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Movements, cover-type selection, and survival of fledgling Ovenbirds in managed deciduous and mixed coniferous-deciduous forests

Henry M. Streby [a,*], David E. Andersen [b]

[a] Minnesota Cooperative Fish and Wildlife Research Unit, Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 200 Hodson Hall, St. Paul, MN 55108, USA
[b] US Geological Survey, Minnesota Cooperative Fish and Wildlife Research Unit, 200 Hodson Hall, St. Paul, MN 55108, USA

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ABSTRACT

We used radio telemetry to monitor movements, cover-type selection, and survival for fledglings of the mature-forest nesting Ovenbird (*Seiurus aurocapilla*) at two managed forest sites in north-central Minnesota. Both sites contained forested wetlands, regenerating clearcut stands of various ages, and logging roads, but differed in mature forest composition; one deciduous with open understory, and the other mixed coniferous-deciduous with dense understory. We used compositional analysis, modified to incorporate age-specific limitations in fledgling movements, to assess cover-type selection by fledglings throughout the dependent (on adult care) post-fledging period. Compared to those that were depredated, fledglings from nests in deciduous forest that survived the early post-fledging period had more older (sapling-dominated) clearcut available, directed movements toward older clearcuts and forested wetlands, and used older clearcuts more than other cover types relative to availability. Fledglings that were depredated had more young (shrub-dominated) clearcut and unpaved logging road available, and used mature forest and roads more than expected based on availability. For birds from nests in mixed mature forest with dense understory, movements and cover-type selection were similar between fledglings that survived and those that were depredated. However, fledglings that were depredated at that site also had more young clearcut available than fledglings that survived. We conclude that Ovenbird fledgling survival is influenced by distance of their nest to various non-nesting cover types, and by the subsequent selection among those cover types, but that the influence of non-nesting cover types varies depending on the availability of dense understory vegetation in mature forest.

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1. Introduction

Compared to studies of adult songbird home-range and territory use (Vega Rivera et al., 1999; Norris and Stutchbury, 2001; Fraser and Stutchbury, 2004; Leonard et al., 2008; Streby et al., in press) studies of fledgling songbird spatial habitat use are uncommon. Studies based on point counts and mist-netting report that many species of forest-nesting songbirds use early successional (regenerating clearcut) cover types during the post-fledging period (Pagen et al., 2000; Marshall et al., 2003; Vitz and Rodewald, 2007; Streby et al., 2011a), the time between nesting and fall migration. These observations have fueled debate about the relative value of non-nesting cover types, specifically clearcuts, to populations of forest-nesting birds (Vitz and Rodewald, 2007) because clearcuts are often associated with decreased nest productivity in adjacent mature forest (e.g., Manolis et al., 2000, 2002). However,

it is not known how post-fledging use of non-nesting cover types is related to fitness, and some cover types may be used even though they are negatively related to survival (e.g., ecological traps).

Point counts and mist nets are useful for detecting cover-type use by songbirds. However, point counts during the post-fledging period rely heavily on visual detection and identification of birds because vocalizations decline after broods fledge (Bicknell, 1884). Therefore, detectability of songbirds during post-fledging point counts is likely to vary among stands that differ in vegetation density and canopy height, and comparing bird abundance among cover types is complicated when detectability is not constant (Caughley, 1977). It is also difficult to use mist nets to sample statistically comparable areas for bird use in cover types that differ greatly in canopy height, because capture rates in taller vegetation can be biased toward birds that concentrate activity near the ground. For example, it is common to sample an early successional stand with a canopy approximately 2.5-m high using standard mist nets (e.g., Vitz and Rodewald, 2007) or to sample slightly taller stands by stacking mist nets (e.g., Streby et al., 2011b). However,

to sample a statistically comparable area of mature forest with a 25-m canopy presents a serious logistical challenge (Marshall et al., 2003). Therefore, while point counts and mist nets can detect cover type use, their utility is limited for comparing relative use or selection among cover types with different vegetation structure.

Radio telemetry is a useful method for monitoring fledgling songbird movements and habitat use (Anders et al., 1998; Vega Rivera et al., 1998; Lang et al., 2002; Fink, 2003; Cohen and Lindell, 2004), and avoids the detectability issues associated with point counts and mist nets. Monitoring individual fledglings from the time they leave nests allows for analysis of cover-type selection using methods designed for radio telemetry data (e.g., compositional analysis (Aebischer et al., 1993)). However, few studies have integrated both space use and availability (e.g., Lang et al., 2002) or considered the relationship between habitat selection patterns and survival (King et al., 2006; Berkeley et al., 2007) for fledgling songbirds.

