledge date, it is assumed to have failed. If a nest is empty on or after the expected fledge date and there are signs of disturbance to the nest-site (e.g. nest broken or destroyed, broken egg shells, feathers, dead young), the nest is assumed to have failed. If a nest is empty on or after the expected fledge date and there is no sign of predation or disturbance, or there are signs of nest success (e.g. rim of nest flattened, faeces on or near rim of nest), the nest is assumed successful. These rules have been used in studies that consequently report having no uncertain nest fates (e.g. Dalley *et al.* 2009) but their reliability is questionable. For example, Thompson *et al.* (1999) video-monitored songbird nests and found that many that were predated showed no disturbance or evidence of predation. Similarly, Stake *et al.* (2005) found that snake predation of songbird nests increases in frequency late in the nestling stage and usually does not disturb the nest, so could be misinterpreted as fledging. These observations suggest that the Nest Condition method may identify some failed nests as successful, and that treating uncertain nest fates with appropriate statistical considerations may be superior to identifying fates based on the condition of empty nests.

A second common assumption in studies of songbird nest success is that observing a fledgling or family group in a territory is reliable confirmation of a successful nest in that territory (e.g. Vickery *et al.* 1992a, Seagle & Sturtevant 2005). Many studies have circumvented the observation of nests by creating indices of reproductive activity (IRA) using observations during surveys and spot-mapping of territories (e.g. Vickery *et al.* 1992a). Proper application of an IRA requires observer knowledge of species-specific nesting phenology and other natural history characteristics (Vickery *et al.* 1992a). For example, an observation of an adult with food could be a sign of courtship feeding, feeding of an incubating mate, feeding of nestlings, feeding of fledglings, feeding of a brood parasite nestling or fledgling, carrying food to caching sites, or simply a prey item that requires extended handling time. Even if an observer has sufficient knowledge to interpret such activities during the nesting period, little is known about movement and habitat use for most songbird species during the post-fledging period (Anders *et al.* 1998). In particular, if fledglings move off their natal territory and into neighbouring territories soon after fledging, they could cause one to assume the nest in the neighbouring territory was successful. For example, the majority of Dickcissel *Spiza americana* (Berkeley *et al.* 2007) and Lark Bunting *Calamospiza melanocorys* (Yackel Adams *et al.* 2001) fledglings were > 100 m and > 250 m from nests, respectively, within the first week after fledging. The assumption that a fledgling or family group in a territory containing a nest that recently contained nestlings confirms fledging of that nest remains untested.

We studied a population of breeding Ovenbirds *Seiurus aurocapilla* in north-central Minnesota and a population of breeding Golden-winged Warblers *Vermivora chrysoptera* in north-western Minnesota, USA, and assessed whether: (1) the condition of an empty nest on or near its expected fledge date is a reliable indicator of nest fate; and (2) the presence of a fledgling or family group within a nesting territory is a reliable confirmation of a successful nesting attempt within that territory. We monitored conditions of nests and used radio-telemetry to monitor survival and movements of juvenile Ovenbirds and Golden-winged Warblers through expected fledging dates and the early post-fledging period. We expected the proportion of nest fates determined incorrectly by nest condition alone to be small but still potentially a source of bias. We further expected most fledglings to remain within or near nesting territories for at least a few days after fledging.

METHODS

Study area

We studied Ovenbirds during May–July 2007 and 2008 at two study sites in the Chippewa National Forest (CNF: 47°31′N, 94°16′W) in north-central Minnesota, and Golden-winged Warblers during May–July 2011 at Tamarac National Wildlife Refuge (Tamarac NWR: 47°02′N, 95°35′W) in north–western Minnesota. Both species are ground-nesting, primarily insectivorous Neotropical migratory wood warblers (Parulidae); Ovenbirds nest primarily in mature forest, and Golden-winged Warblers nest primarily in early successional forest and other open shrubby areas within a forested landscape. The CNF encompasses ~600 000 ha of Cass and Itasca Counties in the northern hardwood–coniferous forest transition zone. Mature forest stands, in which we studied nesting Ovenbirds, were over 50 years after harvest, more than 200 ha in area, ranged from mostly coniferous to mostly deciduous, and were primarily composed of Red Pine *Pinus resinosa*, Sugar Maple *Acer sacharum*, American Basswood *Tilia americana*, aspens *Populus* spp., birches *Betula* spp., White Pine *Pinus strobus* and Northern White-cedar *Thuja occidentalis*.

Tamarac NWR encompasses ~17 000 ha of primarily deciduous forest, interspersed with lakes, grasslands, shrubby wetlands and early-successional forest stands of various ages. Early-successional forest stands, in which we studied nesting Golden-winged Warblers, were 5–15 years after harvest, 10–30 ha in area, and were primarily composed of hazel *Corylus* spp., aspen, birch, sedges and forbs. We also monitored Golden-winged Warbler nests in shrubby wetlands that ranged from 3 to 20 ha and were dominated by alder *Alnus* spp., hazels, and Tamarack *Larix laricina*.

Nest monitoring

We searched for and monitored Ovenbird nests in eight 10-ha plots at each of two study sites. We randomly established each 10-ha nest-searching plot within mature-forest stands to minimize non-independence among nests and broods we monitored. We searched for and monitored Golden-winged Warbler nests in four early-successional forest stands and four shrubby wetlands during the 2011 breeding season. In addition, we captured female Golden-winged Warblers during May 2011, fitted them with radio-transmitters and monitored nests we found by tracking radio-marked females. For both species, we searched each plot every 4 days and visited nests at 4-day intervals. We made more frequent visits (every 1–2 days) during periods of egg-laying and expected hatching to predict the date of fledging. To reduce disturbance of nest-sites, we took different paths to and from nests during each visit, and we sometimes ($\sim 10\%$ of observations) observed nests remotely (> 10 m from nests) with binoculars. We visited each nest 1–2 days before the expected fledging date, removed the nestlings and carried them in a soft cloth bag $\geq$ 10 m from the nest. We ringed all nestlings with numbered aluminium US Geological Survey rings, and attached a radio-transmitter to at least one nestling from each nest. We attached transmitters using a figure-eight harness designed for passerines (Rappole & Tipton 1991). The combined mass of transmitter and harness was 4.3–4.9% of nestling mass. We returned nestlings to their nest within 15 min, and only when no nest predators were seen or heard. We then monitored each nest daily from a distance of several metres until we observed that the nest was empty. Once a nesting attempt was finished, we closely inspected the condition of the nest-site using the Nest Condition method. After determining the fate of a nesting attempt using this method, we then determined the fate (dead or alive) and location of each radio-marked nestling/fledgling. We recorded locations of nests and fledglings using handheld GPS units (100 points averaged, accuracy usually under 5 m).

We fitted logistic exposure models to data we collected using three methods: (1) Telemetry; (2) Nest Condition; and (3) Manolis (Last Active-B in Manolis *et al.* 2000). In all three methods, nests that failed during laying, incubation or early in the nestling period were treated as failures. In the Telemetry method, we determined nest fates based on the fate and location of radio-marked nestlings (tracked after observing nest condition) immediately after the nest was observed empty. In the Nest Condition method, we assigned a fate of failed or successful to each of those nests based on the condition of the nest-site. However, we did not use fledgling activity near an empty nest as a sign of nest success, in contrast to Manolis (1999), because the validity of using fledgling activity as an indicator of nest success is addressed in the telemetry analysis.

Ovenbirds and Golden-winged Warblers in our study populations average a 4-day laying stage, a 12-day incubation stage, and an 8-day (Ovenbirds) and 9.5-day (Golden-winged Warblers) nestling stage, with 10–15% fledging a day earlier and 10–15% fledging a day later (H.M. Streby and D.E. Andersen unpubl. data). For the Nest Condition and Manolis methods, when a previously occupied nest was observed empty on or after the penultimate day of the nestling stage, we used the following rules to determine nest fates based on nest-site condition. If a nest was empty before the penultimate day of the nestling period (i.e. two or more days before the species-specific mean fledging age), we assumed the nesting attempt failed. If a nest was empty on or after the penultimate day and the nest-site was disturbed, we assumed the nesting attempt failed. If a nest was empty on or after the penultimate day and we found any sign of success, we assumed the nesting attempt succeeded. If a nest was empty on or after the penultimate day and the nest-site was not disturbed, we assumed nestlings successfully fledged from the nest (Nest Condition method) or the nest fate was uncertain (Manolis method). These nest-fate determination methods are consistent with the commonly applied BBIRD protocol (Martin *et al.* 1997).

Fledgling monitoring

We used ARC GIS 9.3 (use of trade names does not imply endorsement by either the US Geological Survey or the University of Minnesota) to measure distances from nests for each daily location of marked fledglings to determine if fledglings were inside or outside their natal territory. Although we did not measure territory sizes for Ovenbirds directly, we recorded 5–15 singing males and monitored 4–10 simultaneous nesting attempts per ha in some of our plots. Therefore, using conservative estimates of 4–10 territories/ha, we determined that Ovenbird territories range from 0.10 to 0.25 ha in this population; this is similar to other densely populated regions (e.g. Smith & Shugart

1987). We considered fledgling Ovenbirds to be outside their probable minimum (0.10 ha) and maximum (0.25 ha) territories if the distance between a fledgling and its nest was greater than the radius of a hypothetical exclusive circular territory of each size. Based on point counts, spot mapping, proximity of monitored nests and tracking of radio-marked adults, Golden-winged Warblers nested at *c.* one pair/ha on our study plots at Tamarac NWR (H.M. Streby, D.E. Andersen & J. P. Loegering unpubl. data). We considered fledgling Golden-winged Warblers to be outside their natal territory if the distance between a fledgling and its nest was greater than the radius of a hypothetical exclusive circular 1-ha territory.

