

CHAPTER EIGHT

Survival and Habitat Use of Fledgling Golden-winged Warblers in the Western Great Lakes Region*

Henry M. Streby, Sean M. Peterson, and David E. Andersen

Abstract. Postfledging habitat use and fledgling survival remain unstudied for most songbirds, but this period is critical for understanding breeding habitat associations and full-season productivity. We used radiotelemetry to study movements, cover-type selection, and survival of fledgling Golden-winged Warblers (*Vermivora chrysoptera*) during the dependent postfledging period in managed forest landscapes of the western Great Lakes region. We used logistic exposure models to determine the relative importance of various habitat characteristics for explaining fledgling survival. In addition, we used compositional analysis, corrected for age-specific fledgling movement capabilities, to test for resource selection, as use versus availability, among cover types. We estimated that 48% of fledglings were depredated before independence from adult care at 25 days after fledging. Fledgling survival was lowest immediately after fledging, and 86% of predation occurred in the first 8 days following fledging. Distance from the nest to forest–shrubland edge was the strongest predictor of young fledgling survival, as survival decreased with nest distance into shrubland cover types

and increased with nest distance into forest cover types. Fledglings from nests in shrubland cover types moved toward the nearest forest–shrubland edge, whereas fledglings from nests in forest cover types did not move toward edge. Fledglings selected mature forest and sapling-dominated clear-cuts over all other cover types during the early postfledging period, and fledgling survival in mature forest and sapling-dominated clear-cuts was greater than in shrub-dominated clear-cuts or wetland shrublands. Fledglings that were 9–25 days postfledging experienced high survival (daily survival >0.99) that was independent of any habitat variables we measured, and birds selected mature forest and shrub-dominated clear-cuts over all other cover types during that period. We conclude that sapling-dominated clear-cuts or mature forest with dense understory and shrub layers, cover types traditionally not associated with breeding, are important for fledgling survival, and therefore full-seasonal productivity in Golden-winged Warblers.

Key Words: forest management, habitat selection, postfledging, songbird.

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

Full-season productivity in songbirds is defined as the number of young raised to independence from adult care (Streby and Andersen 2011). Fledgling survival is a critical component of full-season productivity but remains poorly understood in most species (Anders et al. 1997, Anders and Marshall 2005, Faaborg et al. 2010, Streby and Andersen 2011). Without information about fledgling survival and habitat associations, estimates of population productivity and descriptions of species habitat requirements can be incomplete or misleading (Streby and Andersen 2011, 2013a). Many songbirds use areas during the postfledging period that differ in vegetation characteristics from areas used for nesting (Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2007, Streby et al. 2011a). Fledgling survival is affected by habitat use at multiple spatial scales (King et al. 2006, Streby and Andersen 2013b), and fledglings use habitat features associated with greater likelihood of survival disproportionately both before and after independence from adult care (Cohen and Lindell 2004; Streby and Andersen 2012, 2013a; Jackson et al. 2013; Vitz and Rodewald 2013). Predation is the leading cause of fledgling mortality in songbirds, and fledgling predation is greatest during the first few days outside the nest (Anders et al. 1997, Yackel Adams et al. 2006, Moore et al. 2010, Vitz and Rodewald 2011, Streby and Andersen 2013b). Therefore, habitat features associated with the nest site and with early postfledging locations often contribute disproportionately to fledgling survival (Berkeley et al. 2007, Jackson et al. 2013, Streby and Andersen 2013b). However, identifying the features of nest sites and postfledging habitat use associated with fledgling survival requires monitoring fledgling movements and survival.

Songbird population growth rates can be more sensitive to variation in fledgling survival than nest success (Streby and Andersen 2011). Therefore, it is particularly important to investigate postfledging ecology in species of conservation concern for which population growth might be limited by fledgling survival. Nesting habitat associations and nest success of Golden-winged Warblers (*Vermivora chrysoptera*) are relatively well studied (Ficken and Ficken 1968, Will 1986, Klaus and Buehler 2001, Martin et al. 2007, Vallender et al. 2007, Bulluck and Buehler 2008, Confer et al. 2010), especially in recent years (Chapter 7, this volume). Before the current study, information

about Golden-winged Warbler postfledging ecology was limited to one study in which fledglings were banded and resighted in Michigan (Will 1986). Will (1986) provided initial descriptions of brood-division behavior (further explored in Chapter 9, this volume), early postfledging movements, and duration of parental care, although he also described the increasing difficulty of consistently observing fledglings as they aged and developed. Radiotelemetry has been used to monitor fledgling songbirds for two decades starting with large songbirds (Anders et al. 1997), and the technology has advanced to allow repeated and reliable monitoring of birds as small as Golden-winged Warblers (8.5–10 g) for >30 days with no discernible effects on behavior or survival (Streby et al. 2013a).

We used radiotelemetry to study movements, cover-type selection, and survival of fledgling Golden-winged Warblers at two sites in northern Minnesota and one site in southeastern Manitoba. It was particularly important to investigate postfledging habitat associations in Minnesota, which hosts nearly half of the global population of breeding Golden-winged Warblers (Chapter 1, this volume). Population numbers in Minnesota have been stable (Zlonis et al. 2013) or increasing slightly (Chapter 1, this volume), despite a 30% increase in the area of early successional upland forest between 1977 and 2011 (Miles and VanderSchaaf 2012). Our objectives were to determine the relative importance of various habitat characteristics for fledgling survival and to test for cover-type selection based on whether fledglings use cover types associated with high fledgling survival disproportionately relative to availability. As in Streby and Andersen (2013a), we use the term *selection* in a statistical context to refer to comparisons between use and availability of cover types, and not in a behavioral context in which an individual selects or chooses locations, which is probably attributable to the fledglings' parents. Based on previous songbird studies, we expected fledgling survival to increase nonlinearly with age (Anders et al. 1998, Yackel Adams et al. 2006, Berkeley et al. 2007, Moore et al. 2010, Vitz and Rodewald 2011) and to be related to cover-type use and vegetation density at the nest and at early postfledging locations (King et al. 2006, Berkeley et al. 2007, Streby and Andersen 2013a). In addition, we expected fledglings to move into areas of dense

vegetation and to experience relatively high survival when fledging from nests near those areas (Cohen and Lindell 2004, Jackson et al. 2013, Streby and Andersen 2013b).

