

Post-independence fledgling ecology in a migratory songbird: implications for breeding-grounds conservation

H. M. Streby^{1*}, S. M. Peterson¹, G. R. Kramer¹ & D. E. Andersen²

¹ Minnesota Cooperative Fish and Wildlife Research Unit, Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, MN, USA

² Minnesota Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, St. Paul, MN, USA

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Correspondence

*Current address: Department of Environmental Science, Policy and Management, 130 Mulford Hall, University of California, Berkeley, CA 94720, USA. Email: henrystreby@gmail.com

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Abstract

For migratory songbirds, breeding-grounds conservation and management plans are generally focused on habitat associated with locations of singing males and sometimes nesting females. However, habitat structure is often different in areas used for raising fledglings compared with areas used for song territories, and very little is known about habitat use by fledglings after independence from adult care. From 2010 to 2012, we used radiotelemetry to monitor 68 fledgling golden-winged warblers *Vermivora chrysoptera* after independence from adult care in mixed managed forests of Minnesota, US and Manitoba, Canada. This species is of high conservation concern in the US, is listed as threatened in Canada and is listed as near threatened on the International Union for Conservation of Nature Red List. We assessed distance and orientation of independent fledgling movements and we used compositional analysis to test for selection among cover types. Fledglings of this species, commonly described as a shrubland specialist, selected mature forest (78% of locations) over all other cover types, and foraged in forest canopy and understory in mixed-species flocks. Fledgling golden-winged warbler movements were apparently associated with habitat optimization (although prioritizing foraging over predator avoidance), and likely not with commencement of migration, or scouting future breeding territories. Ten days after independence, fledglings were an average of 1238 m north of their nest, which may be related to homing-target formation and the species' northward range expansion. We conclude that consideration for independent fledgling habitat associations is necessary for developing full-fledged forest management plans on the breeding grounds of migratory songbirds.

Introduction

Conservation and management efforts for migratory songbirds on their breeding grounds require a thorough understanding of habitat associations from spring arrival through departure for fall migration. Migratory songbirds breeding in North America are often described by their habitat associations during the nesting season (e.g. grassland birds, shrubland birds, forest birds, etc.), reflecting what may be an oversimplification of full-season habitat associations (Streby & Andersen, 2013a). Data on habitat use during the post-fledging period (i.e. after the young leave the nest but before fall migration) are relatively sparse and very little is known about habitat used by fledglings after independence from adult care for most avian taxa (Rappole & Ballard, 1987; De Frutos & Olea, 2008), especially in migratory songbirds (Faaborg *et al.*, 2010; Mitchell, Taylor & Warkentin, 2010a; Streby & Andersen, 2012). Radiotelemetry and mist-netting studies have shown that

areas used by fledglings before and after independence from adults can differ considerably in vegetation structure from areas used for nesting (e.g. Anders, Faaborg & Thompson, 1998; Pagen, Thompson & Burhans, 2000; Streby & Andersen, 2013a). Such studies have generally focused on forest-nesting birds that use non-nesting cover types (e.g. regenerating clearcuts) during the post-fledging period. It is unknown if there is a reciprocal mid-season switch whereby species nesting primarily in shrublands and early-successional forests move into mature forest during the post-fledging period. However, the consensus that forest birds move into early-successional cover types to exploit higher food resources and to avoid predation (Vitz & Rodewald, 2006) suggests that an opposite movement pattern is unlikely.

We studied movements and cover-type selection by fledgling golden-winged warblers *Vermivora chrysoptera* after independence from adult care in the western Great Lakes region of North America. The golden-winged warbler is a

small (~ 9 g) migratory wood-warbler (Parulidae) that has experienced considerable long-term declines and is consequently listed as threatened under the Canadian Species at Risk Act, is also considered to be of high conservation concern in the US (Buehler *et al.*, 2007) and is listed as near threatened on the International Union for Conservation of Nature Red List. This species is commonly described as an early-successional shrubland specialist (e.g. Confer & Knapp, 1981; Confer, Hartman & Roth, 2011) and its nesting habitat associations are well studied throughout much of its breeding range (Ficken & Ficken, 1968; Will, 1986; Klaus & Buehler, 2001; Martin, Lutz & Worland, 2007; Vallender, Friesen & Robertson, 2007; Bulluck & Buehler, 2008; Confer, Barnes & Alvey, 2010). Golden-winged warblers nest on the ground in shrublands and in forest edge adjacent to shrublands in our study region (Streby *et al.*, 2014a). After nesting, adult golden-winged warblers choose forested cover types to raise their fledglings, and fledglings become independent from adult care ~ 25 days after fledging from the nest (Peterson, 2014). Ours is the first study of post-independence fledgling ecology in this species. We assessed distance and orientation of fledgling movements and we tested whether fledglings selected among available cover types. We intended to also investigate factors influencing fledgling survival. However, we observed evidence of only two (3%) independent fledgling mortalities, resulting in insufficient variation with which to fit models.

