Golden-winged Warbler Demography and Habitat Associations in Minnesota

Final Report

MN State Wildlife Grants Program

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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 (*Molothrus 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.**

For data collection methods, see Appendix I.

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.

1) **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.

2) **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.

3) **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.

4) **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.

5) **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). Published manuscripts are presented in Appendix II.

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.

All referenced literature is included in the Literature Cited of Appendix I.

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 I. Original Grant Proposal

Golden-winged Warbler Demography and Habitat Associations in Minnesota

Grant Proposal

May 1, 2012 – May 31, 2013

Submitted by the State of Minnesota

Department of Natural Resources

Division of Ecological Resources

Prepared by: Dr. Henry Streby, University of Minnesota
Dr. David Andersen, University of Minnesota

Submitted by: Rich Baker, Endangered Species Coordinator
Richard.baker@state.mn.us 651-259-5073

Need

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 pg. 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 listed 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. 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 fill these information needs. The study, which began in 2012, 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 (NWR) in eastern Minnesota, and Sandilands Provincial Forest (PF) in Manitoba. We will use these demographic data 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 proposal only addresses the work being done on the portion of this study being conducted at the Tamarac National Wildlife Refuge from May 1, 2012 through April 30, 2013.**

Objectives

To address the immediate information needs listed above, we will study 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 May 1, 2012 – April 30, 2013.

1) Monitor GWWA nest productivity and fledging survival for 40 – 50 nests.
2) Using radio-telemetry, monitor the movements of 40 – 50 nesting birds and 40 – 50 fledglings.
3) 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.
4) 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.
5) 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.

Expected Results and Benefits

This project will help address the following goals and strategies of Minnesota's State Wildlife Action Plan (MNDNR 2006 pg. 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.

This project will provide a wealth of novel information critical to the conservation of Golden-winged Warblers, their habitats, and the many species of wildlife that share their habitats. The project will include sample sizes of considerably more nests and adults monitored than any previous GWWA study and the first radio telemetry data about fledgling GWWA survival and habitat use. The results of this study and subsequent management recommendations will immediately inform management, including forest management, and conservation planning for this dramatically declining songbird. The results of this study will be immediately useful to the USFWS as they consider a recent petition to list the Golden-winged Warbler under the Endangered Species Act.

Based on preliminary results from our 2010 and 2011 research, we are confident that radio monitoring GWWA will provide novel information about survival and habitat use. We have found that radio-monitored territorial male GWWA use mature-forest stands significantly more than expected based on basic surveys of singing males (Streby et al. 2012). In addition, we have found most adult and fledgling GWWA use mature forest and edges of forested wetlands throughout the post-fledging period. These results contradict current GWWA habitat management plans that call for only increased area of early-successional forest. These results suggest that mature forest provides an important component of GWWA breeding home ranges and post-fledging habitat requirements, and that this species may require a mosaic of forest stand types underappreciated based on surveys of singing males.

Because our study sites span a range that includes the densest known populations of breeding GWWA, our results will be applicable in the management of the majority of breeding GWWA. Because GWWA share similar habitat requirements with other species of management and conservation concern such as American Woodcock (*Scolopax minor*; also a SGCN), the results of this study will potentially also benefit this species.

Economy -- In addition to the conservation of the species and the genetic diversity contained within, songbirds are important for the local, state, and national economy. There are >50,000,000 birders in the United States that spend >$40 billion dollars annually on wildlife watching equipment and activities. Because the northern hardwood-conifer transition zone of the upper Midwest hosts one of the richest communities of songbirds in North America, research that contributes to the maintenance of that species richness will benefit local economies by continuing to attract wildlife watchers. Tamarac NWR hosts >60,000 visitors annually, many of whom travel to the area specifically to view and photograph wildlife including the densest known population of breeding GWWA.

Approach

Study Locations -- We will conduct this research in the densest known population of GWWA breeding range, at Tamarac NWR in northwest Minnesota (Figure 1). This study location has high

GWWA abundance and a wide range of habitat types including mature forest, open wetlands, shrubby wetlands, open grasslands, and early-successional forest stands in various stages of regeneration.

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

Nest Searching -- We have established nest-searching plots in known GWWA nesting areas within Tamarac NWR. We will have 4 full-time field technicians and 1 project leader at the site. Field workers will search for nests following standard procedures described by Martin and Geupel (1993) and Martin et al. (1997) that we have used during a previous study of forest-nesting birds in north-central Minnesota (Streby and Andersen 2011). In addition, we will capture adult female GWWA with mist nets and follow them to nests using radio telemetry, and we will capture and track females from known nests to enable monitoring of subsequent nesting attempts in cases of initial nest failure.