Statistical analysis

For each species, we used PROC GENMOD in SAS (SAS Institute 2008) to fit logistic exposure models (Shaffer 2004) to data collected using each of the three methods (Telemetry, Nest Condition and Manolis). The candidate models we considered included a constant survival model and models including all combinations of nest initiation date, nest age and a quadratic term for nest age. We used Akaike's information criterion corrected for small sample size (AIC_{C}) to rank candidate models, and we report Akaike weights for each best supported model (Burnham & Anderson 2002). Because the Akaike weight of the best supported model was < 0.90 in most cases, we used model-averaged coefficients to calculate daily survival estimates (Burnam & Anderson 2002). We fitted values of daily survival from model-averaged coefficients to visually compare the models produced from each method.

RESULTS

Nest success

Ovenbirds

We monitored 184 Ovenbird nests, 116 (63%) of which contained nestlings during observations 1–2 days prior to their expected fledge date; 68 (37%) nests failed earlier in the nesting period. From the 116 nests that contained nestlings near the expected fledge date, we ringed 375 nestlings and attached transmitters to 130 nestlings. Transmitters fell off 11 nestlings in 11 nests. We found four of those fledged family groups, confirmed identities of ringed fledglings and re-attached transmitters. The fates of the remaining seven nests for which transmitters fell off nestlings were uncertain. Because there was no sign of failure at those seven nest locations, we considered them successful in the Nest Condition method, and uncertain in the Manolis and Telemetry methods.

Using the Telemetry method, we identified 18 failures, 91 successes and seven nests with uncertain fates for the 116 Ovenbird nests that contained nestlings 1–2 days before their expected fledge date. Using the Nest Condition method, we identified 17 failures and 99 successes in the same sample of nests. Of the 99 successful nests in the Nest Condition method, 80 were assumed successful only because there was no sign of failure. Therefore, for the Manolis method, we identified 17 failures, 19 successes and assigned 80 nests uncertain fates (Table 1).

Of fates determined by condition of the 116 nests active during the final visit interval, 11 (9.5%) were incorrectly identified: six as successful and five as failed. Using telemetry, we found dead nestlings (with and without transmitters) or parts of nestlings (i.e. feathers and ringed legs) under leaf litter < 1 m from each of these six undamaged nests. This suggests that predation probably occurred at the nest. Although it is possible that these birds were killed immediately after fledging, thus technically meeting the definition of a successful nest, they nonetheless clearly represent a failed reproductive attempt. In addition, using telemetry, we observed two nests found empty on day 6 after hatching, and three nests that were damaged or destroyed on day 7 or 8 after hatching, but family groups from these nests were subsequently observed (using telemetry) alive.

For all three methods, the best supported model of Ovenbird nest daily survival was the model including linear and quadratic terms for nest age, with Akaike weights of 0.80, 0.53 and 0.91 for the Telemetry, Nest Condition and Manolis methods, respectively. Because similar numbers of Ovenbird nest fates were incorrectly identified as successful and failed, the net bias caused by incorrectly identified fates was relatively small for the Nest Condition method (Fig. 1, Table 1). However, because the nest fates incorrectly identified as successful were considered uncertain in the Manolis method, that method was disproportionately affected by the nest fates incorrectly

Table 1. Estimates of Ovenbird and Golden-winged Warbler nest success from logistic exposure models (using model-averaged coefficients) fitted to data on 184 Ovenbird nests monitored during 2007–2008 in the Chippewa National Forest, Minnesota, and 53 Golden-winged Warbler nests monitored during 2011 at Tamarac National Wildlife Refuge, Minnesota. Each analysis was identical except for the three methods (Telemetry, Nest Condition and Manolis) used to determine fates of nests found empty on or near the expected fledge date.

Species	Method	No. failed (no. incorrect)	No. successful (no. incorrect)	No. uncertain	Nest success estimate[d]	Percentage difference in estimate
Ovenbird	Telemetry[a]	86	91	7	0.427	0
	Nest Condition[b]	85 (5)	99 (6)	0	0.448	+4.9
	Manolis[c]	85 (5)	19	80	0.384	−11.2
Golden-winged Warbler	Telemetry	29	24	0	0.392	0
	Nest Condition	23 (6)	30	0	0.501	+27.8
	Manolis	23	0	30	0.474	+20.9

[a] Nest fates determined by survival of nestlings and fledglings using radiotelemetry. [b] Nest fates determined by condition of nests found empty on or after expected fledge dates. [c] Nest fates determined as in Nest Condition method when predation was evident on nests found empty on or after expected fledge dates, fates of undisturbed empty nests considered uncertain, and exposure for uncertain fates terminated at the end of the last active interval (Last Active B from Manolis *et al.* 2000). [d] Standard Errors of estimates (not shown) were very similar within species, 0.040–0.045 for Ovenbirds and 0.138–0.164 for Golden-winged Warblers.

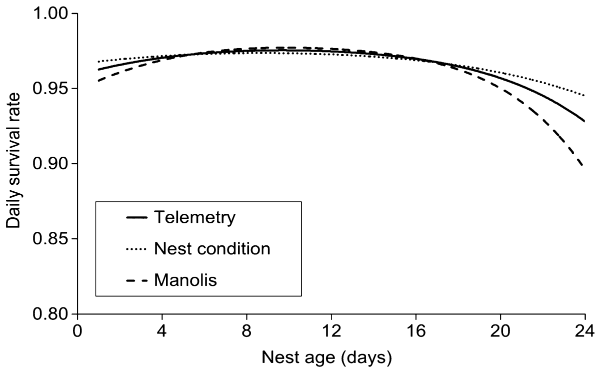

Figure 1. Fitted values from logistic exposure models (from model-averaged coefficients) for data on 184 Ovenbird nests for which fates were determined using three methods (Telemetry, Nest Condition and Manolis) when nests were found empty on or near expected fledge dates. The Manolis method underestimated daily survival because the sample of uncertain nest fates included a disproportionate number of successful nests, resulting from nest failures being more readily identified than nest successes.

determined as failed (Fig. 1) and produced a nest success estimate biased downward (Table 1).

Golden-winged Warblers

We monitored 53 Golden-winged Warbler nests, 30 of which contained nestlings during observations 1–2 days prior to their expected fledge date, whereas 23 (43%) nests failed earlier in the nesting period. From the 30 nests that contained nestlings close to the expected fledge date, we ringed 122 nestlings and attached transmitters to 47 nestlings.

Using the Telemetry method, we identified six failures and 24 successes for the 30 Golden-winged Warbler nests that contained nestlings 1–2 days before their expected fledge date. Using the Nest Condition method, we identified all 30 nests as successful because there was no sign of nest failure at any of those nests. Therefore, we identified all 30 of those nests as having uncertain fates in the Manolis method.

Of fates determined by condition of the 30 nests active during the final visit interval, six (20%) were incorrectly identified: all six failed with no sign of failure at the nest. As with Ovenbirds, using telemetry we found dead nestling Golden-winged Warblers, or parts of nestlings (i.e. feathers and ringed legs), under or on leaf litter < 4 m from each of these six undamaged nests. In addition, we tracked radio-tagged adult female Golden-winged Warblers from those nests and observed them foraging 200–400 m from the nest with no sign of feeding fledglings.

For the Telemetry method, the best-supported model of Golden-winged Warbler nest daily survival included linear and quadratic terms for nest age, with an Akaike weight of 0.60. For the Nest Condition and Manolis methods, the best-supported model included only a linear term for nest age, and had an Akaike weight of 0.48 and 0.57, respectively. Unlike our Ovenbird sample, all incorrectly identified nest fates for Golden-winged Warblers were failed nests that we identified as successful based on nest condition alone, biasing the estimates of nest success from Nest Condition and Manolis methods upward by 28 and 21%, respectively (Fig. 2, Table 1).

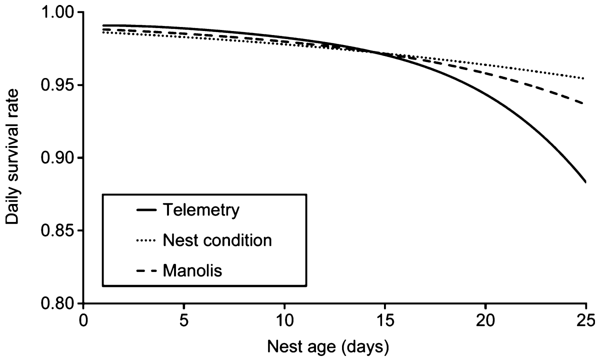

Figure 2. Fitted values from logistic exposure models (from model-averaged coefficients) for data on 53 Golden-winged Warbler nests for which fates were determined using three methods (Telemetry, Nest Condition and Manolis) when nests were found empty on or near expected fledge dates. The Nest Condition and Manolis methods greatly overestimated daily survival because six failed nests were incorrectly identified as successful using those methods.

Fledgling movements

Ovenbirds

We located fledgling Ovenbirds 3–108 m ($\bar{x}$ = 36 m, *n* = 89) from their nests within 24 h of fledging. This suggests that 58–74% of fledgling Ovenbirds were outside their presumed natal territory within 24 h, based on estimated territory sizes ranging from 0.10 to 0.25 ha (Fig. 3). We located fledgling Ovenbirds 37–174 m ($\bar{x}$ = 117 m, *n* = 61) from nests within 5 days of fledging and 86–390 m ($\bar{x}$ = 152 m, *n* = 41) within 10 days of fledging. This suggests that 98 and 100% of fledglings were outside assumed 0.25-ha natal territories within 5 and 10 days of fledging, respectively. We located 8, 17 and 32% of fledgling Ovenbirds outside of the 10-ha plot containing their nest ≤ 24 h, ≤ 5 days and ≤ 10 days after fledging, respectively.

Golden-winged Warblers

We located fledgling Golden-winged Warblers 8–66 m ($\bar{x}$ = 26 m, *n* = 16) from their nests within 24 h of fledging. This suggests that 13% of fledgling Golden-winged Warblers were outside of their presumed natal territory within 24 h of fledging (Fig. 4). We located fledgling Golden-winged Warblers 25–346 m ($\bar{x}$ = 156 m, *n* = 13) from nests within 5 days of fledging, and 126–510 m ($\bar{x}$ = 252 m, *n* = 12) within 10 days of fledging. This suggests that 85 and 100% of fledgling Golden-winged Warblers were outside 1-ha natal territories within 5 and 10 days of fledging, respectively. We located 6, 54 and 83% of fledgling Golden-winged Warblers outside our study plots ≤ 24 h, ≤ 5 days and ≤ 10 days after fledging, respectively.