We used radio telemetry to study movements, cover-type selection, and survival for fledgling Ovenbirds (*Seiurus aurocapilla*) at two managed (for timber harvest) forested sites in north-central Minnesota. It is important to distinguish between our statistical use of the term *selection* to describe cover-types occupied by fledglings relative to cover-type availability, from the behavioral act of selection, or choosing a cover type, which is likely attributable to the adults caring for the fledglings. Ovenbirds nest on the ground nearly exclusively in mature forest (Van Horn and Donovan, 1994), but use at least some non-nesting cover types during the post-fledging period (e.g., Marshall et al., 2003; Vitz and Rodewald, 2007; Streby et al., 2011a). In our study population, fledglings from nests near older sapling-dominated clearcuts and forested wetlands experienced higher survival than those from nests near younger shrub-dominated clearcuts and roads (Streby, 2010; Streby and Andersen, 2011). Our objective was to determine if fledgling survival was associated with availability of (i.e., nesting near) or selection of non-nesting (i.e., non-mature forest) cover types. We hypothesized that fledglings would use sapling-dominated clearcuts and forested wetlands more than expected based on availability, and that both availability and subsequent selection of those cover types would be associated with increased fledgling survival. We further hypothesized that fledglings from nests near those cover types would move toward them soon after fledging and would move shorter distances than fledglings from nests farther from those cover types. Again, it is important to recognize that although we assessed movements and habitat use with respect to fledglings, and refer to cover-type selection in that manner throughout this manuscript, those choices are probably made by their parents. However, we were interested in the relationship between those choices and fledgling survival, and we monitored fledglings because it can be extremely difficult to ascertain accurate individual fledgling location and survival data by tracking adults (H.M. Streby, personal observation).

Vitz (2008) found that fledgling Ovenbirds in Ohio did not select among cover types, but used areas of relatively dense understory within mature forest. Vitz hypothesized that fledgling Ovenbirds might use regenerating clearcuts disproportionately in even-aged forest landscapes in which dense mature-forest understory is less common. Admittedly, we did not consider understory density in the selection of our two study sites, but the considerable difference in mature-forest understory density between our sites allows for a convenient test of Vitz's hypothesis. To that end, we expected that our above hypotheses about cover type selection would be supported by movements of fledglings from nests in open-understory deciduous forest, but might not be supported by movements of fledglings from nests in dense-understory mixed coniferous-deciduous forest.

2. Methods

2.1. Study area

We studied Ovenbirds at two sites in the Chippewa National Forest (CNF), Itasca County, Minnesota. The CNF is located in the transition zone from northern hardwood to northern coniferous forest, and mature-forest stands in the CNF range from entirely deciduous to entirely coniferous. Mature-forest stands at our study sites were 60–120 years old and were interspersed with lakes, marshes, forested wetlands, regenerating clearcut stands (9–15-ha even-aged stands with remnant mature oak (*Quercus* spp.), white pine (*Pinus strobus*) and occasional large snags) ranging from 2 to 20 years after harvest, and logging roads (unpaved roads ranging from open to entirely closed forest canopy cover). Our first site (hereafter: deciduous site) was located in the Suomi Hills region of the CNF, and mature-forest stands at that site were primarily open-understory stands of sugar maple (*Acer saccharum*), American basswood (*Tilia americana*), paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), big-tooth aspen (*Populus grandidentata*), and red maple (*Acer rubrum*). Our second site (hereafter: mixed site) was located in the Cutfoot Sioux region of the CNF, and mature stands at that site ranged from entirely red pine (*Pinus resinosa*) to mixed stands of approximately a 1:1 ratio of red pine to deciduous trees. Mature forest stands at the mixed site had a relatively dense and heterogeneous understory of sugar maple and hazel (*Corylus* spp.).

2.2. Radio telemetry

We monitored movements and survival of fledgling Ovenbirds from nests in mature forest at each site during the 2007–2008 breeding seasons. We searched for and monitored nests following procedures modified from Martin and Geupel (1993) in sixteen 10-ha plots that we randomly selected within mature forest stands at our sites (eight plots at each site). On the seventh day after nestlings hatched in each nest, we banded all nestlings with standard aluminum US Geological Survey leg bands, and attached radio transmitters to ⩾1 nestling in each nest. We carried all nestlings in soft cloth bags 10–15 m from the nest, weighed and banded them, attached transmitters using a figure-eight harness design (Rappole and Tipton, 1991) with elastic leg loops to allow for growth, and returned all nestlings to their nest within 15 min of removal. The 0.67-g transmitters were 4.3–4.9% of nestling mass at time of attachment, and we observed no apparent impacts of transmitters on fledgling activities relative to occasionally observed unmarked siblings.