We sought evidence for each of the four hypotheses summarized by Mitchell, Taylor & Warkentin (2010b) for explaining independent fledgling movements: (1) migration commencement; (2) habitat optimization; (3) breeding-territory prospecting; and (4) homing-target formation. The migration-commencement hypothesis suggests that fledglings orient movements in the direction of eventual fall migration (Rappole & Ballard, 1987). The habitat-optimization hypothesis suggests that fledglings select areas to maximize access to food or for avoidance of predators (e.g. Walsberg, 1986; Rappole & Ballard, 1987). The breeding-territory prospecting hypothesis suggests that fledglings search for potential future nesting territories by observing breeding conspecifics (Brewer & Harrison, 1975; Nocera, Forbes & Giraldeau, 2006; Betts *et al.*, 2008). The homing-target formation hypothesis suggests that fledglings seek out landscape features that will help them recognize their natal area or dispersal area when returning from migration for their first breeding season (Wiltchko & Wiltchko, 1978).

Materials and methods

Study area

We conducted this study at three managed forest sites in the western Great Lakes region of North America. The sites were Rice Lake National Wildlife Refuge (NWR; 46.529°N, 93.338°W) and Tamarac NWR (47.049°N, 95.583°W), Minnesota, US, and Sandilands Provincial Forest (PF; 49.637°N, 96.247°W), Manitoba, Canada (Supporting

Information Appendix S1). All three sites were in the Boreal Hardwood Transition Bird Conservation Region, with boreal forest to the northeast and prairie to the southwest. All sites were surrounded by upland and wetland forest and shrubland with small amounts of agriculture and other human development. Mature-forest stands (canopy > 20 m) comprised 31–62% of each site, and 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 *Pinus resinosa*. Areas within mature forest ranged from 50 to 90% canopy closure and most mature stands contained a patchy and dense understory and shrub layer of maple, aspen, oak and hazel (*Corylus* spp.). Upland forested areas at each site had a management history of harvest and/or prescribed fire for timber production and wildlife management. This resulted in a patchwork of upland shrublands and regenerating forest stands of various seral stages, in addition to shrubby and grassy wetlands, all within the mature forest matrix. Shrublands were composed of forbs, grasses, shrubs, paper birch saplings and aspen propagules. Upland shrublands ranged from 1 to 30 ha and contained sparse individual or small patches of mature trees. Mid-successional stands (i.e. sapling-dominated regenerating clearcuts with canopy 5–15 m) were characterized by dense areas of aspen, birch and sometimes green ash *Fraxinus pennsylvanica*. Wetland shrublands were primarily willow (*Salix* spp.) and alder (*Alnus* spp.) and also contained reeds, grasses and hazel shrubs. Each site also included small forested wetlands of tamarack *Larix laricina* or black ash *F. nigra*, upland and wetland grasslands, fire-breaks and powerline rights-of-way (mostly grass with some shrubs), roads ranging from two-track access trails to two-lane paved roads, small areas of human occupation (houses, outbuildings and lawns) and open water in the form of lakes and small rivers.

Data collection

We monitored fledgling golden-winged warblers after independence from adult care between 2 July and 4 August 2010–2012 at Tamarac NWR, and from 2011 to 2012 at Rice Lake NWR and Sandilands PF. We attached radio transmitters (Blackburn Transmitters, Nacogdoches, TX, USA) to the nestling golden-winged warblers from nests we found by systematically searching our study areas and by radio monitoring females. For detailed description of nest searching and monitoring methods, see Streby *et al.* (2013). We removed each brood from its nest 0–3 (usually 2) days before they fledged and carried them in a soft cloth bag > 10 m from the nest. From each nest, we ringed all nestlings and marked one to five (usually two; more or fewer depending on transmitter availability) randomly selected nestlings with radio transmitters. We monitored when each brood fledged so ages of all birds marked as nestlings were known. In addition, we ringed and attached transmitters to fledglings we opportunistically captured and for which we did not know the nest location. We estimated the age of those

fledglings by comparing their plumage development to the larger sample of known-age birds. We attached transmitters to nestlings and fledglings using an elastic-thread, figure-eight harness design modified from Rappole & Tipton (1991) and identical to methods used by Streby & Andersen (2013b). In previous studies with larger, longer-lived transmitters, this harness degraded and birds dropped transmitters 40–50 days after deployment (H.M. Streby, unpublished data). The same transmitters had no adverse effects on behavior or productivity of adult female golden-winged warblers in this population (Streby *et al.*, 2013). Transmitter mass was 4.5% of mean fledgling body mass at the time of fledging and 4.1% of mean body mass at age of independence.