METHODS

Study Area

We studied Golden-winged Warblers at Tamarac National Wildlife Refuge (NWR; 47.049°N, 95.583°W) and Rice Lake NWR (46.529°N, 93.338°W), Minnesota, and at Sandilands Provincial Forest (PF; 49.637°N, 96.247°W), Manitoba, Canada. All three sites were located in the northern hardwood forest transition zone, with boreal forest to the north and east, and tallgrass prairie (mostly converted to agriculture) to the south and west. We collected all data in portions of these NWRs and PF, but each study site had no official boundaries, and animal movements expanded our perceived study sites almost daily. Each study site covered ~50 km² by the end of the study. The landscape immediately surrounding each study site (within 5 km) was primarily upland and wetland forest, and shrubland, with limited areas (<10%) of agriculture and other human development. Landscapes within the study sites were characterized by similar cover types containing similar tree and shrub species, but individual cover types comprised different proportions of each site (Table 8.1). At all sites, mature forest stands were dominated by maple (*Acer* spp.), oak (*Quercus* spp.), aspen (*Populus* spp.), paper birch (*Betula papyrifera*), and American basswood (*Tilia americana*), with a few mature stands of jack pine (*Pinus banksiana*) and red pine (*P. resinosa*). The term “mature forest” can be ambiguous in managed forests without a specific age or structure when a stand becomes mature. We describe stands by structure rather than age here because (1) forest structure and age are not reliably correlated in our study area, (2) we assume birds respond to vegetation structure rather than age, and (3) forest structure is readily comparable for others drawing inference from our results. Upland forests on our study sites were primarily even-aged stands; we use “mature forest” here to refer to stands that had canopy >20 m. All mature forest stands on our three study sites averaged >60% canopy closure, which is defined as closed tree canopy forest by the U.S. Forest Service (Brohman and Bryant 2005). Sampled locations within mature forest stands ranged from 50% to 96% canopy cover, and most

mature stands contained a patchy and dense shrub layer (vegetation <2 m tall) and understory (vegetation between 2 and ~15 m tall) of maple, aspen, oak, and hazel (*Corylus* spp.). Our estimates of canopy cover percentages are based on analysis of >2,500 digital images and represent percentage of sky obscured by vegetation.

Forested areas at each study site were managed through harvest, prescribed fire, or both, for a combination of timber production and wildlife management resulting in the presence of regenerating forest stands of various seral stages. Age classes provide little useful information and a similar age stand north or south of our study area or on different substrate could have considerably different vegetation structure. Therefore, we include a range of stand ages here, but describe stands primarily by vegetation composition and canopy height. We classified stands dominated by vegetation 1–3 m tall as shrub-dominated clear-cuts. These stands are traditionally described as the vegetative component of Golden-winged Warbler habitat (Chapter 7, this volume) and ranged from five to 15 years postharvest and were composed of shrubs, forbs, grasses, paper birch saplings, and aspen propagule saplings with stems <2 cm in diameter that reached 5 m tall in some areas. Shrub-dominated clear-cuts ranged from one to 30 ha and contained sparse individual or small patches (i.e., <0.25 ha) of trees 10–25 m tall. We classified stands dominated by sapling trees with canopy 5–20 m tall as sapling-dominated clear-cuts. All but two stands classified as sapling-dominated clear-cuts had canopies 10–20 m tall. Sapling-dominated clear-cuts ranged from 15 to 30 years postharvest and were dense stands of aspen, birch, and sometimes green ash (*Fraxinus pennsylvanica*) averaging ~10 cm dbh, but ranging widely in dbh, with sparse individual trees taller than the main canopy, similar to those in the shrub-dominated clear-cuts. We classified stands that were structurally similar to shrub-dominated clear-cuts, but on a wetland substrate and with wetland-associated vegetation, as wetland shrublands. Wetland shrublands were dominated by willow (*Salix* spp.) and alder (*Alnus* spp.) and also contained reeds, grasses, and hazel shrubs. The substrate of wetland shrublands ranged from dry ground to standing or moving water depending on snowmelt and recent rainfall, and in some cases the substrate was sphagnum moss (*Sphagnum papillosum*).

TABLE 8.1

Percentage of each study site comprised by each cover type, and mean percentage of each cover type available to fledgling Golden-winged Warblers the first day outside the nest, based on observed movement distances at Tamarac NWR and Rice Lake NWR, Minnesota, and Sandilands PF, Manitoba, during 2011 and 2012.

| Site | Mature forest | Wetland shrubland | Grassland | Forested wetland | Coniferous forest | Shrub-dominated clear-cut | Sapling-dominated clear-cut | Road | Firebreak | Human development |
|---------------|---------------|-------------------|-----------|------------------|-------------------|---------------------------|-----------------------------|------|-----------|-------------------|
| Tamarac NWR | 62 | 12 | 9 | 9 | <1 | 2 | 3 | 2 | <1 | <1 |
| Rice Lake NWR | 31 | 30 | 2.6 | 8 | <1 | 3 | 1 | <1 | <1 | <1 |
| Sandilands PF | 47 | 15 | 14 | <1 | 14 | 4 | 2 | 2 | <1 | <1 |
| Available | 43 | 12 | 10 | 1 | 2 | 28 | 2 | 2 | <1 | 0 |

Percentages for study sites were measured within arbitrary boundaries that encompassed each study site, not geopolitical boundaries, and percentages vary slightly if boundaries are moved. The values demonstrate the necessity to limit availability to accessible space when analyzing cover-type selection by animals with limited movement capabilities. Specifically, cover-type selection by young fledgling Golden-winged Warblers would have been biased toward a common nesting cover type (shrub-dominated clear-cuts) if we did not limit availability to accessible space.

Other, less common cover types at each study site included forested wetlands of tamarack (*Larix laricina*) or black ash (*Fraxinus nigra*), upland and wetland grasslands, firebreaks and powerline rights-of-way (mostly grass with some shrubs), roads ranging from two-track access trails to two-lane paved roads, and small areas of human occupation (houses, outbuildings, and lawns). Each site also contained open water in the form of rivers and lakes, but we excluded open water from our analysis because we assumed it was not available for use by Golden-winged Warbler fledglings. Sandilands PF also included a few small plantations of young jack pine, several areas apparently used as communal trash dumping sites, and at least one marijuana (*Cannabis sativa*) cultivation site. For details on delineation and classification of cover types for analysis, see Cover-type Selection section.