We used radio telemetry to monitor fledglings following procedures modified from Anders et al. (1998). We relocated fledglings daily from 12 June (first fledged) to 11 August (last transmitter expiration) via ground-based telemetry. We first used triangulation to estimate the location of each fledgling, and then attained visual confirmation of survival or mortality by approaching estimated locations on foot. When fledglings moved beyond the range of ground-based telemetry, either under their own power or by that of a wide-ranging predator (see Streby and Andersen, 2011), we relocated them from the air using standard aerial telemetry procedures (Mech, 1983). We recorded each nest and fledgling location with a handheld global positioning system (GPS) unit (100 points averaged, estimated error <10 m) and noted the cover type of the occupied location. We measured distances from nests to non-nesting cover types and measured minimum daily distances travelled by fledglings (i.e., straight-line distance between subsequent daily locations) in ArcGIS 9.2 (ESRI; use of trade names does not imply endorsement by either the US Geological Survey or the University of Minnesota).

2.3. Cover-type classification and delineation

We used aerial photographs and cover-type layers (US Forest Service Chippewa National Forest 2007) for each study site in a GIS, and edited polygons and descriptive attributes of cover types within our study sites based on extensive ground-truthing (i.e., we visited >1000 locations throughout our study sites and confirmed or adjusted cover-type classification and delineation). We reclassified all cover types into five classes: (1) mature forest, (2) young clearcut, (3) older clearcut, (4) forested wetland, (5) road, and (6) lake. We classified upland cover types as mature forest (stands ⩾ 50 years after harvest), young clearcut (successional stands ⩽6 years after harvest, composed primarily of dense shrub cover), and older clearcut (successional stands 7–20 years after harvest, composed primarily of sapling aspen). We classified tamarack bogs and all ephemerally wet forested stands as forested wetland. We classified all open water and permanently wet open areas as lake. We did not include lake in analyses because open water was not used by fledgling Ovenbirds and is presumably not available to them. Excluding lake, and depending on the position of arbitrarily delineated site boundaries, our deciduous site comprised approximately 69% mature forest, 17% older clearcut, 7% young clearcut, 5% forested wetland, and 2% road, and our mixed site comprised approximately 58% mature forest, 27% forested wetland, 8% older clearcut, 6% young clearcut, and 1% road.

2.4. Cover-type selection

We compared cover-type availability among groups and availability to use within groups using COMPANA (compositional analysis) in the ADEHABITAT package (Calenge, 2006) in Program R (Version 2.11.1, R Development Core Team). Compositional analysis can be used to compare proportions of space available with proportions of space used by radio-tracked animals (Aebischer et al., 1993). However, spatial habitat selection analyses, including the method proposed by Aebischer et al. (1993), are intended for studies of animals for which entire study areas constitute available space and an entire home range is available for use by an animal at all times. However that is not always the case when juvenile animals are being considered. Martin et al. (2008) demonstrated that spatial habitat selection that appeared to be different between two female black bears (Ursus americanus) – one with a dependent cub, and one lone bear – were not different when considerations were made for differences in movement capability associated with the dependent cub. Common assumptions about space availability are also not valid for fledgling songbirds, for which movement capability is limited and increases throughout development. First, the assumption that a home range is selected from all space within a study area is not valid for fledglings, because there is certainly space within a study area that is not available to a fledgling early in the post-fledging period but becomes available as the fledging ages and movement capability increases. For the same reason, a home range, defined as the "area repeatedly traversed by an animal during a specified time period," (Kenward, 2001, p. 208) is not applicable to space used by dependent fledgling songbirds. The area derived from daily locations of a fledgling songbird throughout the dependent post-fledging period (from nest to independence) is almost certain to include space that was not available to the bird early in that period, and therefore should not be considered available, and probably should not be called a home range. In either case, considering space to be available when it actually is not will potentially bias spatial habitat selection results toward the selection of areas relatively close to nests. For songbirds that nest exclusively in one cover type, fledgling habitat selection results may thus be biased toward the nesting cover type. Therefore, modified methods are needed for estimating available space for animals with limited and variable movement capability so that compositional analysis, or other analyses, can be appropriately applied. Here, we develop such a method for analyzing space use by fledgling songbirds.