Fledglings reached independence from adult care (i.e. they foraged entirely on their own and we observed no adult activity) typically 25 days after fledging from the nest (Streby *et al.*, 2014a,b). We assumed movements and survival of all fledglings were statistically independent. We monitored only three pairs of siblings after independence from adult care. The siblings in each of those pairs were cared for by different parents before independence (i.e. brood splitting; Peterson 2014) and we never observed siblings < 200 m (mean = 452 m) from each other after independence from adult care. We monitored each fledgling once daily using standard ground-based telemetry methods. We first triangulated the radio signal and then carefully approached until we observed the fledgling. We recorded each nest and fledgling location with a handheld Global Positioning System unit and averaged 100 locations to achieve accuracy < 5 m. We stopped tracking each fledgling when the fledgling was depredated ($n = 2$) or when the transmitter expired. Transmitter battery life was 30–33 days, and signals became inconsistent during the last 48 h, making transmitter expiration predictable. We measured distance and direction between nest and fledgling locations using ArcMap 10.1 (ESRI, Redlands, CA, USA) GIS software. At each fledgling location we recorded the occupied cover type, occupied vegetation strata (i.e. ground, shrub, understory or canopy), fledgling activity and other birds present (i.e. birds within 10 m of the fledgling). We included observations about flocking to assess whether other shrubland-nesting species commonly used similar areas similar to those used by golden-winged warblers. Flocks often included some unidentified birds, so the rates we report for other species present at fledgling locations are minimums.

Analysis

We used the logistic exposure method (Shaffer, 2004, Streby & Andersen, 2013b) to estimate fledgling daily survival. We used compositional analysis (Aebischer, Robertson & Kenward, 1993) to test for selection among cover types with the ADEHABITAT package (Calenge, 2006) in Program R (version 2.15.3, R Core Team, 2013). We measured cover-type availability as the percentage of each cover type within our study sites after digitizing cover types in each study site from aerial photos in ArcMap with a minimum mapping

unit of 0.25 ha. We measured cover-type availability separately for each study site because they were similar but not identical (H.M. Streby, unpublished data) and we assumed that the entire study site was available to each fledgling at that site because some fledglings made daily movements long enough to nearly traverse a site (i.e. > 2 km). Initial cover-type categories included mature deciduous forest, coniferous forest, mid-successional forest, upland shrubland, firebreak, forested wetland, shrubby wetland, grassland, road, human development and open water. Open water was removed for analysis because we assumed it was not available for use by fledgling golden-winged warblers. No birds used grasslands, coniferous forest or roads, which comprised 17, 5 and 1% of our total study area, respectively. We retained grassland in the analysis as a reference cover type (Aebischer *et al.*, 1993), removed coniferous forest and road for analysis, and recalculated percentages of the remaining available cover types. We used a Rayleigh V test for circular uniformity with a specified mean direction (Durand & Greenwood, 1958; Zar, 2004) and tested whether birds directed movements southward, the direction expected for commencement of migration. We report values as means \pm SE, and we considered statistical tests to be significant at $\alpha = 0.05$ level.

Fledgling movement hypotheses

Four hypothesized explanations for independent fledgling movements include (1) migration commencement; (2) habitat optimization; (3) breeding-territory prospecting; and (4) homing-target formation. We did not experimentally test any of these hypotheses, but we considered evidence for each based on our observations. First, the migration-commencement hypothesis would have been supported by fledgling movements to the south or southeast. Second, the habitat-optimization hypothesis could have been supported if fledglings selected either mature forest for greater food abundance or early-successional stands and dense shrub cover within forest for predator avoidance. The primary prey of golden-winged warblers are small, broad leaf-dwelling caterpillars most abundant in deciduous trees, and fledglings of some songbirds in this region experience lower predation in early-successional stands than in mature forest (e.g. Streby & Andersen, 2013a). Third, breeding-territory prospecting behavior is unlikely in golden-winged warblers because nearly all nesting activities are completed before the first fledgling reaches independence from adult care (H.M. Streby, pers. obs.). Finally, movements along edges of the abundant lakes or rivers in our study area could provide evidence for the homing-target formation hypothesis, similar to movements of two other migratory warblers (Mitchell *et al.*, 2010b).