Data Collection

We attached 0.39-g VHF radio transmitters (Blackburn Transmitters Inc., Nacogdoches, TX) to nestling Golden-winged Warblers from nests we found by systematically searching our study areas and by radiomonitoring breeding females. For detailed description of nest searching and monitoring methods, see Chapter 10 (this volume). Briefly, we established 8–16 plots at each study site within which we captured females and searched for nests. Each plot consisted of one shrub-dominated clear-cut stand or one wetland shrubland (described above) and extended ~50 m into the surrounding forest. Plots were 200 m to 10 km from each other to increase independence of nests in the sample, and the 43% of nests we found using radiotelemetry reduced potential bias inherent to standard nest-searching studies (Powell et al. 2005, Peterson et al. 2015). We removed each brood from its nest 0–3 days before they fledged and carried the young in a soft cloth bag >10 m from the nest. We marked each nestling with an aluminum U.S. Geological Survey leg band, and we marked 1–5 (usually 2) randomly selected nestlings with radio transmitters. We placed each brood back in its nest <15 min after removal. In addition, we banded and attached transmitters to fledglings we opportunistically captured and for which we did not know the nest location. We attached transmitters to nestlings and fledglings using an elastic-thread, figure-eight

harness design modified from Rappole and Tipton (1991) and identical to methods used by Streby and Andersen (2013a). Transmitter and harness weighed 0.39 g, which was 4.5% of mean body mass (8.6 g) at the time of fledging.

After transmitter attachment to nestlings, we monitored nests once or twice daily to determine fledging dates. Some nestlings (12%) force fledged or refused to remain in the nest after we handled them, either as individuals or as entire broods. However, force fledging had no effect on fledging survival (Streby et al. 2013b), so we treated those fledglings as if they had fledged naturally. We monitored each fledgling once per day with some 2–6-day observation intervals because of logistical constraints or inclement weather (<3% of observations), and we recorded fledgling fate as dead or alive at each encounter. Rarely (<3% of observations), when a fledgling was entirely obscured by dense vegetation, we narrowed its location to within ~1 m and recorded the location without visual confirmation of fate. In some cases, the fledgling's parent entered the vegetation with food and we assumed the fledgling was alive. When a transmitter signal emanated from the same obscured location during two consecutive days, we investigated more closely, which typically confirmed fledgling mortality. When an older bird flew away on its own or in response to an approaching observer, we recorded the location where we first observed the fledgling. We recorded each nest and fledgling location with a handheld GPS unit and averaged locations to achieve accuracy <5 m. We measured distance and direction between nest and fledgling locations, and between those locations and the nearest forest–shrubland edge, such as edges between shrub-dominated uplands or wetland shrublands and any taller forest stand, using ArcMap 10.1 (ESRI, Redlands, CA).

At each nest and fledgling location, we estimated canopy cover and lateral cover and recorded observations of fledgling activities as begging, foraging, travelling, or sitting quietly, and adult activities as feeding fledgling, chipping, singing, or not present. We used digital cameras (Vivitar VivCam and Nikon Coolpix, set to 35 mm equivalent focal length) to estimate canopy cover by taking a vertical photograph from 2 m above the ground and analyzing the photograph with ImageJ software (National Institutes of Health) to measure the percentage of sky obscured by

vegetation. We estimated lateral cover using a profile-board method modified from MacArthur and MacArthur (1961) and described in Streby and Andersen (2013a). Briefly, we divided a 2 m × 0.25 m sheet of vinyl cloth into eight squares, hung the sheet from a collapsible stand, and then estimated the percentage of each square obscured by vegetation from a distance of 5 m. We then rotated the sheet 90°, repeated the estimates, and averaged all 16 values to produce one estimate of lateral cover for each location.

Fledgling Survival

We used methods of Streby and Andersen (2013b) to investigate the relative effects of various habitat characteristics on fledgling survival from the nest to independence from adult care. Fledgling Golden-winged Warblers can remain with a parent beyond 30 days (Will 1986), but most fledglings we monitored were independent from adult care by 23–25 days post fledge (Streby et al. 2014a). We chose habitat variables that have been found to influence fledgling survival in previous studies (Cohen and Lindell 2004, Jackson et al. 2013, Streby and Andersen 2013b). We considered the following six habitat variables: nest distance to forest–shrubland edge, nest canopy cover, nest lateral cover, fledgling canopy cover, fledgling lateral cover, and road crossings when consecutive fledgling locations were on opposite sides of a road (Streby and Andersen 2013a). We only included fledglings we tracked from nests ($n = 246$) in these models because nest-site habitat variables were unknown for fledglings captured opportunistically. We used the logistic exposure method to model fledgling survival and we fit models with PROC NLMIXED (Shaffer 2004, SAS Institute 2008). All models included a random effect for brood because preliminary models indicated that survival among broodmates was not independent. Brood identity was a much stronger predictor of survival than age or any habitat variable in single-variable models (H. M. Streby, unpubl. data). In addition, fledgling survival increased nonlinearly with age, as is common in songbirds (Streby et al. 2013a). Therefore, all models except the null model (i.e., constant survival including a random effect for brood) included a quadratic term for fledgling age. We used daily survival measured as whether a fledgling survived a one-day observation interval as the response variable and habitat

characteristics associated with the fledgling location on the first day of the interval as explanatory variables. For example, we used habitat variables at the nest as predictors of a fledgling surviving the first day outside the nest, habitat variables from the first daily location outside the nest as predictors of day 2 survival, and so on. The few observation intervals between two and six days were not problematic because the logistic exposure method incorporates variable interval lengths (Shaffer 2004). In those cases, we associated survival of the observation interval with habitat characteristics measured on the first day of the interval, as we did with the 1-day intervals.

Most predation occurred during the first eight days after fledging so we assessed the effects of habitat characteristics on survival separately for days 0–8 and days 9–25. The set of candidate models was identical for each stage. Preliminary analysis indicated no site or year effects on fledgling survival, so we pooled survival data from 2011 and 2012 and from all three sites (Streby et al. 2014a). As in Streby and Andersen (2013b), our objective was to determine the relative importance of each variable for explaining fledgling survival. To that end, we built a set of 23 candidate models that included a null model, a model including only a quadratic term for age, and models including each variable individually and all pairs of two variables. We ranked models using AICc and we used the cumulative Akaike weight (w) of the models including each variable to determine the relative importance of each variable for explaining fledgling survival (Burnham and Anderson 2002, Arnold 2010, Streby and Andersen 2013b). In addition, we modeled cover-type-specific survival for each cover type for which we had >50 fledgling locations. For each of those cover types, we considered a constant survival model and models with linear and quadratic terms for age. Again, all models included a random term for brood. We used AICc to select the best supported model for fledgling survival in each cover type. No individual fledgling spent the entire postfledging period in a single cover type, but each of these cover types was used by enough fledglings of different ages to produce a model that converged for the entire period. Models of cover-type-specific survival can be useful for explaining why some cover types are used more relative to their availability compared to other cover types by fledglings of different ages. We compared daily

survival among cover types with posthoc Z-tests (Johnson 1979).