DISCUSSION

In this study of Ovenbird and Golden-winged Warbler nest success, the use of radiotelemetry to monitor nestlings and fledglings reduced the number of uncertain nest fates, thus also reducing potential bias in nest success estimation. In addition, using radiotelemetry avoided bias from incorrectly determined fates (i.e. nests for which there was evidence of success or failure but where that

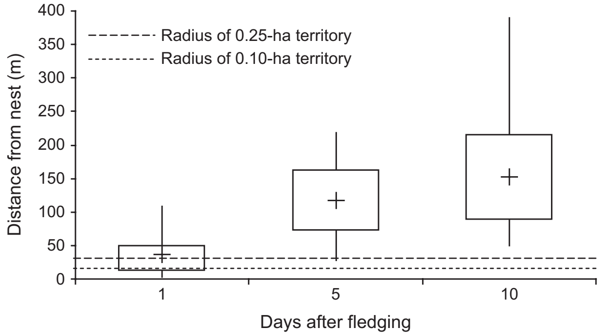

Figure 3. Distances moved from nests by fledgling Ovenbirds within 1 (*n* = 89), 5 (*n* = 61) and 10 (*n* = 41) days after fledging in the Chippewa National Forest, Minnesota. Plus signs, boxes and whiskers represent mean, SD and range, respectively. Dashed lines represent radii of estimated nesting territories of 0.10 and 0.25 ha.

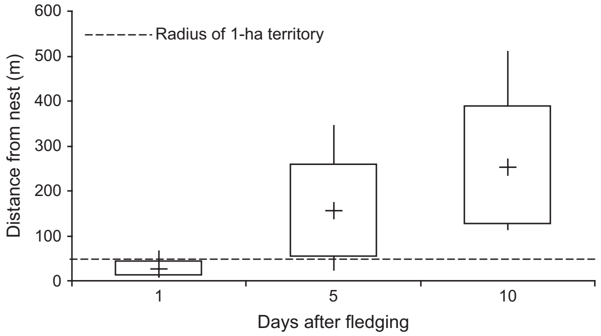

Figure 4. Distances moved from nests by fledgling Golden-winged Warblers within 1 (*n* = 16), 5 (*n* = 13) and 10 (*n* = 12) days after fledging in Tamarac National Wildlife Refuge, Minnesota. Plus signs, boxes and whiskers represent mean, SD and range, respectively. Dashed line represents the radius of an estimated nesting territory of 1.0 ha.

evidence was misleading) based on nest condition alone. Using radiotelemetry, we were able to determine fates of 96% of Ovenbird nests and 100% of Golden-winged Warbler nests, whereas only 57% of nest fates were known correctly without telemetry for each species.

Excluding nests with uncertain fates from nest success estimation is inappropriate (Manolis *et al.* 2000). Observation of the condition of empty nests is often used to determine otherwise uncertain nest fates (e.g. Dalley *et al.* 2009). However, in our study, nest fates were incorrectly determined using nest condition alone for 9.5% of Ovenbird nests and 20% of Golden-winged Warbler nests that contained nestlings near the expected fledge date. Because we did not radiotag all nestlings, it is possible that one or more of the Ovenbird nests for which we determined failure based on telemetry may have experienced partial fledging success. However, for all six Golden-winged Warbler nest failures determined from telemetry, we observed the radiotagged females foraging far from their nests (> 200 m) and not feeding fledglings.

The similarity in Ovenbird nest success estimates produced by the Nest Condition and Telemetry methods obscures the fact that the Nest Condition method included incorrectly identified nest fates. In this study, the Nest Condition method produced an estimate similar to that of the Telemetry method simply because nest successes and failures were similarly likely to be incorrectly assigned. If that were the case in all study populations, incorrectly identified fates in the Nest Condition method would cause little or no net bias in estimates of nest success. However, our estimates of Golden-winged Warbler nest success demonstrate the possible severity of the bias caused by incorrectly determined nest fates when all of those fates are incorrectly determined as either succeeded or failed. Studies of video-monitored nests suggest that incorrectly identified fates are likely to be unbalanced, with failed nests misdiagnosed as successful more often than successful nests are misdiagnosed as failed (Thompson *et al.* 1999, Stake *et al.* 2005), biasing nest success estimates upward as in both of our examples. Another potential problem highlighted by our study is the importance of data from the laying stage in analyses of nest success. We discovered > 50% of nests on or before the day the first egg was laid (H.M. Streby unpubl. data), and nest survival was lower during the laying stage than in any other period until the end of the nestling stage for Ovenbirds (Fig. 1) but not Golden-winged Warblers (Fig. 2). This suggests that excluding the laying stage from analysis can potentially bias nest success estimates upward even more than excluding only the end of the nestling stage.

One might speculate that our ringing and radio-tagging activities could have attracted predators to nests or made tagged birds more vulnerable to predation, thereby increasing predation in the final days of the nestling period. However, predation rates increased throughout the nestling stage for both species we studied, consistent with nests monitored by video (Stake *et al.* 2005) and with the hypothesis that nest predation increases as nestlings grow and with the increased activity of adults and nestlings (Haskell 1994, Martin *et al.* 2000, McDonald *et al.* 2009). Therefore, when all nestlings alive within a few days prior to fledging are considered fledged (e.g. Murphy 2007), the inherent assumption that predation is either absent or greatly reduced in the final days of the nestling stage is more precarious than our assumption that our activities did not increase predation rates. Importantly, terminating all nest observations at the last active visit (‘Early Termination’ in Manolis 2000) requires the similarly unsupported assumption that nest failure rates do not increase during the final 1 or 2 days of the nestling stage.

The potential pitfalls of right-censored data in survival analysis, including the consequences of falsely assuming that censoring does not impact survival estimates, have been discussed at length (e.g. Lagakos 1979). It is important to note that incorrectly determined fates cause bias only when either survival or mortality is more likely to be incorrectly identified. However, our Ovenbird example demonstrates that a very small imbalance in incorrectly identified fates can bias an estimate of nest success meaningfully even when the sample size is reasonably large. It is also important to note that imbalances in incorrectly identified fates cause bias, not imprecision, and therefore cannot be compensated for with increased sample size. In other words, samples of nests are likely to include a similar proportion and imbalance of incorrectly identified fates regardless of sample size. The percentage of successful or failed nests with incorrectly determined fates probably varies due to differences among species’ nesting ecology, rules used to determine fates and predator groups, and our results demonstrate that these factors can have notable influences on nest success estimates. We cannot presume to know whether other nest success estimates based on the Nest Condition method include a net bias as small as our Ovenbird estimate or as large as our Golden-winged Warbler estimate. However, in many cases a very small range determines whether 95% confidence intervals overlap or statistical tests of differences between estimates are significant, and it is these sometimes small differences on which conclusions about treatment effects (e.g. Manolis *et al.* 2002) or whether populations are sources or sinks (e.g. Confer *et al.* 2010) depend.

We did not include observations of fledglings near a nest as a sign of its success, as is typical in methods not using telemetry (Martin *et al.* 1997). However, our observations of fledgling movements during telemetry work demonstrated the potential for additional bias in nest success estimates when assuming that fledglings near a nest came from that nest. Because most Ovenbirds and some Golden-winged Warblers travelled beyond presumed natal territories within 24 h of leaving the nest, presence of a fledgling or family group within a nesting territory is not confirmation of nest success in that territory for Ovenbirds or Golden-winged Warblers in our study populations. We observed fledglings up to 510 m from their nests within 10 days of fledging, even though fledglings may not appear capable of undertaking movements of that magnitude. Therefore, although an observation of a young fledgling or family group certainly indicates a successful nest, that successful nest may be anywhere within the surrounding 82 ha (in our study populations) if the observed bird fledged 10 days earlier. Ralph *et al.* (1993), Martin and Geupel (1993) and Martin *et al.* (1997) are commonly cited sources for nest-monitoring methodology and each caution that some species move up to 100 m within hours of fledging, and that fledglings from neighbouring territories may be attributed incorrectly to a nest territory. We reiterate that caution, and suggest that observations of fledglings should not be used as indicators of nest success unless fledglings can be individually identified and linked to their nests. If fledgling activity near a nest is used as a sign of success, nest success estimates are likely to be inflated, especially in areas of high nesting density. This effect may be smaller in populations or species with larger territories and less mobile fledglings. However, in a population of Lark Buntings with approximately one pair per hectare (Yackel Adams *et al.* 2006) broods moved 256 m (range 16–800 m) from their nests in the first 7 days after fledging (Yackel Adams *et al.* 2001), suggesting that our study populations are not extreme examples. Furthermore, we photographed development of fledgling Ovenbirds of known age throughout this study (H.M. Streby unpubl. data), and we determined that individual variation in development (especially during the first few days after fledging) limits accurate ageing of fledgling Ovenbirds to a range of 3–4 days. Thus age estimates of unmarked fledglings are unlikely to be useful for determining a range of potential proximity to the nest of origin.

Seagle and Sturtevant (2005) used territory density and post-fledging observations of adults and fledglings within territories to demonstrate that Ovenbird reproductive success is predicted by forest productivity. However, density is not a reliable indicator of habitat quality (Van Horne 1983, Vickery *et al.* 1992b) and our results demonstrated that observed fledglings may not have been produced within 10-ha study plots, and fledglings are more likely than not to be outside natal territories within 24 h of fledging. We suggest that Seagle and Sturtevant (2005) found that Ovenbird post-fledging habitat use, but not necessarily reproductive success, was predicted by forest productivity.