Nest Monitoring -- We will record the location of each nest using a handheld GPS unit. We will monitor each discovered nest following standard songbird nest-monitoring procedures (Martin and Geupel 1993, Martin et al. 1997) that we have used in previous research (Streby and Andersen 2011). We will visit nests at 3-4-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 nest visit, we will record adult activity and nest contents (i.e., number of eggs, number of nestlings) and the condition of those contents (e.g., age of nestlings). We will band nestlings with standard U.S. Geological Survey leg bands on the seventh day after hatching, which is 2 days prior to the expected fledge date. We will use the Logistic Exposure method (Shaffer 2004) to estimate nest productivity and to model the effects of habitat characteristics on nest productivity.

Radio Telemetry -- We will monitor birds using radio telemetry methods described by Anders et al. (1998) and Vega Rivera et al. (1998) that we have used during previous research (Streby and Andersen 2011). We have confirmed the availability of (and have already used in 2010 and 2011) transmitters <5% of average GWWA body mass with ≥30-day battery life. We will attach 0.39-g transmitters to adult and nestling birds using a figure-eight harness design for passerines (Rapolle and Tipton 1991). Each transmitter will be positioned above the sacrum of the bird to minimize the impact on their center of gravity, and therefore daily activity, and the elastic harness is designed to break free 40-60 days after attachment. 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 monitor the adult female from each nest and ≥2 fledglings from each successful nest using standard radio telemetry techniques to monitor survival, habitat use, and parental care. We will record locations of monitored birds using handheld GPS units, and sample vegetation characteristics around each location. 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 characteristics on survival. In addition, we will color band all adult GWWA handled during this study and assess annual return rates.

Habitat Assessment **–** We will survey nesting territories using vegetation sampling protocols established by the Golden-winged Warbler Working Group. In addition, we will sample vegetation characteristics at each adult and fledgling location during telemetry monitoring. We will use data about vegetation characteristics to model their influence on adult and fledgling survival across the geographic range of the study.

Population Modeling -- We will build female-based stochastic models of GWWA population growth including all habitat variables we measure. These models will be used to identify the habitat characteristics most influential to GWWA population growth, and to make management recommendations to promote site-specific and range-wide population growth.

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Estimated Costs

The Minnesota Department of Natural Resources uses a detailed cost coding system to identify all costs associated with this grant. The costs associated with grant activities include labor, direct and indirect costs, travel, materials, supplies, equipment, and contracts necessary to accomplish the objectives of this project. This grant will be implemented through a contract with the University of Minnesota. The University may assess indirect charges of 16.51% on 65% of the salary reimbursed under this grant (including the University's share of FICA, insurance and retirement costs) which represents the federally funded portion (65%) of the contract to be developed with the University. **Matching funds are from state sources only.**

Total expenditures	**$64,225**
State Share (35%)	$22,479
Federal Share (65%)	$41,746

Program Income

No activities included in this project generate program income incidental to their purpose.

Reports

Products will include a final project report only, because the term of this project is only one year. The final report, due to MNDNR by May 31, 2013, will discuss the results of objectives 1-5 and include management recommendations for maximizing GWWA population growth. Outside of the grant, a number of reports and presentations are expected, including: a graduate student thesis, presentations of results at state, regional, and national conferences, and publications in primary peer-reviewed scientific journals. This project has already produced two annual reports from the 2010 and 2011 seasons and one manuscript currently in press with the *Wildlife Society Bulletin*.

Compliance Procedures

This project complies with all federal and state laws, regulations, and policies. Birds will be captured, handled, banded, and marked with radio transmitters following protocol #1004A80575 approved by the University of Minnesota Institutional Animal Care and Use Committee.

National Environmental Policy Act

The Minnesota Department of Natural Resources, Division of Ecological Resources, believes that this grant complies with the Department of the Interior - Final Revised Implementation Procedures for the Fish & Wildlife Service as published in the Federal Register on January 16, 1997 (Vol. 62, No. 11). Surveys, as outlined in this grant proposal, are deemed to have no impact and are covered by categorical exclusion 1.4B (1). A NEPA Compliance Checklist has been prepared for this grant and is attached.