We used locations and condition of fledgling and transmitter remains to identify probable predators for each predation event. We attributed predation to mammals when we found remains buried under leaf litter or in mammal burrows and if we observed tooth marks on transmitters. We attributed predation to avian predators when a transmitter was recovered in a pile of plucked feathers or when a transmitter signal came from a raptor nest. We attributed predation to garter snakes (*Thamnophis radix* and *T. sirtalis*) when a transmitter was ingested by a snake or when we recovered a transmitter with the distinct pungent odor of garter snake feces. Rare causes of fledgling death (<4% total) included exposure during cold and wet nights, drowning during a flood, blowfly (*Trypocalliphora braueri*) infection acquired in the nest, apparent starvation following parental disappearance, and fatal injury from a hailstone. We excluded birds with non-predation-related deaths from analysis because those deaths likely were not related to the habitat characteristics used as explanatory variables in our survival models.

Cover-Type Selection

We used aerial photographs for each study site in ArcMap 10.1 to create a digital cover-type map and added descriptive attributes for each cover-type polygon based on ground-truthing. We

visited >2,500 locations throughout our study sites and confirmed or adjusted cover-type classification and delineation. We used 1-m resolution digital orthophoto quadrangles (2009, Minnesota Department of Natural Resources) for the NWRs and we used orthorectified satellite images (2010 imagery) from Google Earth™ (version 6.2) for Sandilands PF. We classified all polygons into 10 classes based on cover types described above: (1) mature forest, (2) sapling-dominated clear-cut, (3) coniferous forest, (4) shrub-dominated clear-cut, (5) wetland shrubland, (6) forested wetland, (7) grassland, (8) road, (9) firebreak, and (10) human development.

We analyzed cover-type selection (i.e., use versus availability) with compositional analysis using the adehabitat package in Program R (Aebischer et al. 1993, Calenge 2006). We defined the space or area available to fledglings based on the current location of the fledgling and the fledgling's age-specific movement capability to avoid bias associated with assuming an entire study site is available (Streby and Andersen 2013a). We used the daily estimated availability (DEA) method to determine the space available to fledgling Golden-winged Warblers of each age, days 0–24 postfledge (Streby and Andersen 2013a). We used the greatest distance traveled by any fledgling between consecutive daily locations as an estimate of the maximum straight-line movement capability by a fledgling of each age (Figure 8.1). We used each of those maximum daily distances as the radius of a

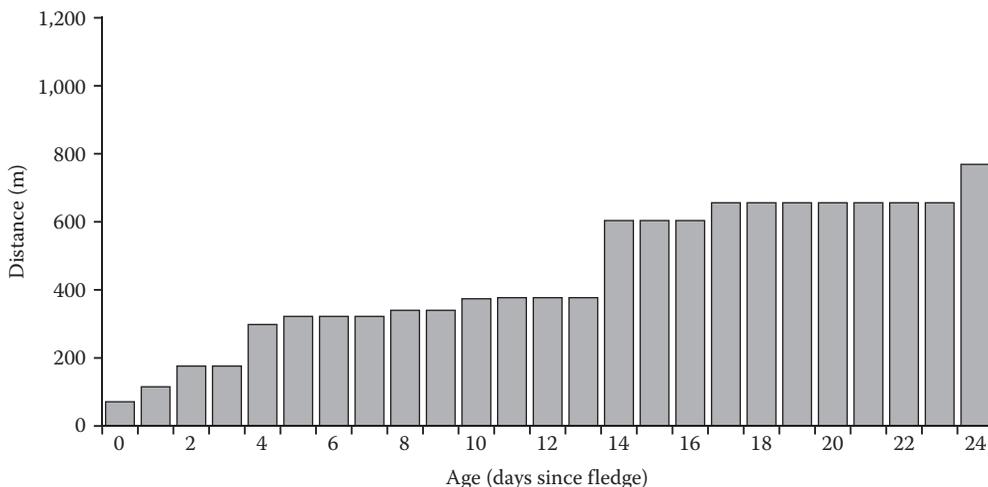


Figure 8.1. Age-specific daily movement capability for fledgling Golden-winged Warblers 0–24 days after fledging in Minnesota, and Manitoba, Canada during 2011 and 2012. Values were used as radii of circles delineating the DEA of space for cover-type selection analysis.

DEA circle defining available space for fledglings of each age. We then drew DEA circles around each fledgling location in GIS and measured the percentage of each DEA circle comprised by each cover type. By averaging the percentages of each cover type available each day throughout the postfledging period, we standardized cover-type availability by age-specific movement capability for each fledgling Golden-winged Warbler. We defined cover-type use as the cover type occupied by a fledgling within the DEA circle from the previous day. Therefore, we estimated availability for days 0–24 and recorded use for days 1–25.

We analyzed cover-type selection separately for the two stages defined in the survival analysis because cover-type selection might differ between the high-predation period of days 0–8 and the remaining lower predation period of days 9–25. We converted cover-type use and availability to percentages for each bird for compositional analysis. Similar cover-type availability among broodmates does not cause pseudoreplication in compositional analysis because availability is usually identical for entire populations in most such analyses. However, cover-type use was not independent among broodmates during days 0–8, nor among subbroodmates, defined as broodmates with one parent after parents split the brood. During days 9–25, movement patterns but not cover-type use, of male- and female-reared subbroods diverged (Chapter 9, this volume). We therefore averaged use and availability values for broodmates during days 0–8 and for subbroodmates during days 9–25. We excluded fledglings that were depredated in the first 24 h after fledging from cover-type selection analysis because they provided no information for cover-type use. We included fledglings we captured opportunistically in cover-type selection analysis because use and availability were measured daily and did not require knowledge of nest locations after day 1. Cover-type selection analysis included 94 broods for days 0–8 and 127 subbroods for days 9–25. Most of the fledglings we captured opportunistically ($n = 25$; 11% of total) were captured within a few days of fledging. We assigned these fledglings to an age class by comparing their developmental morphology to our sample of known-age birds. Accurate aging of fledgling songbirds can be difficult (Streby et al. 2013c) and we conducted cover-type selection analyses with and without the opportunistically

captured fledglings. Statistical significance and the order of cover-type selection were unaffected if we excluded opportunistically captured fledglings from analysis (H. M. Streby, unpubl. data), so we report results for cover-type selection analysis including all fledglings.