In conclusion, our results demonstrate that using radiotelemetry or other methods of individually identifying fledglings or family groups, rather than using nest condition, can improve accuracy of determination of nest fates, and improve nest success estimates. In the absence of individual identification of fledglings or family groups, our results suggest that treating all nests found empty on or near the expected fledge date, regardless of nest condition, as uncertain fates does not necessarily reduce bias as suggested by Manolis *et al.* (2000), because daily nest survival is rarely constant. In addition, radiotelemetry or other methods of individually identifying birds to confirm nest success within a territory or larger study area provides more accurate estimates of nest success than observations of birds from nests of unknown location. Without knowledge of species-specific post-fledging movements and habitat use, and considering the large movements made by fledglings of species that have been studied (e.g. Yackel Adams *et al.* 2001, Berkeley *et al.* 2007), an observation or capture of a fledgling or family group during the post-fledging period is evidence of no more than the use of the sampled area by that species during that period.

We acknowledge that radiotelemetry and other technology can be costly and time-consuming and may not be available for use in every study. However, due to the potential limitations of nest success studies conducted without such efforts, we suggest that telemetry, nest cameras or some other method should at least be used when possible to test whether their absence results in large bias (e.g. Golden-winged Warblers) in nest success estimates or relatively small bias (e.g. Ovenbirds). It is possible that the net bias caused by incorrectly identified nest fates is inconsequential for many species. Without testing that assumption, however, we are left to question the value of many affordable but potentially inaccurate studies compared with fewer costly but accurate ones.

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Radio-transmitters do not affect seasonal productivity of female Golden-winged Warblers

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ABSTRACT. Investigating the potential effects of handling and marking techniques on study animals is important for correct interpretation of research results and to effect progress in data-collection methods. Few investigators have compared the reproductive output of radio-tagged and non-radio-tagged songbirds, and no one to date has examined the possible effect of radio-tagging adult songbirds on the survival of their fledglings. In 2011 and 2012, we compared several parameters of reproductive output of two groups of female Golden-winged Warblers (*Vermivora chrysoptera*) breeding in Minnesota, including 45 females with radio-transmitters and 73 females we did not capture, handle, or mark. We found no difference between groups in clutch sizes, hatching success, brood sizes, length of incubation and nestling stages, fledging success, number of fledglings, or survival of fledglings to independence. Thus, radio-tags had no measurable impact on the productivity of female Golden-winged Warblers. Our results build upon previous studies where investigators have reported no effects of radio-tagging on the breeding parameters of songbirds by also demonstrating no effect of radio-tagging through the post-fledging period and, therefore, the entire breeding season.

RESUMEN. **Radio trasmisores no afectan la productividad estacional en las hembras de *Vermivora chrysoptera***

Investigar los efectos potenciales de las técnicas de manipulación y marcaje en estudios de animales es importante para interpretar correctamente los resultados de las investigaciones y para llevar a cabo los avances en los métodos de colecta de datos. Pocos investigadores han comparado el rendimiento reproductivo de las aves paserinas con o sin radios trasmisores, y nadie hasta la fecha ha examinado el posible efecto en la supervivencia de los juveniles de aves marcadas con radios trasmisores. En el 2011 y 2012 comparamos varios parámetros reproductivos en dos grupos de hembras de *Vermivora chrysoptera* reproduciéndose en Minnesota, los cuales incluían 45 hembras con radio trasmisores y 72 hembras que no capturamos, manipulamos o marcamos. No encontramos diferencias entre los grupos en el tamaño de la nidada, éxito de eclosión, numero de polluelos, duración del periodo de incubación o polluelos, éxito de salida de los polluelos del nido o supervivencia de los juveniles hasta su independencia. En consecuencia, radio trasmisores no tienen un impacto apreciable en la productividad de hembras de *V. chrysoptera*. Nuestros resultados aportan ha estudios anteriores en donde investigadores no han encontrados efecto de los radio trasmisores sobre parámetros reproductivos de aves paserinas y también demuestra que no hay un efecto de los radio trasmisores sobre la supervivencia de los juveniles a lo largo del periodo después del abandono del nido, y por ende durante toda la temporada reproductiva.

Key words: methods, nest success, post-fledging survival, songbird, transmitter effect, *Vermivora chrysoptera*

A meta-analysis of the effects of radio-transmitters and other dataloggers on birds revealed that their negative impacts on behavior, survival, and productivity are widespread (Barron et al. 2010). However, that analysis was heavily weighted toward waterbirds (i.e., penguins, waterfowl, and seabirds), and Barron et al. (2010) acknowledged that there is likely a file-drawer effect (Rosenthal 1979) from under-publication of studies finding no effect of marking devices. Negative effects of transmitters on songbirds reported to date have been species- or technology-specific. For example, nestling Louisiana Waterthrushes (*Parkesia motacilla*) fitted with transmitters were expelled from nests by adults causing their death (Mattsson et al. 2006), and bulbous antenna tips left some endangered Palilas (*Loxioides bailleui*) dangling from antennas stuck in vegetation (Dougill et al. 2000). However, many studies of songbirds

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have revealed no apparent deleterious effects of transmitters (Neudorf and Pitcher 1997, Streby et al. 2009, Vitz and Rodewald 2011, but see Hill and Elphick 2011).

Detecting transmitter-induced changes in condition, behavior, survival, or productivity of songbirds is best accomplished by comparing marked and unmarked birds. However, the difficulty of observing unmarked songbirds is usually what necessitates radio-telemetry, likely explaining the rarity of such comparisons (Neudorf and Pitcher 1997, Hill et al. 1999, Anich et al. 2009, Gow et al. 2011, Townsend et al. 2012). These comparative studies have revealed no measurable effects of transmitters on songbirds. For example, radio-tagging had no effect on annual return rates of either adult male Swainson's Warblers (*Limnithlypis swainsonii*; Anich et al. 2012) or male and female Bicknell's Thrushes (*Catharus bicknelli*; Townsend et al. 2012). Townsend et al. (2012) also found that transmitters had no effect on the body condition of Bicknell's Thrushes during the non-breeding season. In addition, transmitters had no effect on clutch sizes, nest survival, or number of young fledged from nests of Common Blackbirds (*Turdus murela*; Hill et al. 1999) or Wood Thrushes (*Hylocichla mustelina*; Gow et al. 2011) or the provisioning rates of female Hooded Warblers (*Setophaga citrina*; Neudorf and Pitcher 1997).

An important component of productivity typically excluded from songbird studies is survival of fledglings after they leave nests, but remain under adult care, that is, the dependent post-fledging period (Streby and Andersen 2011).Differences between fledgling survival and nest survival can generate estimates of seasonal productivity (i.e., young raised to independence from adult care) that differ greatly from productivity estimates based on nesting data alone (Streby and Andersen 2011). Considering fledgling survival when estimating productivity is important because some stressors that have no apparent effect on nest success can have detrimental effects on fledging survival. For example, blowflies (*Protocalliphora* spp. and *Trypocalliphora braueri*) usually cause no reduction in fledging success, but can increase fledgling mortality rates (Streby et al. 2009). In addition, although many songbirds can successfully raise broods that include nestling Brown-headed Cowbirds (*Molothrus ater*), the burden of continuing to feed fledgling cowbirds might cause starvation of host fledglings (Rasmussen and Sealy 2006, Peterson et al. 2012) and reduce the number of young recruited into the breeding population (Payne and Payne 1998).Similarly, if effects of carrying a transmitter accumulate over time, fledgling survival may be impacted even if there was no apparent effect on nesting parameters. In the only previous study to assess the effects of transmitters on breeding songbirds through an entire breeding season, Gow et al. (2011) did not report fledgling survival, but did report no decline in physiological condition of adult Wood Thrushes through post-breeding molt. Such results suggest that songbirds can carry transmitters through the entire breeding season without deleterious effects, but the effects on fledgling survival remain untested.

We compared reproductive parameters of marked and unmarked female Golden-winged Warblers (*Vermivora chrysoptera*) during nesting and the dependent post-fledging period. Golden-winged Warblers are smaller (8.5–10.0 g) than species for which similar comparisons have been made, and our study extends the measure of productivity to include survival of dependent fledglings. If our capture and marking methods and the additional mass and aerodynamic effects of radio-transmitters negatively impacted condition or behavior of breeding females, then one or more measures of productivity should differ between marked and unmarked females. For example, physiological stress could result in smaller clutch sizes or lower quality eggs less likely to hatch. In addition, the increased energetic demands of the transmitter load could require birds to spend more time foraging, which might lengthen the incubation or nestling periods or reduce the number of eggs that hatch or number of young that fledge.

METHODS

We studied female Golden-winged Warblers at Tamarac National Wildlife Refuge (47°2′N, 95°35′W), Becker County, Minnesota, in 2011 and 2012. Golden-winged Warblers are small migratory songbirds of high conservation concern (Buehler et al. 2007). These warblers are a multi-nesting, single-brooded species, with females typically renesting after initial nest failure, but only producing one brood of fledglings per year. The short breeding season in our study area in the northern portion of the species range limits most females to one (rarely two) additional attempts after initial failure. This species has been considered sensitive to transmitter effects based on an unpublished pilot study (referenced in Confer et al. 2011), where two of four adult males were not seen again after radio-tagging. However, subsequent telemetry studies with larger numbers of male Golden-winged Warblers have revealed no apparent effects on survival (Streby et al. 2012, M. Frantz, unpubl. data).

We captured, handled, banded, and attached radio-transmitters to adult females to monitor their survival, find and monitor their nests, and to attach transmitters to nestlings and monitor fledgling survival. We captured female Golden-winged Warblers in mist nets from 13 to 20 May 2011–2012, after females arrived at our study area, but before most females initiated nests. Each captured female (hereafter marked) was banded with one U.S. Geological Survey aluminum band and a unique combination of three plastic color bands. In addition, we attached a 0.39-g (3.9–4.3% of body mass) radio-transmitter (Blackburn Transmitters, Nacogdoches, TX) using an elastic-thread, figure-eight harness modified from Rappole and Tipton (1991). Transmitter antennas were flexible and nylon-coated, and we trimmed antennas to ~7 cm to avoid curling and kinking we observed in a pilot study that could potentially lead to entanglement. We did not attempt to capture, handle, or mark females in the unmarked group.