2.5. Cover-type daily estimated availability

To analyze cover-type selection (use relative to availability) by fledgling Ovenbirds, we first needed to determine the space accessible, and therefore available to fledglings, and how that space changes over time. Because it is unlikely that fledglings move in straight lines from one daily location to the next, minimum daily distance between locations on successive days does not accurately reflect movement capability. Therefore, we used the frequency distribution of minimum daily distances (grouped by 10-m intervals) for all fledglings of similar age (i.e., days after fledging) to estimate maximum movement capability for fledglings of each age (Fig. 1). We fit a quadratic regression curve to the frequency distribution of minimum daily distance traveled from day t to day $t + 1$, and used the right intercept of that curve and the x-axis as our estimate of age-specific maximum daily movement capability (rounded up to the nearest 10 m). If the regression curve crossed the x-axis at a distance lower than the greatest minimum daily distance traveled by a fledgling, we instead used that greatest minimum daily distance as the estimated maximum movement capability. We repeated this analysis to estimate maximum movement capability for fledglings of each age from 0 to 24 days after fledge (Fig. 2). This method assumes that all fledglings of similar age are capable of traveling a similar distance. Another possible method for estimating maximum movement capability is the bounded-count
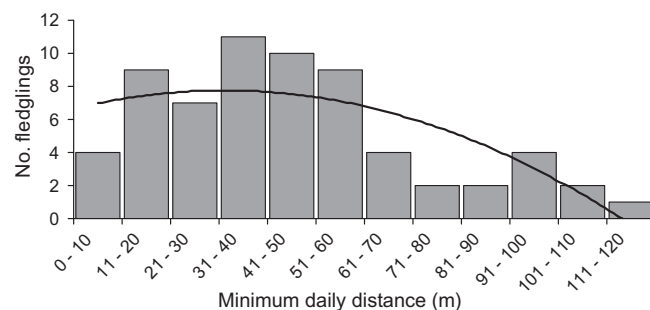
Fig. 1. Minimum distances traveled by fledgling Ovenbirds within 1 day of fledging in the Chippewa National Forest, Minnesota. We estimated the maximum daily movement capability of day-zero (fledge day) fledglings as the intercept between the regression curve and the x-axis, rounded up to the nearest 10 m (120 m in this case). We repeated this analysis for each fledgling age, 0–24 days after fledging.
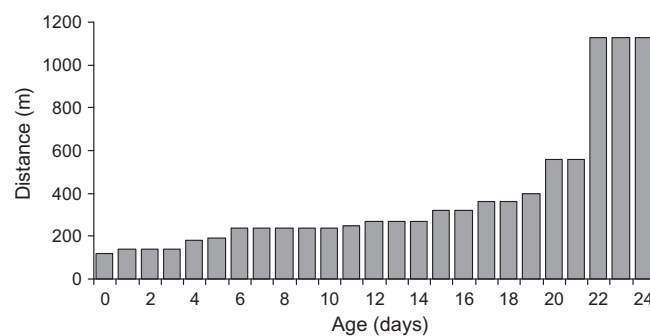
Fig. 2. Age-specific maximum daily movement capability for fledgling Ovenbirds, derived by repeating the analysis from Fig. 1 for fledglings aged 0–24 days after fledging in the Chippewa National Forest, Minnesota.

estimator, or two times the highest value minus the second-highest value (Johnson et al., 2007). A linear regression of the results from our quadratic method with those from the bounded-count estimator indicated that the two methods produced nearly identical estimates ($r^2 = 0.99$, $F_{1,24} = 2381.14$, $P < 0.01$) for our dataset.

Using GIS software, we overlaid nest and fledgling locations onto the cover-type layer. We used our estimates of age-specific maximum daily movement capability as radii for circles (GIS buffers) of daily estimated availability (DEA) of space around each fledgling location. The DEA circle for age zero was drawn around the nest, and DEA circles for subsequent ages were drawn around subsequent fledgling locations (Fig. 3). We then measured the area of each cover type within each DEA circle, and calculated proportions of available cover types. We assumed that lake was not available for use by fledgling Ovenbirds. Therefore, we removed lake contained within any DEA circle, and recalculated proportions for the remaining available cover types. For each fledgling, we calculated the proportional availability of each cover type for the entire post-fledging period as the mean of all daily proportional availabilities. We thereby standardized cover type availability by age-specific movement capability.
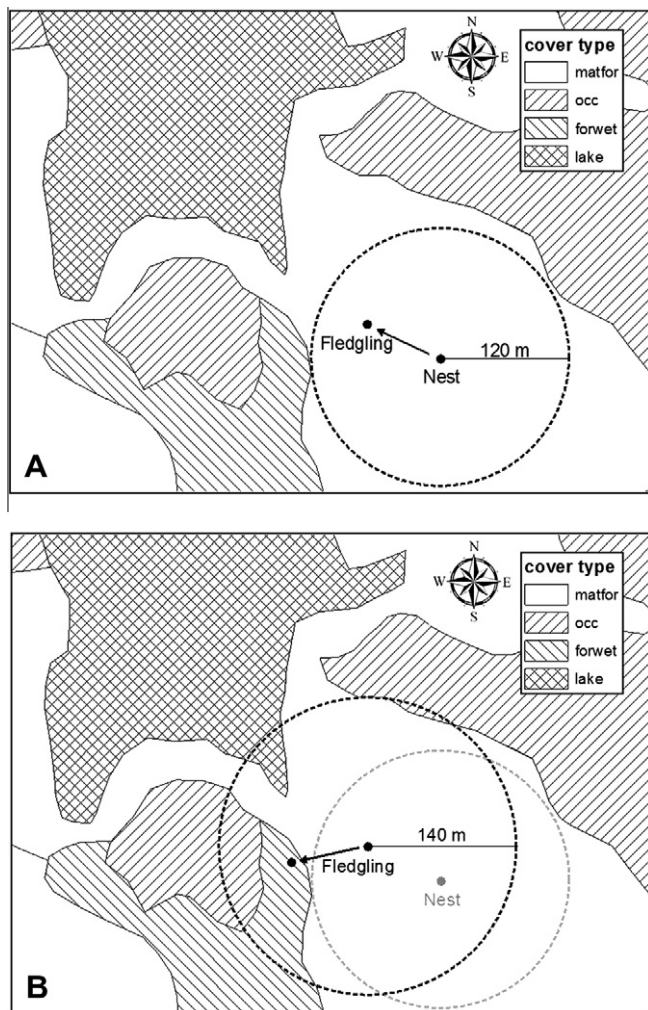
Fig. 3. An example of daily estimated availability (DEA) for a fledgling Ovenbird (first 2 days off of nest) in the Chippewa National Forest, Minnesota. Mature forest (matfor) comprised 100% of available space for this fledgling for day 1 (A). Mature forest, 7–20 year-old clearcut (occ), forested wetland (forwet), and lake were within the DEA circle for day 2 (B). This process was repeated for each location during the 24-day dependent post-fledging period. Lake was removed for analysis based on the assumption that it is not available to fledgling Ovenbirds.