Fledgling Golden-winged Warblers did not consistently move in any cardinal direction during our study (Peterson 2014). However, based on the results of survival and cover-type selection analysis, we examined whether early postfledging movements during first the 24 h after fledging were oriented toward cover types associated with high fledgling survival including sapling-dominated clear-cuts and mature forest. We used Rayleigh V tests for circular uniformity with a specified mean direction (Durand and Greenwood 1958, Zar 2004). We conducted separate tests of oriented movement for fledglings from nests in shrublands (shrub-dominated clear-cuts and wetland shrublands) and for fledglings from nests in forest (mature forest and sampling-dominated clear-cuts). For both groups, we tested whether movements were oriented toward the nearest shrubland–forest edge. We considered all statistical tests to be significant at $\alpha = 0.05$ level.

RESULTS

Fledgling Survival

We estimated that 48% of fledgling Golden-winged Warblers were depredated before reaching independence from adult care 25 days after fledging. Most (75%) fledgling predation events occurred during the first three days after fledging, and 86% of predation events occurred in the first eight days. Based on location and condition of fledgling and transmitter remains, we attributed predation of day 0–3 fledglings to mammals (86%), snakes (9%), and avian predators (5%). The percentage of fledgling predation attributable to avian predators increased with fledgling age, with 73% of predation during days 9–25 attributed to raptors, whereas 27% and 0% of predation was attributable to mammals and snakes, respectively, during that period.

Survival of fledgling Golden-winged Warblers during the first eight days after fledging was best explained by a model including nest distance to forest–shrubland edge (Figure 8.2; all models included a random term for brood and a quadratic

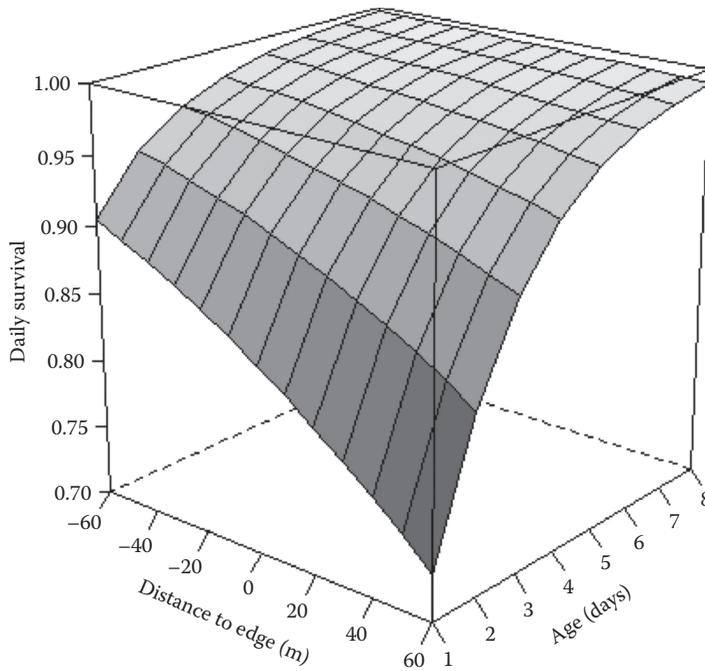


Figure 8.2. Probability of daily survival for 246 fledgling Golden-winged Warblers during the first eight days after fledging from nests in Minnesota, and Manitoba, Canada during 2011 and 2012. The best supported model (lowest AICc) included a quadratic effect of fledgling age and a linear effect of nest distance to edge. Positive values of distance to edge are for nests in shrublands and negative values are for nests in forest. Variance excluded for clarity of presentation.

term for age), and nest distance to edge was the strongest predictor of fledgling survival during that period ($w = 0.73$). Other than fledgling age, which fit the expected pattern for fledgling songbird survival (Figure 8.2), nest distance to edge was the only variable with a statistically significant relationship with fledgling survival ($\beta = -0.010$; 95% CI = -0.020 to -0.001 ; $t = -2.18$, d.f. = 93, $P = 0.03$). Fledgling survival was greatest from nests in forest, lowest from nests in shrublands, and intermediate from nests closest to forest-shrubland edge (Figure 8.2). Nest canopy cover ($w = 0.27$), nest lateral cover ($w = 0.19$), fledgling canopy cover ($w = 0.15$), fledgling lateral cover ($w = 0.22$), and fledgling road crossings ($w = 0.12$) each received less Akaike weight than nest distance to edge during the first eight days after fledging and all of these factors had regression coefficients with confidence intervals overlapping zero. Fledgling survival during days 9–25 was best explained by the null model, suggesting that none of the variables we measured, including fledgling age, explained a meaningful amount of variation

in survival after the first eight days postfledging. For comparison, the null model for the first eight days ranked worse than other models with a ΔAICc of 51.8 from the best supported model.

Cover-type-specific survival models indicated that fledgling survival was least in shrublands and greatest in forests ($Z > 3.00$ and $P < 0.01$ for all comparisons between shrubland types and forest types; Figure 8.3). Daily survival was statistically similar between mature forest and sapling-dominated clear-cuts ($Z = 0.87$, $P = 0.38$) and between the two types of shrublands ($Z = 0.39$, $P = 0.70$). The differences in survival between forested and shrubland cover types were apparent during the first ~8 days, after which fledgling survival was generally high (0.993 ± 0.003 SE) in all cover types. The probability of a fledgling surviving to day 25 and independence from adult care, if it spent the entire dependent postfledging period in one cover type was $0.84 (\pm 0.09)$ in sapling-dominated clear-cut, $0.75 (\pm 0.06)$ in mature forest, $0.46 (\pm 0.16)$ in wetland shrubland, and $0.40 (\pm 0.10)$ in a shrub-dominated clear-cut.

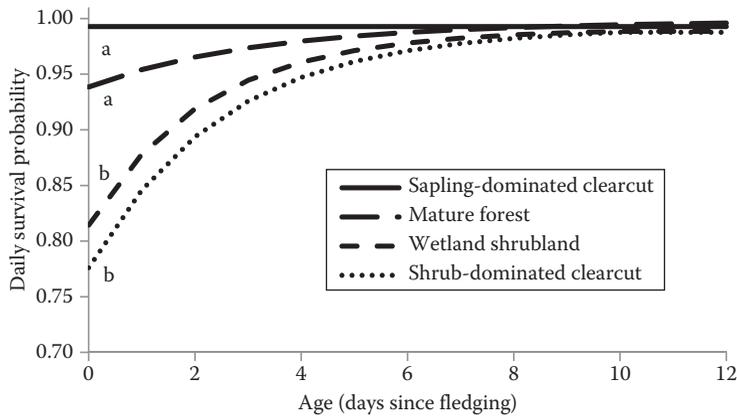


Figure 8.3. Probability of daily survival for 246 fledgling Golden-winged Warblers in each of four cover types in northern Minnesota, and Manitoba, Canada during 2011 and 2012. Shown for each cover type are fitted values for best supported logistic exposure models (lowest AICc) selected from a constant survival model and models with linear and quadratic terms for fledgling age. Values are fitted from models of survival for fledglings 0–24 days after fledging, but days 0–12 are shown to illustrate the differences among cover types that occurred during only the first ~8 days. Letters (a, b) indicate significantly different groups. SE in text, excluded for clarity of presentation.