Nest searching and monitoring. We located marked birds using standard ground-based radio-telemetry methods once or twice daily until we found their nests during building, egg-laying, or early incubation. When tracking, we first triangulated the signal and then carefully approached until we observed the bird on the nest, flushed it from the nest, or observed that the bird was not at the nest. We found nests of unmarked birds by systematically searching the study area and by observing adult behavior. If a nest was discovered under construction and subsequently found to be the nest of a marked female ($N = 10$), then that female was included in the marked group and not in the unmarked group. Nests of marked and unmarked birds did not differ in nest concealment or canopy cover (S. M. Peterson, unpubl. data). We monitored all nests at 4-d intervals, and more frequently when events such as the onset of incubation and hatching were expected, so we could accurately determine clutch sizes, length of incubation and nestling periods, hatching success, and predict fledging dates.

Fledgling survival. We used radio-telemetry to monitor survival of fledglings from successful nests of marked and unmarked females. On the seventh day of the nestling period (1–2 d before typical fledging age), we banded nestlings with a standard U.S. Geological Survey leg band and attached a radio-transmitter to 1–4 (usually 2) nestlings per nest using the same methods as used with adults. We visited nests once or twice daily and monitored locations of radio signals from 5 to 10 m away to determine the day of fledgling. We monitored radio-marked adults and nestlings/fledglings to determine fates of nests because visual assessment of recently fledged or predated nests can lead to erroneous nest fate assignment in this species (Streby and Andersen 2013). We monitored each radio-tagged fledgling once daily (with an occasional 2-d interval for some birds) until it died or survived 24 d after fledging, the approximate age of independence. Importantly, only radio-tagged fledglings were included in our comparison of survival rates of fledglings of marked and unmarked females. Fledgling Golden-winged Warblers move beyond nesting territory boundaries soon after leaving nests (Streby and Andersen 2013), and often move >500 m from nests in unpredictable directions before independence from adult care (S. M. Peterson, unpubl. data). As a result, locating unmarked fledglings consistently is nearly impossible, and determining their fates is even harder (Streby and Andersen 2013).

Statistical analysis. Our methods were identical in both years and our estimates of population productivity were similar between years, so we combined data from both years for analysis. All comparisons were made between nests and fledglings of marked and unmarked females. We compared clutch and brood sizes, the length of incubation and nestling stages, number of fledglings, and possible interactions of those parameters between marked and unmarked females with an unbalanced MANOVA (Proc GLM; SAS Institute 2008). We monitored two consecutive nesting attempts for 7% of marked and 3% of unmarked females, so we averaged the values of each parameter from both nests for those females to avoid psuedoreplication. Only

Table 1. Reproductive parameters for female Golden-winged Warblers during 2011–2012 in Minnesota. Marked females were captured and marked with an aluminum leg band, three color bands, and a radio-transmitter weighing ~4% of body mass; unmarked females were not captured, handled, or fitted with transmitters. Hatching success and fledging success are shown as proportions; all others are means ± SE.

	Marked		Unmarked	
Parameter	*N*	Estimate	*N*	Estimate
Clutch size	45	4.7 ± 0.6	60	4.7 ± 0.6
Incubation-stage length (d)	17	11.6 ± 0.6	21	11.5 ± 0.8
Brood size	32	4.5 ± 0.7	49	4.6 ± 0.8
Nestling-stage length (d)	20	9.0 ± 1.0	27	8.7 ± 0.8
Number of fledglings	19	4.3 ± 1.0	31	4.4 ± 0.9
Hatching success	24	0.71	35	0.63
Fledging success	34	0.62	52	0.60
Fledgling daily survival[a]	19	0.981 ± 0.006	31	0.974 ± 0.006

[a] Sample sizes for fledgling survival reflect number of broods because brood was included as a random effect in those models to avoid pseudoreplication.

nests where a parameter of interest was known were included in each analysis. For example, nests that failed during laying were not included in the comparison of clutch size, and nests that failed during incubation were included in comparisons of clutch size and hatching success, but not of incubation-stage length. We compared hatching success and fledging success using chi-square tests of independence. We calculated daily survival for fledglings of marked and unmarked females from regression coefficients of a logistic exposure model (Shaffer 2004) for each group using the NLMIXED procedure in SAS. Both models included a random effect for brood because survival among brood-mates was found to be non-independent in preliminary analysis. We compared the resultant fledgling survival estimates for marked and unmarked females using a Z-test (Johnson 1979).

RESULTS

We monitored nests of 45 marked and 73 unmarked female Golden-winged Warblers, and monitored marked fledglings of 19 marked ($N=$ 35 fledglings) and 31 unmarked ($N = 61$ fledglings) females. Nest failures ($N = 70$) were due to predation (94%), females being predated by accipiters (3%), and apparent abandonment by unmarked birds that either died away from nests or abandoned nests (3%). Fledgling mortality ($N = 50$) was due to predation (98%), apparent exposure during an unusually cold and wet night (1%), and blunt-force-trauma to the head during a hailstorm (1%).

We found no differences between marked and unmarked females for any of the parameters measured (Table 1). Marking females had no effect on clutch size, brood size, the length of incubation or nestlings stages, or number of fledglings (Wilks' $\lambda = 0.8$, $F_{5,15} = 0.9$, $P = 0.51$; Table 1). In addition, we found no difference between marked and unmarked females in either hatching ($\chi^2 = 0.4$, $P = 0.52$) or fledging ($\chi^2 = 0.04$, $P = 0.84$) success (Table 1). Importantly, we also found no difference in survival of fledglings of marked and unmarked females ($Z = 0.8$, $P = 0.41$; Table 1). One aspect of productivity we could not compare was the probability of nesting. However, all 45 radio-tagged female Golden-winged Warblers in our study nested, indicating no reduction in nesting probability.

DISCUSSION

We found no effect of capturing, handling, banding, and attaching transmitters on the seasonal productivity of female Golden-winged Warblers. Similar results have been reported in previous studies of marked and unmarked songbirds (Neudorf and Pitcher 1997, Hill et al. 1999, Gow et al. 2011). In addition, our results suggest that radio-tagging females had no effect on fledgling survival, a critical component of seasonal productivity (Streby and Andersen 2011). Thus, our results, in combination with those of previous studies where investigators compared radio-tagged and non-radio-tagged songbirds during the breeding season (Neudorf and Pitcher 1997, Hill et al. 1999, Gow et al. 2011), indicate that many songbirds can carry radio-transmitters from spring arrival to the onset of fall migration without apparent deleterious effects on condition or seasonal productivity.

Our results add to the growing number of studies indicating that radio-transmitters do not influence songbird behavior (Neudorf and Pitcher 1997, Gow et al. 2011), body condition (Rae et al. 2009), or annual survival in breeding (Powell et al. 1998, Anich et al. 2009) and wintering (Townsend et al. 2012) areas. However, we caution that investigators should not assume transmitters will have no effect when beginning telemetry work in a new system. Deleterious effects of transmitters and other marking devices are usually identified when a species or age group is marked for the first time (e.g., Dougill et al. 2000, Mattsson et al. 2006) or when attachment techniques are being assessed for the first time (e.g., Sykes et al. 1990), and may also be related to researcher inexperience (Hill and Elphick 2011). All of these are important reasons to test new (to the researcher or to the species) marking techniques initially with extra caution, and to include empirical assessments of transmitter effects in publications.

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Research

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Retirement investment theory explains patterns in songbird nest-site choice

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When opposing evolutionary selection pressures act on a behavioural trait, the result is often stabilizing selection for an intermediate optimal phenotype, with deviations from the predicted optimum attributed to tracking a moving target, development of behavioural syndromes or shifts in riskiness over an individual's lifetime. We investigated nest-site choice by female golden-winged warblers, and the selection pressures acting on that choice by two fitness components, nest success and fledgling survival. We observed strong and consistent opposing selection pressures on nest-site choice for maximizing these two fitness components, and an abrupt, within-season switch in the fitness component birds prioritize via nest-site choice, dependent on the time remaining for additional nesting attempts. We found that females consistently deviated from the predicted optimal behaviour when choosing nest sites because they can make multiple attempts at one fitness component, nest success, but only one attempt at the subsequent component, fledgling survival. Our results demonstrate a unique natural strategy for balancing opposing selection pressures to maximize total fitness. This time-dependent switch from high to low risk tolerance in nest-site choice maximizes songbird fitness in the same way a well-timed switch in human investor risk tolerance can maximize one's nest egg at retirement. Our results also provide strong evidence for the adaptive nature of songbird nest-site choice, which we suggest has been elusive primarily due to a lack of consideration for fledgling survival.

1. Introduction

Selection pressures acting on a single trait but in opposite directions can result in stabilizing selection for that trait [1–3]. It is not uncommon for selection pressures on individual components of fitness, for example survival of different life stages, to oppose each other [4–6], and the resulting stabilizing selection can optimize an individual's total fitness at the expense of failing to maximize particular components of fitness. When the trait of interest is a behavioural strategy, stabilizing selection can result in all individuals behaving in a similar way, with trait values centred around the optimum phenotype and little variation among individuals or over time [5]. However, theoretical and empirical studies have presented several hypotheses to explain why mean trait values might deviate from the optimum value predicted under pure stabilizing selection. First, environmental variation may cause selection pressures to vary over time, such that the optimal strategy is a moving target (the Red Queen hypothesis [7]). Second, syndromes may develop in which some individuals are consistently conservative in their behavioural strategies while others adopt a bolder, risk-taking strategy (disruptive selection [8–10]). Finally, individuals may change their behaviour over their lifetime, taking greater risks as they age because they have less to lose in terms of future reproductive output [11–14]. In the latter two examples, the population trait mean is centred around the optimum phenotype, but variation in trait values is due to variation

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among individuals (behavioural syndromes) or within individuals over a lifetime (increased riskiness with age), even when opposing selection pressures are constant.