We analyzed cover-type selection separately for the two study sites because of differences between sites in understory vegetation density of mature forest stands. The understory of the mature forest stands at the mixed site had large areas of dense hazel and sugar maple that were not present at the deciduous site. To quantify this difference, we estimated understory vegetation density at 50 randomly selected points within mature forest stands at each site using a profile board method modified from MacArthur and Mac-Arthur (1961). We used a 2 m × 0.25 m board divided into eight squares to measure the density of vegetation at successive 25-cm intervals ranging from ground level to 2 m above ground. We viewed the board from 10 m in a computer-generated random direction and estimated the percent of each square obscured by vegetation. We then turned the board 90 degrees and repeated the procedure from a second direction. We used the mean of the 16 cover estimates as the estimate of understory vegetation density at each point.

2.6. Statistical analysis

For cover-type selection analysis, we randomly chose one fledgling from each nest for which we tracked multiple siblings to avoid pseudoreplication. Which bird we chose had very little influence on results because we marked >1 sibling in only 10% ($n = 6$) of broods included in analysis and siblings occupied the same cover type on 84% of days tracked. We excluded fledglings that were depredated within 24 h of fledging from cover-type selection analysis because we had no data about cover-type use for those animals. To investigate the relationship between cover type selection and survival, we analyzed cover type selection separately for fledglings that survived through the dependent post-fledging period (24 days) and for fledglings that were depredated during that period. For each fledgling group (survived or depredated) we used compositional analysis and ranked cover types from most used to least used relative to availability and reported statistically significant (i.e., $P < 0.05$) differences in among-cover-type selection (Λ; Aebischer et al., 1993). We also used compositional analysis to compare cover-type availability between fledglings that survived and fledglings that were depredated to investigate whether fledgling survival was associated with nest location relative to non-nesting cover types. For the comparison of availability, we randomly removed either depredated or surviving fledglings from the sample to achieve balanced sample size for compositional analysis. We limited our comparisons of availability to the first eight post-fledging days because we were most interested in differences in cover-type availability associated with nest location and early movements.

We tested whether survival was similar among cover types using a χ^2 test of independence on the number of mortalities and number of daily fledgling location in each cover type. For each site we compared distance and direction of initial post-fledging movements (i.e., distances traveled from nest in the first 4 days) between fledglings from nests ⩽100 m from non-nesting cover types associated with higher survival and fledglings from nests >100 m from those cover types. We chose 100 m because that was the apparent distance between nests and edges within which fledgling survival was associated with non-nesting cover types (Streby and Andersen, 2011). We compared distances traveled from nests using a 2-tailed *t*-test for unequal samples. We tested for directional orientation of fledgling movements using Rayleigh tests for circular uniformity with a specified mean direction (Durand and Greenwood, 1958). For that analysis, we standardized the specified mean direction among fledglings by converting to North (0°) the direction from each nest to the nearest non-nesting cover type associated with higher survival. We compared understory vegetation density between the two study sites with a 2-tailed

Student's t-test. All tests were considered significant at the $\alpha = 0.05$ level.

3. Results

3.1. Fledgling survival

We attached transmitters to 109 fledglings from 91 successful Ovenbird nests. After we randomly selected one fledgling from each brood with >1 radio-marked fledgling, removed birds from analysis that slipped out of their harness or were depredated within 1 day of fledging ($n = 23$) and birds that died associated with blow fly infection ($n = 8$; Streby et al., 2009) or of apparent starvation due to a Brown-headed Cowbird brood mate ($n = 1$; Peterson et al., 2012), 62 fledglings from 62 nests remained for analysis (31 from each site). Of the 31 fledglings monitored at the deciduous site, 15 survived to independence and 16 were depredated during the dependent post-fledging period. Of the 31 fledglings monitored at the mixed site, 14 survived to independence and 17 were depredated during the same period.