Protection of Historic Properties

Section 106 of the National Historic Preservation Act of 1966 (NHPA) requires federal agencies to consider the effects of their actions on historic properties and cultural resources. As this project does not involve any activities that meet the definition of "undertaking" under the NHPA no notification or consultation with the State Historic Preservation Office or Indian communities will be done.

Floodplain Management, Executive Order 11988

The project will be in full compliance with this Executive Order.

Protection of Wetlands, Executive Order 11990

This grant will be in full compliance with this Executive Order.

Pesticides

The application of pesticides will not take place under this project.

Protection of Threatened and Endangered Species

The MN DNR believes that this grant will be in full compliance with the Endangered Species Act of 1973. A Section 7 Phase 1 review has been completed and is attached.

Implementation of this grant will not jeopardize the continued existence of any federally listed, threatened, endangered, or candidate species or result in the destruction or adverse modification of critical habitat of these species.

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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

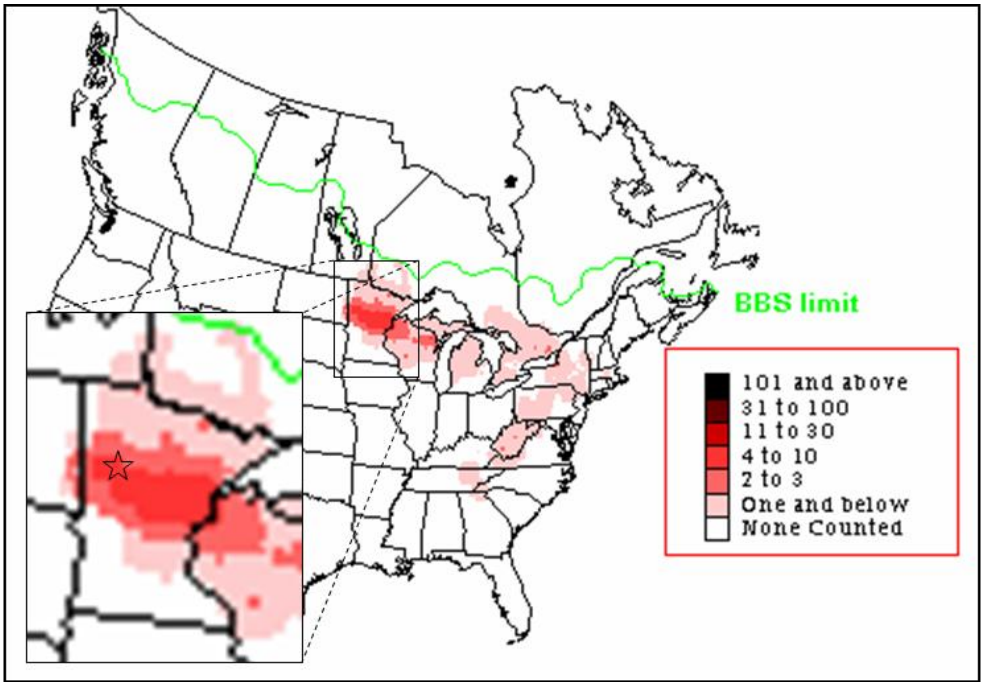

Figure 1. Relative abundance of Golden-winged Warblers across the species' breeding range. Color range represents mean number of birds counted per route during the North America Breeding Bird Survey. Star in callout box identifies our study site at Tamarac National Wildlife Refuge.

Appendix I. Peer-reviewed publications including results from activities supported by this SWG-funded project

IBIS The International Journal of Avian Science
Ibis (2013), **155**, 327–337

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.

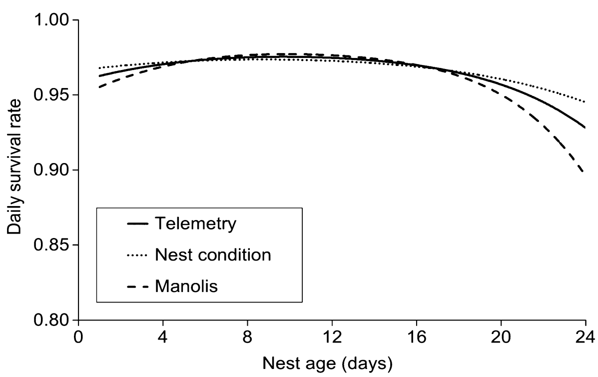

Figure 1. Fitted values from logistic exposure models (from model-averaged coefficients) for data on 184 Ovenbird nests for which fates were determined using three methods (Telemetry, Nest Condition and Manolis) when nests were found empty on or near expected fledge dates. The Manolis method underestimated 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).