Predation is the primary cause of mortality for songbird nests and fledglings [15,16]. Therefore, minimizing risk of nest predation is probably a driver of nest-site choice in avian systems [17]. However, although some positive and negative relationships have been identified, most avian studies have found no relationship between nest-site choice and nest success [16,17], and it is often concluded that nesting habitat selection could be maladaptive in terms of nest success [18]. One explanation for these seemingly incongruous results is that selection for nest sites that optimize one trait, for example nest success, may be opposed by selection acting on other traits, as demonstrated in a variety of non-avian systems (reviewed in [19]). For example, phytophagous lichen moths lay eggs on the species of host plant with the highest nutritional value for late-instar larvae, thus favouring rapid growth of older larvae over high growth rates of early-instar larvae [20]. Similarly, female turtles adjust their nest-site choice to prioritize their own survival over that of their offspring when predation risk increases [6,21]. In some birds, nest sites are chosen to minimize physiological stress on [22–24] or predation risk to [18,25,26] the incubating adult. Although predation on nests and incubating adults is probably rarely independent, nest sites were chosen in all of these examples for reasons other than, or in addition to, maximizing nest or egg survival. Thus, studies attempting to identify nest-site choice variables that predict nest or egg survival in these cases would be likely to yield unclear results because selection for nest or egg survival was not the ultimate driver of nest-site choice.

Logistical constraints historically precluded most research on the fledgling stage (after young leave the nest but remain under adult care; also called the dependent post-fledging period) of songbird systems. However, over the past two decades radio-telemetry micro-technology has made studies of this important life stage feasible for songbirds of all sizes [27,28]. Telemetry studies of fledgling songbirds have demonstrated for many species that habitat used during the post-fledging period differs from that used for nesting [28–30], fledgling survival is typically low in the first few days off the nest [27,28,31], and fledgling survival is directly influenced by nest location [28–31]. These studies demonstrate that it is critical to include the fledgling stage when considering a species's reproductive ecology. Indeed, studies of other taxa have demonstrated that selection for survival of juvenile stages, analogous to the avian fledgling stage, drives nest-site choice (e.g. insects [32], fish [33], amphibians [34] and reptiles [35]). Therefore, we hypothesized that selection for fledgling survival might explain nest-site choice in avian systems as well.

Here, we investigated nest-site choice by female golden-winged warblers throughout the nesting season and examined the relative influences of nest success (i.e. the probability of a nest producing fledglings) and fledgling survival (i.e. the probability of fledglings surviving to complete independence from adult care) on nest-site choice. We considered the selection pressure imposed by predation on the nest and fledgling life stages, which correspond to two different components of an adult's reproductive fitness that must be balanced by females choosing nest sites. As discussed above, predation on adults attending the nest is also an important driver of nest-site choice in some species [25,26,36]. However, because predation on an adult not only results in a failed reproductive attempt, but also precludes all future reproduction [37], and because we observed no evidence of adult mortality at nests in our study, we assumed that adult survival produced negligible variation in nest-site choice in our study system, and we therefore focused only on nest success and fledgling survival. We predicted that the optimal nest site would represent an equal trade-off between opposing selection pressures (i.e. stabilizing selection) on nest success and fledgling survival.

2. Material and methods

We studied golden-winged warblers (*Vermivora chrysoptera*) at three sites in the region of the species's densest breeding populations, spanning approximately 400 km in Minnesota and Manitoba. Sites were Tamarac National Wildlife Refuge (NWR) and Rice Lake NWR in northern Minnesota, USA, and Sandilands Provincial Forest (PF) in southeastern Manitoba, Canada. All sites were generally characterized by a mature forest matrix interspersed with regenerating forest stands of various ages, upland and wetland shrublands, and forested wetlands. Golden-winged warblers used all of those cover types to some degree throughout the breeding season, but nesting was concentrated in the open upland and wetland shrublands, and in adjacent forest. Vegetation at all study sites was reflective of managed northern hardwood–coniferous forests of the region. Shrublands were dominated by shrubs, sedges, grasses, forbs and patches of trees more than 5 m tall, and often contained remnant individual or sparse clusters of mature trees. The upland shrublands were in early stages of regeneration after forest harvest. Some of the shrublands consisted of a mosaic of both upland and wetland areas. The forest surrounding each shrubland was characterized by canopy trees more than 10 m tall, a dense and patchy understorey and shrub-layer, and relatively sparse ground vegetation compared with the shrublands. The shrubland–forest edge was generally abrupt owing to its origin in forest harvest.

Golden-winged warblers are Neotropical migratory songbirds that winter in montane forests from Guatemala to central Venezuela, and breed across the Great Lakes region of the United States and Canada, and along the Appalachian Mountains. Males establish nesting territories, nearly all of which include forest edge and extend more than 40 m on either side of the edge, such that they include both forest and shrubland [38]. The edge, or boundary between forest and shrubland, was generally abrupt and clearly defined at our study sites owing to its origin in forest harvest. Females build small open-cup nests on or very near the ground, typically at the base of grasses, shrubs or stems of sapling trees less than 1 cm in diameter. The species's nesting ecology has been well studied [39]. However, the ecology of its post-fledging stage is virtually unknown, as is true of most passerines [29]. Golden-winged warblers, like many songbirds, are a multi-nesting, single-brooded species, which means they will renest after initial nest failure, but can or will only successfully raise one brood in a breeding season. In our study, individuals renested up to two times after initial nest failure. A typical successful reproductive attempt, from first egg laid to independence of all young, takes 48 days: 24 days from first egg to fledging young from the nest, and 24 days to raise fledglings to complete independence.

Potential and confirmed predators of golden-winged warbler eggs and nestlings at our study sites are mammals, including thirteen-lined ground squirrel (*Ictidomys tridecemlineatus*), eastern chipmunk (*Tamias striatus*), red squirrel (*Tamiasciurus hudsonicus*), striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*) and black bear (*Ursus americanus*), and reptiles, including plains garter snake (*Thamnophis radix*) and common garter snake (*Thamnophis sirtalis*). Fledgling golden-winged warblers are depredated by the preceding predators as well as avian predators including American crow (*Corvus brachyrhynchos*), blue jay (*Cyanocitta cristata*), red-shouldered hawk (*Buteo lineatus*), broad-winged hawk (*Buteo platypterus*), sharp-shinned hawk (*Accipiter striatus*) and Cooper's hawk (*Accipiter cooperii*).

(a) Data collection

In 2011 and 2012, we used radio telemetry and standard nest-searching methods to locate golden-winged warbler nests. At each of the three study sites, we established four to eight study plots, each composed of a shrub-dominated upland, wetland or a mix of both, as well as the adjacent surrounding forest. After birds arrived from migration, but before most nesting began, we used mist nets to capture female golden-winged warblers. Each day, we placed 20–50 mist nets (each 12 × 2.5 m) throughout at least one study plot and captured birds passively for 3–7 h. We placed nets such that they bisected or paralleled edges and dense shrubby areas commonly used for foraging by warblers (Parulidae) during the pre-breeding period. We fitted a 0.39 g radiotransmitter (3.9–4.3% of body mass) to each captured female golden-winged warbler using a figure-eight harness design modified from Rappole & Tipton [40]. We monitored each female once or twice daily using standard ground-based telemetry methods until we identified her nest site during the building, laying or early incubation stage.

In addition to locating nests by radio-tracking females, from 15 May to 30 June, we searched for nests in each study plot on a 4-day cycle following standard nest-searching protocols [41]. We walked through each plot searching for nests in areas with vegetation structure typical of nest sites of the species [39] and by observing adult behavioural cues. We monitored each nest every 4 days and more often during late incubation to accurately document the hatching date and predict the fledging date. We also attached radiotransmitters to some females whose nests we found during nest-searching. In those cases, we flushed the bird from the nest into a mist net during incubation, radio-marked the bird and monitored it for the remainder of the nesting season. When a nest was depredated, we resumed daily tracking of the female until we found her subsequent nesting attempt, until the transmitter expired or until all known nests were no longer active, after which we assumed no new nests were initiated.

One to three days before the expected fledge date for each nest, we removed the entire brood of nestlings and carried it in a soft cloth bag more than 10 m from the nest. We ringed each nestling with a standard US Geological Survey aluminium legband and fitted transmitters to one to five (usually two) randomly selected nestlings before returning the entire brood to the nest within 15 min. After we attached transmitters to nestlings, we checked nests once or twice daily from a distance of more than 3 m to identify the day and approximate time of fledging. After fledglings left the nest, we located each radio-marked fledgling once daily using ground-based telemetry methods. We first used triangulation to estimate fledgling location, and then carefully approached the transmitter's location to achieve visual confirmation of fledgling fate (dead or alive) and cause of mortality.

We focused analysis on mortality caused by predation, and we censored from survival analysis the few nests that failed and fledglings that died from other causes. Specifically, we excluded nests that failed because females were depredated away from the nest (known from telemetry monitoring; $n = 6$) and fledglings that died due to apparent exposure ($n = 11$) during cold and wet nights. Exposure was a cause of mortality we observed primarily at Sandilands PF and that we assumed was related to the proximity of that site to the species's northern range limit, and not due to local nest-site choice. In addition, we excluded from survival analysis a nest ($n = 1$) and fledglings ($n = 3$) that drowned in an extreme flooding event at Rice Lake NWR, because drowning in the highest water level recorded since the establishment of the refuge in 1935 was probably not related to within-season nest-site choice.

Predation on adult songbirds attending nests is generally uncommon, and its occurrence is usually evident from the presence of adult feathers around a depredated nest [29]. Although we observed evidence of predation on six radio-marked adult females 10–145 m away from their nests, we observed no evidence of predation on females while attending their nest, indicating those mortalities were likely to be independent of nest location. We therefore assumed that female survival was either consistently unimportant in nest-site choice, or, more likely, it was consistently the highest priority, which should produce no discernible variation in nest-site choice. We consequently considered only selection pressures on nest survival and fledgling survival for analysis.