Fledgling survival was different among cover types ($\chi_4^2 = 43.45$, $P < 0.01$). There were no mortalities associated with 106 fledgling locations in older clearcuts and only one mortality associated with 53 fledgling locations in forested wetlands. Mature forest hosted slightly lower survival, with 18 mortalities in 699 fledgling locations, while use and survival of young clearcuts (one mortality in five locations) and roads (three mortalities in six locations) were both very low. Among non-nesting cover types, we therefore considered older clearcuts and forested wetlands to be associated with higher survival, and the young clearcuts and roads to be associated with lower survival in analysis of direction and distance of early fledgling movements.

3.2. Cover-type selection

Mature forest understory was denser ($t_{98} = 2.44$, $P = 0.02$) at the mixed site ($\bar{x} = 48.9\%$) than at the deciduous site ($\bar{x} = 39.7\%$), as expected. Heterogeneity in mature forest understory density was also greater at the mixed site ($V = 0.76$) than at the deciduous site ($V = 0.57$), reflecting patchy areas of very dense understory. Based on that confirmation of our presumption about differences in understory vegetation density and heterogeneity, we proceeded by conducting analyses separately for each site.

At the deciduous site, there were different proportions of cover types available to birds that survived than to those that were depredated ($\Lambda = 0.08$, $P < 0.01$). Birds that survived had more older clearcut available, whereas birds that were depredated had more young clearcut and road available. Fledglings that survived the post-fledging period at the deciduous site selected ($\Lambda = 0.05$, $P < 0.01$) older clearcut and mature forest significantly more than forested wetland and road, and selected against young clearcut relative to all other cover types. Depredated fledglings at the deciduous site selected ($\Lambda = 0.11$, $P < 0.01$) mature forest and road more than older clearcut and forested wetland, and selected against young clearcut relative to all cover types except forested wetland.

At the mixed site, there were different proportions of cover types available to birds that survived than to those that were depredated ($\Lambda = 0.07$, $P < 0.01$). Birds that were depredated had more young clearcut available, whereas birds that survived had more of all other cover types available. Fledglings that survived the post-fledging period at the mixed site selected ($\Lambda = 0.03$, $P < 0.01$) mature forest significantly more than all other cover types, which they used relative to availability (although statistically similarly) in the order: older clearcut > forested wetland > young clearcut > road. Depredated fledglings at the mixed

site also selected ($\Lambda = 0.05$, $P < 0.01$) mature forest more than all other cover types, which they used relative to availability (although statistically similarly) in the order: road > older clearcut > forested wetland > young clearcut.

3.3. Direction and distance of initial fledgling movements

At the deciduous site, fledglings from nests $\leqslant 100$ m from non-nesting cover types associated with higher survival moved shorter distances from nests in the early post-fledging period than did fledglings from nests >100 m from those cover types ($t_{24} = 3.11$, $P < 0.01$; Fig. 4). Regardless of nest location at the deciduous site, fledglings moved toward the nearest non-nesting cover type associated with higher survival: fledglings from nests $\leqslant 100$ m from a higher-survival cover type moved toward them ($u_{11} = 2.91$, $P < 0.01$), and so did fledglings from nests >100 m from a higher-survival cover type ($u_7 = 3.57$, $P < 0.01$).

At the mixed site, fledglings from nests $\leqslant 100$ m from non-nesting cover types associated with higher survival moved similar distances to those from nests >100 m from those cover types ($t_{16} = 1.38$, $P < 0.18$; Fig. 4). Fledglings did not consistently move toward the nearest higher-survival non-nesting cover type at the mixed site: fledglings from nests $\leqslant 100$ m from a higher-survival cover type did not move toward them ($u_{0.05,8} = 0.79$, $P = 0.22$) and neither did fledglings from nests >100 m from a higher-survival cover type ($u_{0.05,18} = 0.33$, $P < 0.50$).
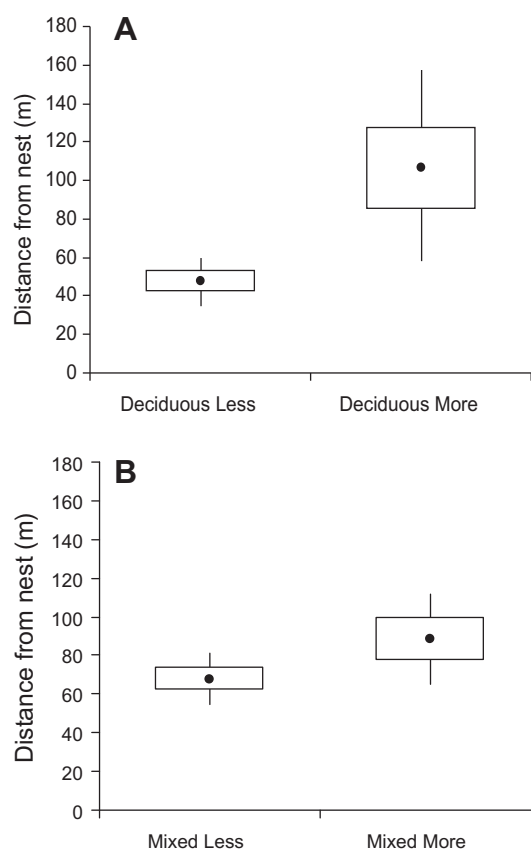
Fig. 4. Distance traveled from nests by fledgling Ovenbirds 4 days (period of highest mortality) after fledging. Distances are compared between fledglings from nests $\leqslant 100$ m from (less), and nests >100 m from (more), cover-types associated with higher survival (i.e., clearcuts 7–20 year since harvest and forested wetlands at (A) a deciduous mature forest site with open understory, and (B) a mixed coniferous-deciduous mature forest site with dense understory in the Chippewa National Forest, Minnesota. Values are reported as mean, SE, and 95% CI. Differences are in the same direction, but statistically significant at only the deciduous forest site.