Results

Movements and cover-type selection

We monitored 68 fledgling golden-winged warblers for 2–20 ($\bar{x} = 6$) days after independence from adult care. Daily

survival probability for fledglings during the observation period was 0.995 ± 0.003 . Fledglings moved 154 m (± 18 m) per day during the first 5 days after cessation of parental care (Fig. 1). They then travelled considerably greater daily distances during days 6 and 7, after which daily distances were highly variable (Fig. 1). Independent fledglings used cover types disproportionately with respect to availability ($\Lambda = 0.036$, $P < 0.01$). They selected mature forest (78% of locations) over all other cover types, used mid-successional forest, firebreaks and upland shrublands slightly less than expected based on availability, and selected against forested wetlands, wetland shrublands, grasslands and human development. We observed no birds using coniferous forest or roads. Fledglings in mature forest occupied forest canopy, shrubs and understory trees during 43, 38 and 19% of observations, respectively, and we did not observe any fledglings on the ground.

The fledglings we monitored ≥ 10 days after independence (≥ 35 days after fledging; $n = 13$) did not direct movements southward ($u_{13} = -0.442$, $P = 0.989$). Rather, despite moving in no consistent direction under parental care

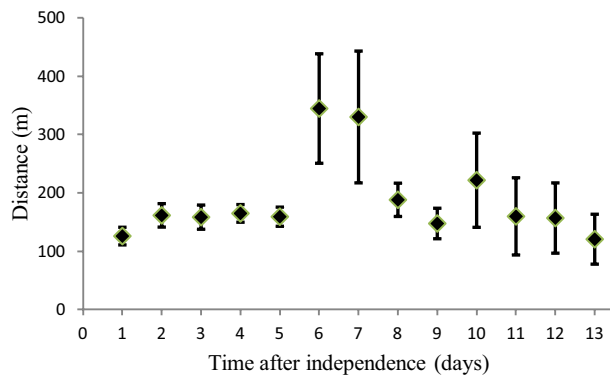


Figure 1 Minimum daily distance (mean \pm SE) travelled by fledgling golden-winged warblers after independence from adult care in Minnesota, US and Manitoba, Canada. Age is measured since day 24 after fledging (i.e. 0 = day 24) because fledglings were typically independent from adult care on day 25.

(Peterson, 2014), independent fledglings were 907 m (± 372 m) north ($u_{13} = 0.442$, $P = 0.011$) of their last location of parental care, and those with known nest locations ($n = 9$) were 1238 m (± 528 m) north ($u_9 = 0.453$, $P = 0.027$) of their nests 35 days after fledging (Fig. 2). Northward movements apparently started soon after independence because fledglings 5 days after independence (30 days after fledging; $n = 29$) were north ($u_{13} = 0.477$, $P = 0.009$) of their last location at which we observed parental care. On the last day we monitored them, four (31%) of the 13 oldest fledglings were in mature forest < 50 m from grassy wetlands, lakes or rivers, one (8%) was in a shrubby wetland and eight (61%) were in mature forest > 50 m from any apparent landscape feature that might be used for homing-target formation. Of those fledglings, only one (the one in a shrubby wetland) was in an area with vegetation structure consistent with golden-winged warbler nesting territories.

Species associations

We observed fledglings alone (i.e. no other birds observed within 10 m) during only 6% of observations. Fledglings were in mixed-species flocks of adults and fledglings (80% of observations), or with only conspecifics (14% of observations) during most observations. Flock species composition differed little among sites, with black-capped chickadee *Poecile atricapillus* (24% of observations), American redstart *Setophaga ruticilla* (19%), chestnut-sided warbler *S. pensylvanica* (19%), red-eyed vireo *olivaceus* (13%), black-and-white warbler *Mniotilta varia* (13%), ovenbird (11%) and common yellowthroat *Geothlypis trichas* (11%) present during $> 10\%$ of fledgling observations. Yellow warblers *S. petechia* were also present during 10% of fledgling observations at Tamarac NWR, our only site where that species was a common breeder. Of the species that commonly flocked with fledglings, chestnut-sided warblers, common yellowthroats and yellow warblers also nested in shrublands at our study sites. Fledglings were accompanied by adult (non-ringed, non-parent) and fledgling (non-ringed, non-sibling) conspecifics during 81% (Tamarac NWR), 44% (Rice Lake NWR) and 37% (Sandilands PF) of