(b) Statistical analysis

We used the logistic exposure method [42] to model nest and fledgling daily survival. The logistic exposure method accounts for the fact that not all nests are found on the initiation date, and incorporates an appropriate likelihood estimator for interval data. In most nesting bird studies, it is necessary to estimate nest success from a model of nest daily survival because apparent success can be biased when not all nests are found on or before the day the first egg is laid [43]. In addition, modelling fledgling survival was necessary in our analysis because we could not track every fledgling from every brood owing to logistical constraints. We fitted nest survival models using PROC GENMOD [44], after initial models showed no effect of year or study site on either nest or fledgling survival. We fitted fledgling survival models in PROC NLMIXED to allow inclusion of a random effect for brood. In a preliminary model-ranking procedure, we used Akaike's information criterion corrected for small sample size (AICc [45]) to rank 14 (nest survival) and 26 (fledgling survival) models including null models, linear and curvilinear effects of nest distance to forest edge, and vegetation characteristics at nest and fledgling locations. The linear model of nest distance to edge was the best-supported model (lowest AICc [45]) for nest and fledgling survival (H. Streby 2011–2012, unpublished data). All other models had $\Delta\text{AICc} > 3.9$ and were therefore not considered competitive [45].

We assessed whether selection pressures were consistent throughout the breeding season by testing for an effect of the interaction between nest-site distance to edge and nest initiation date on both nest success and fledgling survival. We used Wald's χ^2 tests and t-tests to assess whether selection patterns (i.e. regression coefficients from daily survival models) were different from zero (i.e. significant) for the general linear models (GLMs) and mixed models, respectively. We calculated period survival, or the probability of a nest succeeding (nest success) or a fledgling surviving to independence from adult care, as daily survival raised to the power of 24, the number of days in each period. We estimated the number of young predicted to be produced (raised to independence from adult care) from a nest site as the product of the probability of nest success, the number of young produced from a successful nest and the probability of a fledgling surviving to independence from adult care. We then calculated relative total maternal fitness for a female that chooses a nest site at a particular distance to edge as the number of young predicted to be produced from each nest site divided by the mean number of young predicted to be produced from all nest sites.

Our models of nest success (figure 1*a*) and fledgling survival (figure 1*b*) illustrate selection patterns analogous to, but not mathematically equivalent to, selection gradients used in other

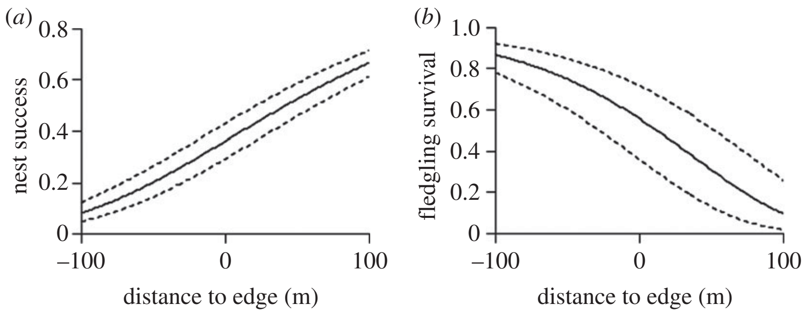

Figure 1. Opposing selection pressures on nest-site choice by female golden-winged warblers with respect to distance from forest edge. Negative distances are in mature forest and positive distances are in shrublands, with zero corresponding to the shrubland–forest edge. An even trade-off between (*a*) the probability of successfully fledging young from a nest and (*b*) the survival probability for fledglings that emerge from that nest results in (*c*) the prediction of stabilizing selection with nest sites close to the forest edge producing the highest relative maternal fitness. The vertical dotted line in (*c*) represents the nest location predicted to maximize relative total fitness, which occurs at +5 m from forest edge.

systems [46,47]. For reasons described above, calculating nest success and fledgling survival from models of nest and fledgling daily survival was necessary. Therefore, calculation of traditional selection gradients was not possible. However, we calculated approximate selection gradients as $1/\hat{W}$ [46], where $\hat{W}$ was mean maternal fitness from our models for each fitness component, to place the patterns of selection we observed in context with similar studies.

We examined the relationship between nest-site distance to forest edge and nest initiation date using linear and quadratic general linear models and a general additive model (GAM) in program R. We ranked the GLMs and GAM using AICc. A GLM with the strongest support (lowest AICc) would indicate a linear or curvilinear relationship between nest-site distance to edge and nest initiation date, and suggest a gradual change in nest-site choice priorities throughout the season. A GAM with strong support may indicate a temporal threshold in nest-site choice, suggesting an abrupt strategy switch as opposed to a gradual change. We used the inflection point of the GAM to separate early and late nesting attempts (figure 2). The inflection point was identified visually and consistently as the same value by seven independent observers. Repeating this analysis with the similar method of piecewise regression produced identical results (H. Streby 2013, unpublished data), but we chose the GAM *a priori* for its superior performance in, among other things, fitting complex curvilinear relationships [48]. We used a Student's *t*-test to compare mean distance from forest edge for early- and late-season nest sites. To avoid bias in nest-site distance to edge associated with standard nest-searching methods (S. Peterson 2010–2012, unpublished data), we included only nests ($n = 95$) found by radio-tracking adult females ($n = 110$) in comparisons of early and late nest-site locations. Those 95 nests included all nests found by radio-tracking females, regardless of nest fate. Owing to the limited battery life of the transmitters (approx. 30 days), and because renesting only occurs after nest failure, we monitored consecutive nesting attempts found using radio telemetry for only 15 females, and six of those renests were initiated during the early nesting period. We used a paired *t*-test to compare mean distance from forest edge for early- and late-season nests for the nine females for which we monitored consecutive nesting attempts initiated during the early and late season. We report regression coefficients ± s.e. We considered all tests significant at $\alpha = 0.05$.

3. Results

We monitored 226 nests and 198 fledglings. Overall, nest sites were distributed approximately normally with respect to edges, with more than 95% of nests placed within 100 m of either side of the edge. Regardless of nest location, golden-winged warblers usually moved their fledglings into forest within 10 days of leaving the nest, or kept them there if the nest was in forest. As is common among songbirds [29], most (85%) fledgling mortality occurred within the first week after leaving the nest.

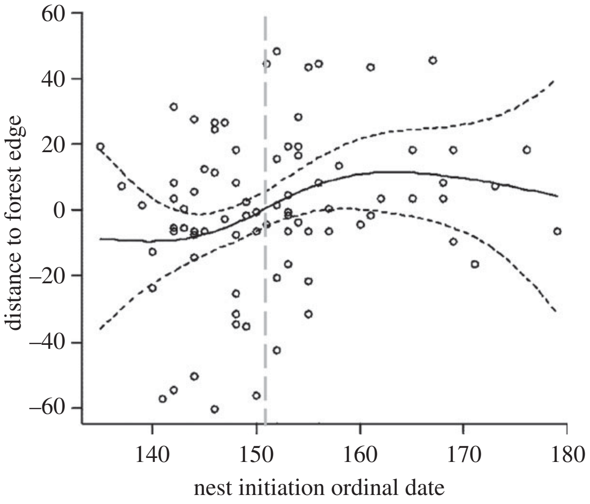

Figure 2. Locations of golden-winged warbler nests initiated throughout the breeding season in the western Great Lakes region, USA. All nests in this analysis ($n = 95$) were found using radio telemetry to track females, removing potential human searching bias. The inflection point (vertical dotted line, ordinal date 151) in the GAM indicates the date of an apparent strategy switch in nest-site choice, whereby nests initiated before that date were close to or in forest and nests initiated on or after that date were generally in shrublands. GAM is presented with 95% CI.

Our models indicated that nest survival did not differ among study sites ($\chi^2 = 0.04$, d.f. = 2, $p = 0.838$) or between years ($\chi^2 = 0.10$, d.f. = 1, $p = 0.755$), and that fledgling survival did not differ among study sites ($t = -0.44$, d.f. = 93, $p = 0.664$) or between years ($t = -0.23$, d.f. = 93, $p = 0.821$). Consistent among sites and years, the selection pattern for nest sites with respect to distance to forest edge was positive (regression coefficient = 0.0093 ± 0.0037) and significant for nest daily survival ($\chi^2 = 6.35$, d.f. = 1, $p = 0.012$), and was negative (regression coefficient = −0.0160 ± 0.0079) and significant for fledgling daily survival ($t = -2.03$, d.f. = 93, $p = 0.045$). These regression coefficients are for models of nest and fledgling daily survival, and are not equivalent to selection gradients [46]. Approximate selection gradients calculated from our models of nest success ($\beta = 0.65$) and fledgling survival ($\beta = 0.45$) are similar to those from studies on phenotypic traits [49]. The selection patterns we observed illustrate strong opposing selection pressures on nest-site choice for maximizing nest success and maximizing fledgling survival (figure 1*a*,*b*). Mean fledged brood size was 4.2 (± 0.09), which varied slightly among years and sites, but not with respect to nest-site distance to forest edge ($F_{1,93} = 0.18$, $p = 0.668$). Multiplying the probability of successfully nesting by 4.2 (fledglings from a successful nest) and then by the probability of survival to independence for fledglings from nest sites at particular distances from edge, and dividing by the mean total fitness for all nest sites, resulted in highest predicted relative total fitness for females nesting +5 m from forest edge (figure 1*c*).

We found no effect of a nest-site distance to edge × nest initiation date interaction on either nest success ($\chi^2 = 0.08$, d.f. = 1, $p = 0.777$) or fledgling survival ($t = 0.71$, d.f. = 93, $p = 0.480$), indicating that the opposing selection pressures on nest-site choice persisted throughout the breeding season. Therefore, any temporal change in nest-site choice with respect to distance to forest edge probably represents either a gradual change or an abrupt switch in the relative prioritization of selection pressures by the birds. The GAM outperformed the linear and quadratic GLMs (ΔAICc linear = 2.54, ΔAICc quadratic = 2.06, ΔAICc null model = 7.30) for explaining nest-site distance to edge over time with a good fit to the data (GAM approximate fit of smoothed terms, $F = 2.11$, $p = 0.08$), and the shape of the GAM indicated a short-term switch in nest-site choice instead of a gradual change throughout the season (figure 2). The ΔAICc values for the GLMs suggested that they received some support, but the GAM was superior. The inflection point in the GAM was at ordinal day 151, which we considered the estimated switching point. Early nest sites (initiated before day 151) and late nest sites (initiated on or after day 151) were in significantly different locations relative to forest edge ($t = 2.71$, d.f. = 93, $p = 0.008$), with early nests in locations that prioritized fledgling survival over nest success and later nests in locations that prioritized nest success over fledgling survival (figure 3). Although the estimated switching point was day 151, there was variation around that estimate, suggesting the switch may have occurred slightly before or after that date. Moving the switching date forward or backward by 1 or 2 days resulted in similarly significant differences in early and late nest locations (all $p < 0.03$), indicating the switch could have occurred during or across this short period.