Cover-Type Selection

Fledglings used cover types disproportionately with respect to availability ($\Lambda = 0.054$, $P < 0.01$) during the first eight days after fledging. Young fledglings selected for mature forest and sapling-dominated clear-cut over all other cover types, selected against road and grassland, and used shrub-dominated clear-cut, wetland shrubland, firebreak, and forested wetland in accordance with availability. Fledglings also selected ($\Lambda = 0.068$, $P < 0.01$) among cover types during days 9–25 after fledging. Older fledglings selected for mature forest over all other cover types and selected for shrub-dominated clear-cut over all other cover types except mature forest. During days 9–25, fledglings selected against road and grassland and used wetland shrubland, firebreak, and forested wetland in accordance with availability. First-day movements of fledglings from shrubland nests were oriented toward shrubland–forest edge ($u_{77} = 4.11$, $P < 0.01$), but first-day movements of fledglings from forest nests were not oriented toward shrubland–forest edge ($u_{20} = 0.24$, $P < 0.78$).

DISCUSSION

We found that survival of fledgling Golden-winged Warblers was greater in mature forest and sapling-dominated clear-cuts than the shrub-dominated clear-cuts and wetland

shrublands with which the species is typically associated (Buehler et al. 2007). In addition, we found that the best predictor of fledgling survival was the location of the nest relative to a forest–shrubland edge. Our results support the contention that fledgling survival is strongly influenced by nest-site choice, which may explain why Golden-winged Warblers rarely nest in areas that maximize nest success (Streby et al. 2014a). The importance of forest stands in later seral stages than stands traditionally associated with breeding Golden-winged Warblers could prove critical for future management plans in the western Great Lakes region. Population trends in Minnesota are stable or growing slightly (Zlonis et al. 2013; Chapter 1, this volume) despite a 30% increase in early successional upland vegetation in the past 35 years (Miles and VanderSchaaf 2012). Refining conservation goals to include postfledging habitat requirements could be key to improving population growth rates in Golden-winged Warblers.

Areas used during the postfledging period differ in vegetation structure from areas used for nesting in many songbirds (Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2007, Streby et al. 2011a), and postfledging habitat use is associated with fledgling survival, especially in the first few days after fledging (Anders et al. 1998, Yackel Adams et al. 2006, Berkeley et al. 2007, Moore et al. 2010, Vitz and Rodewald 2011). We found

that early postfledging movements were oriented toward forest–shrubland edge for fledglings from nests in shrublands but not for fledglings from nests in forested cover types. Our results indicate that adult Golden-winged Warblers direct or lead their fledglings to forested cover types, or keep them in those cover types, regardless of nest location. Similarly, fledgling Ovenbirds (*Seiurus aurocapilla*), Eastern Bluebirds (*Sialia sialis*), and White-throated Robins (*Turdus assimilis*) move toward habitat features associated with high survival shortly after fledging (Cohen and Lindell 2004, Jackson et al. 2013, Streby and Andersen 2013a). Crossing roads had no meaningful influence on survival of fledgling Golden-winged Warblers despite having a considerable impact on survival of fledgling Ovenbirds in the same region (Streby and Andersen 2013b). The difference in mortality associated with road crossings might be related to the manner in which these species move through their environment. Young fledgling ovenbirds spend most of their time on the ground and hop or walk across roads, thereby exposing themselves to predation in the open space of the road (Streby and Andersen 2013b), whereas fledgling Golden-winged Warblers primarily occupy shrubs and understory trees and cross roads relatively quickly by flying (H. M. Streby, pers. obs.).

Fledgling survival differed among cover types for the first eight days, and fledglings selected cover types associated with high fledgling survival (mature forest and sapling-dominated clear-cuts) over all other cover types during that period. Fledgling survival was unaffected by cover-type use or by any other habitat variable we measured during days 9–25, but fledglings still used cover types disproportionately to their availability by selecting mature forest and shrub-dominated clear-cuts over all other cover types. Our results suggest that cover-type selection during the early postfledging period is driven by predator avoidance but is driven by other factors later as fledglings develop and as predation risk declines. Some songbirds choose areas of abundant food resources during the postfledging period (White and Faaborg 2008, Streby et al. 2011b). Leaf-roller caterpillars (*Archips* spp.) made up 89% of stomach contents in fledgling Golden-winged Warbler in our study population (Streby et al. 2014b) and were abundant in broad-leafed trees and shrubs at all of our study sites, possibly explaining the selection of stands abundant in these plants by

fledglings starting to forage. We observed fledglings following foraging adults and starting to attempt foraging at about two weeks after fledging; self-feeding increased until independence (H. M. Streby and S. M. Peterson, unpubl. data).

Many areas within the mature forest stands at our study sites were characterized by dense and patchy understory and shrub layer. Golden-winged Warblers selected mature forest throughout the dependent postfledging period, but young fledglings were most often observed in the shrub layer while their parents foraged elsewhere (Chapter 9, this volume), often >300 m away (H. M. Streby and S. M. Peterson, unpubl. data). Use of shrubs and understory trees within mature forest by young fledglings suggests that early postfledging habitat might be limited for Golden-winged Warblers in landscapes with primarily contiguous closed-canopy forest with limited shrub–sapling vegetation. Ovenbirds, which nest on the ground in mature forest, select sapling-dominated clear-cuts over mature forest during the postfledging period, but only when dense understory vegetation is not available in the mature forest (Streby and Andersen 2013a). Once postfledging habitat associations are considered, it is clear how two species like Golden-winged Warblers and Ovenbirds, with seemingly disparate breeding habitat requirements, can experience strong full-season productivity in the same landscape. Indeed, we regularly observed fledgling Ovenbirds and other mature forest birds while tracking fledgling Golden-winged Warbler in sapling-dominated clear-cuts and mature forest areas with dense understory.

Postfledging survival is important to breeding habitat selection (Streby et al. 2014a) and full-season productivity in songbirds (Streby and Andersen 2011). The presence of cover types associated with high fledgling survival is likely necessary to increase breeding densities and full-season productivity or the number of fledglings raised to independence from adult care. Our results suggest that creating and maintaining young, shrub-dominated stands within an open-understory mature forest matrix is problematic for maximizing density or full-season productivity for Golden-winged Warblers. Rather, the presence of dense forest understory, sapling-dominated clear-cut stands, or both adjacent to shrublands is likely associated with higher density and full-season productivity.