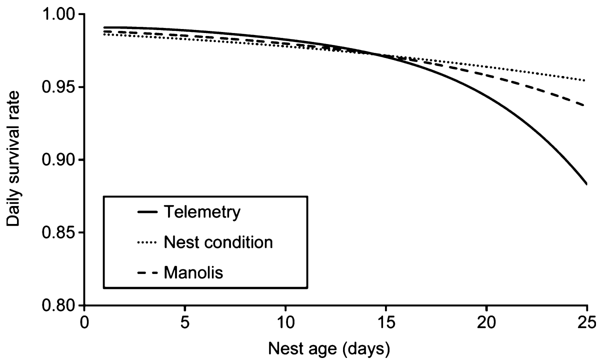

Figure 2. Fitted values from logistic exposure models (from model-averaged coefficients) for data on 53 Golden-winged Warbler nests for which fates were determined using three methods (Telemetry, Nest Condition and Manolis) when nests were found empty on or near expected fledge dates. The Nest Condition 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

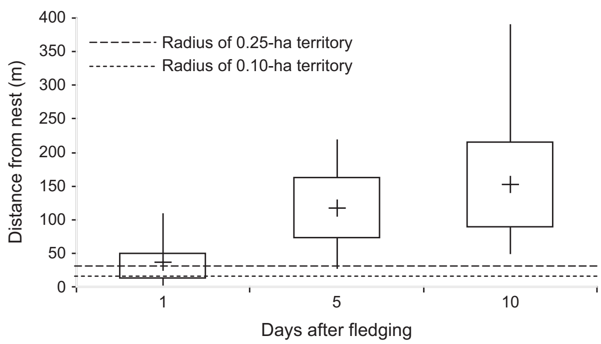

Figure 3. Distances moved from nests by fledgling Ovenbirds within 1 (n = 89), 5 (n = 61) and 10 (n = 41) days after fledging in the Chippewa National Forest, Minnesota. Plus signs, boxes and whiskers represent mean, SD and range, respectively. Dashed lines represent radii of estimated nesting territories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

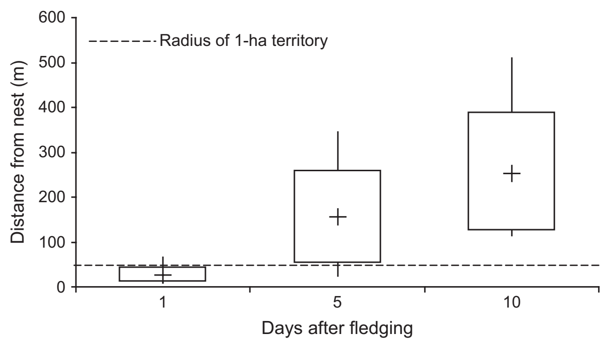

Figure 4. Distances moved from nests by fledgling Golden-winged Warblers within 1 (n = 16), 5 (n = 13) and 10 (n = 12) days after fledging in Tamarac National Wildlife Refuge, Minnesota. Plus signs, boxes and whiskers represent mean, SD and range, respectively. Dashed line represents the radius of an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

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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).

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

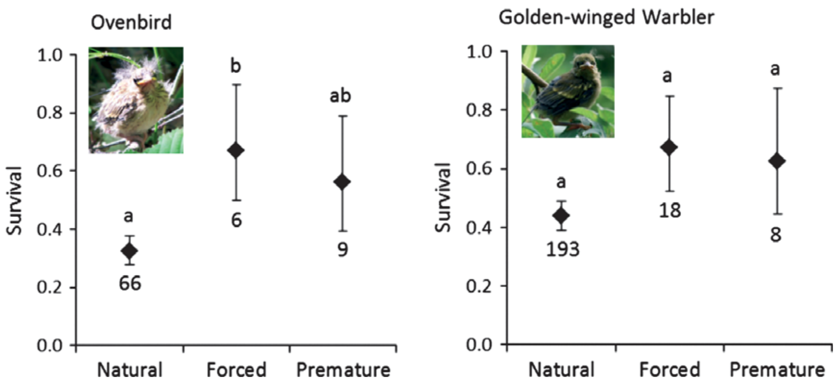

Figure 1. Survival from fledging to independence from adult care for Ovenbirds and Golden-winged Warblers that fledged from nests independent of investigator activity (natural), and those that fledged in response to investigator activity at a typical fledging age (forced) or earlier than typical fledging 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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