The behavioural switch we observed is consistent with time limitation caused by the impending end of the nesting season. The latest nest we observed was initiated on ordinal day 179 (28 June), suggesting that ordinal day 179 is the approximate limit for initiating new nests. The maximum time between subsequent nesting attempts is 28 days if a nest fails on the day before nestlings fledge (nest-cycle day 23) and the next nest is initiated 5 days later (typical from our observations). Therefore, approximately 28 days before ordinal day 179 is the last day a nest can be initiated with certainty that there is time remaining for renesting if that nest fails. In other words, any nest initiated on or after day 151 is likely to be a female's last nesting attempt of the season. Importantly, the switch in nest-site choice we observed was related to a specific time in the nesting season rather than to the number of previous nesting attempts made by a female. Depending on when a nest fails in the 24-day nesting cycle, the final nesting attempt of the season could be a second or a third nest attempt for females in our study population. Using radio telemetry, we identified two subsequent nest sites, one initiated before and one initiated after the switching date, for nine individual females. Early nest sites chosen by those females ($\bar{x} = -6 \pm 5$ m from edge) were in significantly different locations relative to edge ($t = 2.34$, d.f. = 8, $p = 0.047$) than their later nest sites ($\bar{x} = 23 \pm 12$ m from edge), confirming that the switch in nest-site choice we observed occurred within individuals and was not indicative of multiple strategies, or syndromes, among individuals. None of these females initiated a nest within 2 days of day 151, so moving the switching date forward or backward 1 or 2 days did not affect this result.

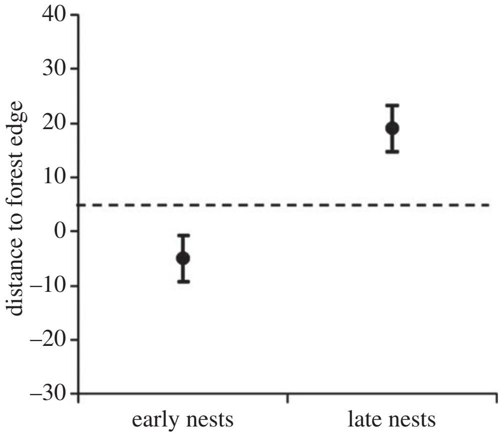

Figure 3. Nest sites (mean ± s.e.) chosen by golden-winged warblers before (early nests) and after (late nests) a risk-tolerance threshold related to the time limitation of the breeding season. Instead of choosing nest sites that optimally balanced opposing selection pressures (dotted line; reproduced from figure 1*c*), early nest sites were in locations that prioritized fledgling survival over nest success, whereas later nest sites were in locations that prioritized nest success over fledgling survival. This significant shift in nest-site choice suggests that individuals risk early nest failure in exchange for greater potential fledgling survival to maximize total maternal fitness, but make relatively conservative choices after early nests fail and time to renest becomes limited, to increase the probability of salvaging moderate total maternal fitness.

4. Discussion

Golden-winged warblers consistently deviated from the predicted optimal behaviour when choosing nest sites because they could make multiple attempts at one fitness component, nest success, but only one attempt at the subsequent component, fledgling survival. We observed positive selection for nest success with respect to distance to forest edge and negative selection for the survival of fledglings from those same nest locations. That is, nest success was highest in shrublands and lowest in forest, while fledgling survival was lowest from nests in shrublands and highest from nests in forest. Both life stages experienced intermediate survival near edges. These relationships, analogous to selection gradients, illustrate strong opposing selective pressures on nest-site choice for maximizing nest success and maximizing fledgling survival, with the greatest relative total fitness predicted for females that chose nest sites close to forest edge. The opposing selection pressures on nest-site choice persisted throughout the breeding season, but, importantly, females did not balance these selection pressures evenly throughout the season. Early nest sites were farther into forest, thereby prioritizing fledgling survival, whereas later nest sites were farther away from forest, thereby prioritizing nest success, compared with what was predicted assuming pure stabilizing selection resulting from evenly balancing opposing selection pressures on nest success and fledgling survival.

The within-season switch in nest-site choice was not concurrent with any apparent phenological shift in vegetation structure or food availability. Golden-winged warblers arrived on our study sites during leaf out of trees and shrubs, and vegetation gradually developed throughout the nesting season. There was no apparent change in vegetation structure that co-occurred with the shift in nest-site choice. Golden-winged warblers at our study sites preyed upon leaf-dwelling invertebrates, especially leafroller caterpillars (*Archips* spp.). There was no apparent change in foraging locations used by radio-marked females throughout the nesting season, although they tended to follow a daily pattern of foraging farther from their nest later in the day throughout the nesting season (H. Streby 2010–2012, unpublished data). Therefore, there was no apparent spatial shift in food availability to correspond with the shift in nest-site choice. Additionally, plant phenology, and thus that of leaf-dwelling invertebrates, was more than one week earlier in 2012 than in 2011 across our study sites, and was a few days later at Sandilands PF than at the Minnesota sites in both years. However, the timing of the shift in nest-site choice was consistent among sites and years, indicating its relation to the end of the nesting season regardless of when the nesting season began. There was variation around the estimated switching point in the GAM, suggesting that the switching point may have occurred slightly before or after day 151, or could have occurred over a few days around day 151. We suspect at least some of this variation is due to females taking 5 days between a failed nesting attempt and the initiation of a subsequent nest. This delay between nesting attempts could give the impression of a multi-day period of switching even if the true switching point was on a single day. Regardless of the switch occurring over one day or over a few days, our results indicate that the switch was brief and significant with respect to distance to edge.

The opposing selection pressures were consistent throughout the season; therefore, the switch in the fitness component females prioritized was not consistent with the optimal nest site being a moving target the birds were attempting to track [7]. In addition, the switch in nest-site choice occurred within individuals, which is not consistent with the presence of behavioural syndromes among individuals [8]. Instead, the switch in nest-site choice was consistent with a risk-tolerance threshold, or a switch in the relative prioritization of two fitness components in response to a change in time limitation. Given a successful nest, a female's total reproductive fitness depends entirely on fledgling survival and is represented by the selection pattern illustrated in figure 1*b*. Consequently, there is minimal fitness cost to risking nest failure early in the season, when time to renest is not limited, for the reward of maximizing fledgling survival and thereby maximizing total fitness. But if early nests fail and time to renest becomes limited, the fitness benefit switches to the prioritization of nest success because potential fledgling survival is unimportant if the final nesting attempt fails to produce fledglings.

The period within which nest-site choice switched was brief and occurred 28 days before the last observed nest initiation date. The longest period between consecutive nest initiation dates for this species is 28 days, which corresponds to a nest that fails on the 23rd and final day before fledging plus the typical 5-day period between nest failure and renest initiation. The 28-day threshold for switching nest-site choice to prioritize nest success over fledgling survival thus coincides with the date after which an initiated nest is likely to be an individual's final nest of the season.

We emphasize that the strategy of switching between nest sites with high to low nest predation risk within a season is not inconsistent with strategies in which risky behaviour increases over an individual's lifetime [12]. In such systems, the risk to total fitness is that of adult mortality, which is traded off with some parameter of reproduction such that older animals become more risky with their own lives for the potential reward of reduced risk to their current nest or offspring [11,14]. In our study system, the fitness trade-off is between success of the nest and survival of the fledglings that might emerge from that nest, and the risk-tolerance threshold is associated with adult females facing a time-limited breeding season. Therefore, a switch in priorities between fledgling survival and nest success should be expected during every breeding season, and should occur regardless of a breeding female's age.

Our observation of a risk-tolerance threshold in songbird nest-site choice in response to the time limitation of the breeding season represents a novel perspective on parental investment theory [50]. Traditionally, predictions based on parental investment theory pertain to the quantity or proportion of energy adults allocate to reproduction based on the age, quantity or quality of offspring [50]. Our study demonstrates an additional component of parental investment, wherein adults change the physical location of their energetic investment in reproduction, rather than the amount of investment, to maximize their total fitness. This risk-tolerance threshold is analogous to human retirement investment theory, wherein individuals investing early in their careers can afford to seek greater returns by choosing higher-risk investment options because they have time to recoup losses and even start over if they lose their entire investment [51]. By contrast, individuals time-limited by impending retirement have a lower risk tolerance and instead should make conservative investment choices to ensure modest returns while avoiding great losses. The relationship between time to retirement and investor risk tolerance is non-linear [51], as observed in our study, suggesting that there may be a threshold during which switching from a high- to low-risk strategy is optimal for humans as well. Departures from such a financial strategy, on average, result in a less than optimal nest-egg at retirement. Similarly, departures from the strategy of switching nest locations during the breeding season are likely to result in lower annual and lifetime fitness for songbirds, suggesting that the switching behaviour we observed is adaptive.

Choice of nest site affects a variety of fitness components across multiple life stages in oviparous animals [37], and trade-offs are regularly observed when selection pressures between individual fitness components or on different life stages are in opposition [35,52]. However, when individual fitness components or life stages are studied in isolation, rather than examining all components of an individual's total fitness, the resulting correlations between nest-site choice and proxies for fitness are likely to be incongruous

[16] and yield incomplete conclusions regarding the reasons for and consequences of nest-site choice. Evidence for the adaptive nature of nest-site choice has so far been elusive in bird studies [15,16], but we believe results similar to those found here will be observed in additional avian systems as more studies consider the contribution of fledgling survival to total fitness, and therefore the influence of fledgling survival on nest-site choice.

We collected data following Protocol no. 1004A80575, approved by the University of Minnesota Institutional Animal Care and Use Committee.

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Data accessibility. These data are a product of research conducted by a US federal government employee and they are therefore in the public domain. They are stored and accessible through the Minnesota Cooperative Fish and Wildlife Research Unit.

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