Two potential management options for providing an early postfledging habitat component are thinning of the canopy of mature forest adjacent to shrublands or maintaining a close association between shrublands and sapling-dominated regenerating stands through rotational harvest. In smaller forested areas, or areas where rotational harvest might remove too much mature forest from the landscape to maintain densities of Golden-winged Warblers or other species of conservation concern, thinning the mature forest around maintained shrublands could provide adequate postfledging habitat by increasing density of shrub-sapling layer in the mature forest. Based on distances fledglings move from nests in the early postfledging period (Chapter 9, this volume) when predation is highest, we suggest that a 100-m buffer of thinned mature forest around managed shrublands could provide the vegetation structure associated with high survival of fledgling Golden-winged Warblers.

Our dataset is large and collected from sites spanning a broad geographic range within the western Great Lakes region where a majority of the species breeds, but inference from our results might not apply outside our study region. We described cover types by structure instead of age so the general structure of the vegetative habitat components can be understood and considered elsewhere. However, before applying recommendations based on Golden-winged Warbler-habitat associations in the Great Lakes breeding-distribution segment to the Appalachian breeding-distribution segment, similar studies of postfledging movements, habitat selection, and survival need to be conducted in the Appalachian Mountains portion of the species breeding distribution, where nest productivity is similar to that in our study region (e.g., Confer et al. 2010, Percy 2012), but where many populations of Golden-winged Warblers are declining (Chapter 1, this volume).

ACKNOWLEDGMENTS

Field data were collected during a project funded by the U.S. Fish and Wildlife Service, U.S. Geological Survey, and Minnesota Department of Natural Resources through Research Work Order no. 87 at the Minnesota Cooperative Fish and Wildlife Research Unit. We collected data following Protocol #1004A80575, approved by the University of Minnesota Institutional Animal

Care and Use Committee. Use of trade names does not imply endorsement by the U.S. Geological Survey, University of Minnesota, or any other organization supporting this research. We thank P. Blackburn, W. Brininger, W. Faber, W. Ford, J. Loegering, M. McDowell, H. Saloka, and R. Vallender for equipment and logistical support, and J. Kelley for graphics consulting. We thank L. Arnold, S. Barlow, D. Bradshaw, J. Bruggman, R. Carr, M. Dawson, L. Deets, J. Feura, A. Fish, R. Franta, C. Gesmundo, A. Jensen, M. Johnson, G. Kramer, J. Lehman, T. McAllister, D. McNeil, Z. Orbaz, E. Pokrivka, R. Poole, A. Rehmann, J. Refsnider, R. Refsnider, N. Seeger, E. Sinnot, and B. Vernasco for assistance with field data collection, J. Refsnider and S. Loss for constructive comments on early drafts, and two anonymous referees for comments improving the manuscript.

LITERATURE CITED

- Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313–1325.
- Anders, A. D., D. C. Dearborn, J. Faaborg, and F. R. Thompson III. 1997. Juvenile survival in a population of migrant birds. *Conservation Biology* 11:698–707.
- Anders, A. D., J. Faaborg, and F. R. Thompson III. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. *Auk* 115:349–358.
- Anders, A. D., and M. R. Marshall. 2005. Increasing the accuracy of productivity and survival estimates in assessing landbird population status. *Conservation Biology* 19:66–74.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management* 74:1175–1178.
- Berkeley, L. I., J. P. McCarty, and L. L. Wolfenbarger. 2007. Postfledging survival and movement in Dickcissels (*Spiza americana*): implications for habitat management and conservation. *Auk* 124:396–409.
- Brohman, R. J., and L. D. Bryant (editors). 2005. Existing vegetation classification and mapping technical guide version 1.0. USDA Forest Service General Technical Report WO-67. Washington, DC.
- Buehler, D. A., A. M. Roth, R. Vallender, T. C. Will, J. L. Confer, R. A. Canterbury, S. B. Swarthout, K. V. Rosenberg, and L. P. Bullock. 2007. Status and conservation priorities of Golden-winged Warbler (*Vermivora chrysoptera*). *Auk* 124:1439–1445.

- Bulluck, L. P., and D. A. Buehler. 2008. Factors influencing Golden-winged Warbler (*Vermivora chrysoptera*) nest-site selection and nest survival in the Cumberland Mountains of Tennessee. *Auk* 125:551–559.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer-Verlag, New York, NY.
- Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519.
- Cohen, E. B., and C. A. Lindell. 2004. Survival, habitat use, and movements of fledgling White-throated Robins (*Turdus assimilis*) in a Costa Rican agricultural landscape. *Auk* 121:404–414.
- Confer, J. L., K. W. Barnes, and E. C. Alvey. 2010. Golden- and Blue-winged Warblers: distribution, nesting success, and genetic differences in two habitats. *Wilson Journal of Ornithology* 122:273–278.
- Durand, D., and J. A. Greenwood. 1958. Modifications of the Rayleigh test in analysis of two-dimensional orientation data. *Journal of Geology* 66:229–238.
- Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux Jr., P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, S. C. Latta, D. J. Levey, P. P. Marra, C. L. Mekord, E. Nol, S. I. Rothstein, T. W. Sherry, T. S. Sillett, F. R. Thompson III, and N. Warnock. 2010. Conserving migratory land birds in the New World: do we know enough? *Ecological Applications* 20:398–418.
- Ficken, M. S., and R. W. Ficken. 1968. Territorial relationships of Blue-winged Warblers, Golden-winged Warblers, and their hybrids. *Wilson Bulletin* 80:442–451.
- Jackson, A. K., J. P. Froneberger, and D. A. Cristol. 2013. Habitat near nest boxes correlated with fate of Eastern Bluebird fledglings in an urban landscape. *Urban Ecosystems* 16:367–376.
- Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96:651–661.
- King, D. I., R. M. Degraaf, M. L. Smith, and J. P. Buonaccorsi. 2006. Habitat selection and habitat-specific survival of fledgling Ovenbirds (*Seiurus aurocapilla*). *Journal of Zoology* 269:414–421.
- Klaus, N. A., and D. A. Buehler. 2001. Golden-winged Warbler breeding habitat characteristics and nest success in clearcuts in the southern Appalachian Mountains. *Wilson Bulletin* 113:297–301.
- MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* 42:594–598.
- Martin, K. J., R. S. Lutz, and M. Worland. 2007. Golden-winged Warbler habitat use and abundance in northern Wisconsin. *Wilson Journal of Ornithology* 119:523–532.
- Marshall, M. R., J. A. DeCecco, A. B. Williams, G. A. Gale, and R. J. Cooper. 2003. Use of regenerating clearcuts by late-successional bird species and their young during the post-fledging period. *Forest Ecology and Management* 183:127–135.
- Miles, P. D., and C. L. VanderSchaaf. 2012. Minnesota's forest resources, 2011. Northern Research Station Research Note NRS-134. USDA Forest Service, Newtown Square, PA.
- Moore, L. C., B. J. M. Stutchbury, D. M. Burke, and K. A. Elliott. 2010. Effects of forest management on postfledging survival of Rose-breasted Grosbeaks (*Pheucticus ludovicianus*). *Auk* 127:185–194.
- Pagen, R. W., F. R. Thompson III, and D. E. Burhans. 2000. Breeding and post-breeding habitat use by forest migrant songbirds in the Missouri Ozarks. *Condor* 102:738–747.
- Percy, K. L. 2012. Effects of prescribed fire and habitat on Golden-winged Warbler (*Vermivora chrysoptera*) abundance and nest survival in the Cumberland Mountains of Tennessee. M.S. thesis, University of Tennessee, Knoxville, TN.
- Peterson, S. M. 2014. Landscape productivity and the ecology of brood division in Golden-winged Warblers in the western Great Lakes region. M.S. thesis, University of Minnesota, St. Paul, MN.
- Peterson, S. M., H. M. Streby, J. A. Lehman, G. R. Kramer, A. C. Fish, and D. E. Andersen. 2015. High tech or field techs: radio-telemetry is a cost-effective method for reducing bias in songbird nest searching. *Condor* 117:386–395.
- Powell, L. A., J. D. Lang, D. G. Krementz, and M. J. Conroy. 2005. Use of radio telemetry to reduce bias in nest searching. *Journal of Field Ornithology* 76:274–278.
- Rappole, J. H., and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62:335–337.
- SAS Institute. 2008. SAS/STAT 9.2 user's guide. SAS Institute, Cary, NC.
- Shaffer, T. L. 2004. A unified approach to analyzing nest success. *Auk* 121:526–540.
- Streby, H. M., and D. E. Andersen. 2011. Seasonal productivity in a population of migratory songbirds: why nest data are not enough. *Ecosphere* 2:78.