4. Discussion

Fledgling Ovenbirds in north-central Minnesota used all available cover types during the dependent post-fledging period, and they used those cover types non-randomly. Fledglings used mature forest as much as or more than each non-nesting cover type relative to availability. However, some non-nesting cover types were selected more than others at both sites, and that pattern differed between fledglings that survived and those that were depredated at the deciduous site. Fledgling Ovenbird survival in older clearcuts and forested wetlands was high, whereas survival in young clearcuts and on roads was low. Whether fledglings used non-nesting cover types seemed to be influenced by the availability of dense areas of understory vegetation within mature forest, the only apparent difference in vegetation structure between our study sites. These observations support the hypothesis of Vitz (2008) that fledglings of forest nesting birds might use non-nesting cover types more often when dense understory vegetation is not available in mature forest. Fledgling movements at the deciduous site were toward cover types associated with higher survival, and distances moved differed depending on proximity of nests to those cover types. However, distance and direction of fledgling movements at the mixed site were independent of distance to non-nesting cover types. We observed differences in availability of cover types between surviving and depredated fledgling Ovenbirds. At both study sites, depredated fledglings had more young, shrub-dominated clearcut available than did surviving fledglings in the early post-fledging period, suggesting that nesting near young clearcuts increased the probability of fledgling predation. Conversely, surviving fledglings at the deciduous site had higher older clearcut availability than did depredated fledglings, suggesting that nesting near older, sapling-dominated clearcuts increased the probability of fledgling survival when dense mature forest understory was unavailable.

In addition to differences in cover type availability, there were differences in cover type selection between surviving and depredated fledglings. Not only did surviving fledglings at the deciduous site have higher availability of older clearcut, but they also used that cover type at more than others relative to availability. However, those differences in older clearcut availability and selection were not apparent at the mixed site. The difference in understory vegetation density between study sites may explain the difference in cover-type selection. Based on cover-type-specific survival rates, it is likely that adult birds take fledglings into older clearcuts and forested wetlands to reduce exposure to predation. These results suggest that although forest-nesting birds choose areas within non-nesting cover types based primarily on food availability (Streby et al., 2011b), predator avoidance in the relatively dense vegetation may be the reason birds are initially drawn to these stands. Presumably, the higher vegetation density of those cover types provides increased cover for fledglings compared to the relatively open mature-forest understory. However, where dense and heterogeneous understory is available (e.g., our mixed site), that understory vegetation is apparently used similarly to older clearcuts and forested wetlands. These results suggests that birds choosing territories and nest sites are likely considering post-fledging habitat when making those choices (Refsnider and Janzen, 2010; Streby and Andersen, 2011).

It is important to consider how fledgling movement and space use choices are made. Individual fledglings probably choose specific cover objects or perches, and those choices likely influence survival to some degree (King et al., 2006). However, at larger scales, as in the current study, fledgling space use is largely dependent on choices made by adults, especially early in the post-fledging period. Studies of fledgling movement patterns suggest that adult songbirds may have two movement strategies for rearing broods. Birds that rear their young within presumed nesting territories are described as following a stationary strategy, while birds that move their young from the natal territory are following a drifting strategy (Anders et al., 1998; White and Faaborg, 2008). Birds following the drifting strategy have been reported as moving significantly farther from nests than birds following the stationary strategy (White and Faaborg, 2008). However, that is circular reasoning, because a statistical difference in distance traveled between two groups is meaningless when the groups are first classified based on distance traveled. It is more appropriate to group birds based on an *a priori* ecologically based hypothesis, and then test for movement differences between groups. The same is true for directional orientation of fledgling movements. In our study, fledglings did not move in any distinct compass direction at either site, but movements were toward cover types in which fledgling survival was highest. This observation is consistent with that of Mitchell et al. (2010) who reported movements of independent (from adult care) juvenile Yellow-rumped Warblers (*Setophaga coronata*) and Blackpoll Warblers (*Setophaga sriata*) are more consistent with landscape composition than to any particular compass direction (discussed further in McNair and Nisbet, 2011 and Mitchell et al., 2011).