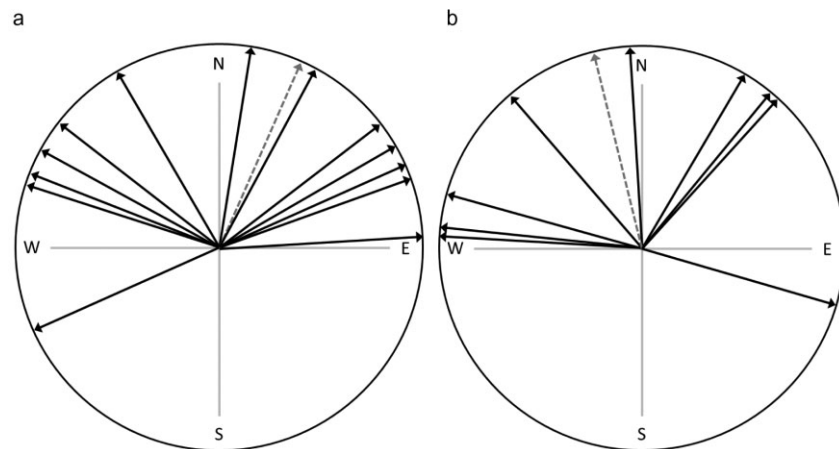


Figure 2 Directions travelled by fledgling golden-winged warblers from (a) their last location of parental care and (b) their nest of origin to their location 10 days after independence from adult care (35 days after fledging from the nest). Dotted grey lines are mean directions.

observations. Those percentages approximately reflect differences in breeding density and productivity among the sites, both of which are highest at Tamarac NWR and lowest at Sandilands PF (H.M. Streby, unpublished data).

Fledgling movement hypotheses

Fledgling movements did not indicate migration commencement, as movements were oriented north, the opposite direction of eventual migration. Fledglings selected mature forest and fledglings were foraging during most observations, supporting the food acquisition portion of the habitat-optimization hypothesis. We did not observe evidence that any fledgling occupied an active golden-winged warbler nesting territory, suggesting no support for the breeding-territory prospecting hypothesis. Although some fledglings were near wetlands on the final day we tracked them, we observed no evidence that fledglings spent multiple days moving along any apparent landscape feature that might have indicated homing-target formation. However, it is possible that fledglings formed homing targets after our observation period.

Discussion

Fledgling golden-winged warblers travelled long and variable distances each day after independence from adult care. They selected mature forest over all other cover types, and they spent relatively little time in the shrublands with which the species is generally associated during nesting. Fledglings of few migratory songbirds have been monitored beyond independence from adult care (Mitchell *et al.*, 2010a). Independent fledglings of mature forest-nesting ovenbirds selected sapling-dominated clearcuts and forested wetlands over their nesting habitat (Streby & Andersen, 2012), and independent fledglings of mature forest-nesting wood thrushes *Hylocichla mustelina* also moved into non-nesting cover types including early-successional forest and riparian forest (Anders *et al.*, 1998). In addition, independent fledglings of blackpoll warblers *S. striata* and yellow-rumped warblers *S. coronata*, both typically associated with coniferous or mixed forest during nesting, directed movements along riparian areas of river valleys (Mitchell *et al.*, 2010b). Mist-netting studies demonstrate that many other mature-forest birds use non-mature forest cover types, often shrublands and early-successional forest, later in the summer (Pagen *et al.*, 2000; Marshall *et al.*, 2003; Vitz & Rodewald, 2007; Streby *et al.*, 2011a; Streby, Peterson & Andersen, 2011b). To our knowledge, ours is the first study to demonstrate the opposite pattern in which a shrubland-nesting species selects mature forest as its primary cover type during the post-fledging period. Our anecdotal observations of adult and fledgling chestnut-sided warblers, common yellowthroats and yellow warblers in mixed-species flocks with golden-winged warblers in mature forest suggest at least some other shrubland-nesting species follow this pattern.