- Streby, H. M., and D. E. Andersen. 2012. Movement and cover-type selection by fledgling Ovenbirds (*Seiurus aurocapilla*) after independence from adult care. *Wilson Journal of Ornithology* 124:621–626.
- Streby, H. M., and D. E. Andersen. 2013a. Movements, cover-type selection, and survival of fledgling Ovenbirds in managed deciduous and mixed-coniferous forests. *Forest Ecology and Management* 287:9–16.
- Streby, H. M., and D. E. Andersen. 2013b. Survival of fledgling Ovenbirds: influences of habitat characteristics at multiple spatial scales. *Condor* 115:403–410.
- Streby, H. M., S. M. Peterson, and D. E. Andersen. 2011b. Invertebrate availability and vegetation characteristics explain use of non-nesting cover types by mature forest songbirds during the post-fledging period. *Journal of Field Ornithology* 82:406–414.
- Streby, H. M., S. M. Peterson, C. F. Gesmundo, M. K. Johnson, A. C. Fish, J. A. Lehman, and D. E. Andersen. 2013a. Radio-transmitters do not affect seasonal productivity of female Golden-winged Warblers. *Journal of Field Ornithology* 83:316–321.
- Streby, H. M., S. M. Peterson, J. A. Lehman, G. R. Kramer, K. J. Iknayan, and D. E. Andersen. 2013b. The effects of force-fledging and premature fledging on the survival of nestling songbirds. *Ibis* 155:616–620.
- Streby, H. M., S. M. Peterson, J. A. Lehman, G. R. Kramer, B. J. Vernasco, and D. E. Andersen. 2014b. Do digestive contents confound body mass as a measure of relative condition in nestling songbirds? *Wildlife Society Bulletin* 35:308–310.
- Streby, H. M., S. M. Peterson, T. L. McAllister, and D. E. Andersen. 2011a. Use of early-successional managed northern forest by mature-forest species during the post-fledging period. *Condor* 113:817–824.
- Streby, H. M., J. M. Refsnider, S. M. Peterson, and D. E. Andersen. 2014a. Retirement investment theory explains patterns in songbird nest-site choice. *Proceedings of the Royal Society of London B* 281:20131834.
- Streby, H. M., B. Scholtens, A. P. Monroe, S. M. Peterson, and D. E. Andersen. 2013c. The Ovenbird (*Seiurus aurocapilla*) as a model for testing food-value theory. *American Midland Naturalist* 169:214–220.
- Vallender, R., V. L. Friesen, and R. J. Robertson. 2007. Paternity and performance of Golden-winged Warblers (*Vermivora chrysoptera*) and Golden-winged × Blue-winged Warbler (*V. pinus*) hybrids at the leading edge of a hybrid zone. *Behavioral Ecology and Sociobiology* 61:1797–1807.
- Vitz, A. C., and A. D. Rodewald. 2007. Vegetative and fruit resources as determinants of habitat use by mature forest birds during the postbreeding period. *Auk* 124:494–507.
- Vitz, A. C., and A. D. Rodewald. 2011. Influence of condition and habitat use on survival of post-fledging songbirds. *Condor* 113:400–411.
- Vitz, A. C., and A. D. Rodewald. 2013. Behavioral and demographic consequences of access to early-successional habitat in juvenile Ovenbirds (*Seiurus aurocapilla*): an experimental approach. *Auk* 130:21–29.
- White, J. D., and J. Faaborg. 2008. Post-fledging movement and spatial habitat-use patterns of juvenile Swainson's Thrushes. *Wilson Journal of Ornithology* 120:62–73.
- Will, T. C. 1986. The behavioral ecology of species replacement: Blue-winged and Golden-winged Warblers in Michigan. Ph.D. dissertation, University of Michigan, Ann Arbor, MI.
- Yackel Adams, A. A., S. K. Skagen, and J. A. Savidge. 2006. Modeling post-fledging survival of Lark Buntings in response to ecological and biological factors. *Ecology* 87:178–188.
- Zar, J. H. 2004. *Biostatistical analysis*. Pearson, Upper Saddle River, NJ.
- Zlonis, E. J., A. Grinde, J. Bednar, and G. J. Niemi. 2013. Summary of breeding bird trends in the Chippewa and Superior National Forests of Minnesota—1995–2013. NRRI technical report NRRI/TR-2013/36. University of Minnesota Duluth, Duluth, MN.