Proposed explanations for brood movement patterns include whether adults attempt a subsequent brood (Vega Rivera et al., 2000) and whether the birds occupy landscapes fragmented by undesirable cover types (Fink, 2003). There may also be differences in movements between adult males and females when broods are split (Vega Rivera et al., 2000). Our results demonstrate that proximity of nests to brood-rearing areas associated with higher fledgling survival can influence both distance and direction of fledgling movements during the early post-fledging period. Therefore, birds with nesting territories that include, or are adjacent to, brood-rearing areas associated with higher fledgling survival (which can be non-nesting cover types) may move shorter distances than birds nesting farther from those areas. This hypothesis is supported by observations that dickcissel (*Spiza amaricana*) fledgling survival is significantly correlated with high density of forbs at the nest site (Berkeley et al., 2007), Swainson's thrush (*Catharus ustulatus*) fledglings use dense thickets near nests within 1–2 days of fledging (White and Faaborg, 2008), and white-throated robins (*Turdus assimilis*) move more quickly from pasture into forest than from coffee plantation into forest, presumably due to a lack of cover in pastures (Cohen and Lindell, 2004). In addition, White and Faaborg (2008) reported that some Swainson's thrush broods were led by adults to areas of abundant fruit, suggesting that food availability, in addition to cover, may be an important factor in brood-rearing habitat selection. If future studies continue to explore relationships between spatial habitat-use patterns and fledgling survival, rather than separating the two, they will provide more useful information about habitat requirements and population responses to management actions and better inform management decisions.

A common criticism of habitat selection studies using individual locations of animals is that locations are likely serially autocorrelated, or not statistically independent (De Solla et al., 1999). However, autocorrelation in animal movement studies is not undesirable (De Solla et al., 1999; Martin et al., 2008). In fact, the inherent autocorrelation in such studies contains ecologically important information that should be integrated, not removed (Martin et al., 2008). For example, the concept of a home range not only includes, but requires, autocorrelation of locations within a landscape (De Solla et al., 1999). Locations of fledgling songbirds, for which movement capability is low (compared to adults) and increases with age, are potentially highly autocorrelated. Our analysis implicitly assumes autocorrelation of fledgling locations, and

integrates that autocorrelation by allowing availability to vary with each daily location and with age-specific fledgling movement capability. A second common criticism of habitat selection studies is that estimates of availability are often defined by arbitrary study area or legal boundaries (Cooper and Millspaugh, 1999). Available space should be defined using biological knowledge and information about the movement capability of the studied animals (Martin et al., 2008). Our method also accounts for that issue by standardizing availability by age-specific movement capability.

4.1. Management implications

The difference in movements and cover type selection between our study sites seems to be associated with the relative availability of dense understory vegetation in mature forest. Our results suggest that areas of dense understory are important to mature-forest songbirds, but that sapling-dominated successional forest stands can provide similar habitat in landscapes with open-understory mature forest. A key difference between surviving and depredated fledglings at both sites was the relative use of roads. Roads at our sites were unpaved logging roads under open to entirely closed forest canopy. Roads ranked last (mixed site) and second-to-last (deciduous site) in cover-type selection by fledglings that survived, but ranked second in relative use by depredated fledglings at both sites. Roads were the least available cover type to all fledglings, and we observed only six fledglings on roads and six others in dense vegetation alongside roads within forest. However, of those 12 fledglings, four were tracked to hawk nests the following day. Therefore, although roads were a relatively rare landscape feature (<2% of available space), they were associated with 17% of fledgling mortality. Additionally, in a separate analysis we found that fledglings that crossed at least one road within the first 8 days after fledging were 50% less likely to survive than fledglings that did not cross roads (Streby, 2010). Throughout our study, we regularly observed Broad-winged Hawks (*Buteo platypterus*), Cooper's Hawks (*Accipiter cooperii*) and Sharp-shinned Hawks (*Accipiter striatus*) coursing roads, and we commonly observed plucked feathers of passerines, woodpeckers (Picidae), and Ruffed Grouse (*Bonasa umbellus*) on those roads. Our results and observations suggest that logging roads provide an area of unusually high mortality for ground-dwelling birds. Indeed, in a current study of American Woodcock (*Scolopax minor*) chick survival in Minnesota, predation appears common along unpaved roads and trails (K. Daly, personal communication). Road removal is sometimes used to reduce the ecological and hydrological impacts of the nearly 900,000 km of roads fragmenting US federal lands (Switalski et al., 2004). Our results suggest that in addition to the intended goals of road removal, the process might positively impact populations of ground-dwelling forest birds by reducing the prevalence of a landscape feature associated with high juvenile mortality.

Acknowledgements

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