The use of areas with different vegetation structure during the post-fledging period compared with those used for nesting has been hypothesized to be driven by food availability, predator avoidance or both (Vitz & Rodewald, 2006). Studies investigating this mid-season habitat-association switch have focused on mature-forest birds that move into dense early- to mid-successional forest stands after nesting. Early-successional stands are described as having greater density of both vegetation and food resources including invertebrates and fruits (Vitz & Rodewald, 2006). The greater density of both cover and food in early-successional stands makes comparisons of the relative importance of predator avoidance and food availability in these stands difficult. This has resulted in incongruent conclusions about the relative importance of food and cover in habitat use by fledglings of forest-nesting songbirds that move into early-successional stands (e.g. Vitz & Rodewald, 2007; Streby *et al.*, 2011b). Our observations of the movement of golden-winged warblers from early-successional stands into less dense vegetation of mature-forest canopy, and the high survival they experienced despite occupying less dense vegetation, suggests that they choose these areas for food and not for predator avoidance. Leaf-roller caterpillars (*Archips* sp.) constitute a majority of fledgling golden-winged warbler diet (Streby *et al.*, 2014b). These lepidopteran larvae are primarily found rolled up in the leaves of deciduous trees in our study area, and golden-winged warblers use a specialized gaping behavior (i.e. prying rolled leaves open with the bill) to access them (Confer *et al.*, 2011). If mature forest birds move into early-successional forest late in the summer for the relative density of fruits and some invertebrate taxa, then perhaps those movements only appear to be associated with the dense vegetation that hosts their preferred prey. Regardless of the reason for these mid-season switches in cover-type associations, our results demonstrate that having patches of early-successional forest and mature forest adjacent to one another can have post-fledging benefits for species nesting on both sides of the forest edge.

Mature forest is also where adult golden-winged warblers do much of their foraging during the nesting season (Streby, Loegering & Andersen, 2012). Together, these findings demonstrate that the golden-winged warbler, often described as an early-successional shrubland specialist (Confer & Knapp, 1981; Confer *et al.*, 2011), in fact spends much of its time on the breeding grounds in mature forest. This may explain why the species tends only to nest in and around shrublands within otherwise primarily mature-forest landscapes (Buehler *et al.*, 2007). Although shrublands provide a crucial component of golden-winged warbler breeding habitat, this species exemplifies the risk in assuming song territories and nest locations adequately represent breeding-grounds habitat requirements for a migratory songbird.

We found no evidence that independent fledglings prospected future breeding territories (Nocera *et al.*, 2006; Betts *et al.*, 2008) or moved southward to commence migration (Rappole & Ballard, 1987). Instead, our observations support the habitat-optimization hypothesis (Rappole &

Ballard, 1987), and specifically that fledglings moved to access food resources. Similarly, fledgling blackpoll warblers, yellow-rumped warblers (Mitchell *et al.*, 2010b) and ovenbirds (Streby & Andersen, 2012) move to access local resources and not to commence migration or scout future breeding territories. Interestingly, fledgling golden-winged warblers directed their movements northward despite no apparent geographic or habitat-related feature consistently north of all fledglings. This suggests that golden-winged warblers do not seek out large landscape features for homing target formation, as might be the case in other warblers (Mitchell *et al.*, 2010b). The cover type most commonly occupied by fledgling golden-winged warblers (i.e. mature forest) was similarly available within 5 km north and south of each of our study sites (see Supporting Information Appendix S1). It is possible that the northward movements were related to, or preceded homing-target formation behavior that we did not observe. The northward movements or fledglings are consistent with the steady northward expansion of the species' range (Buehler *et al.*, 2007), but more study is needed to understand if these phenomena are related.

The high survival of independent fledgling golden-winged warblers is consistent with that of ovenbirds (Streby & Andersen, 2011, 2012; Vitz & Rodewald, 2013), worm-eating warblers *Helminthos vermivorum* (Vitz & Rodewald, 2011) and eastern meadowlarks *Sturnella magna* (Kershner, Walk & Warner, 2004). This high survival should not give the impression that habitat used by independent fledglings is less important to the species than that used for nesting or raising dependent fledglings. Migration can be a high mortality period for songbirds (Sillett & Holmes, 2002) and condition before migration can be related to future fitness (Marra, Hobson & Holmes, 1998). Therefore, even if mortality is low during this premigratory period, access to adequate habitat structure and food resources is important to long-term survival and subsequent population growth. Consequently, future studies investigating habitat requirements during this period have strong potential for improving conservation and management plans, especially when the habitat requirements prove to be considerably different from those associated with nesting.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Study sites in Minnesota (Tamarac National Wildlife Refuge and Rice Lake National Wildlife Refuge) and Manitoba (Sandilands Provincial Forest) where fledgling golden-winged warblers (*Vermivora chrysoptera*) were radio tracked after they were independent from adult care during 2010–2012.