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SURVIVAL OF FLEDGLING OVENBIRDS: INFLUENCES OF HABITAT CHARACTERISTICS AT MULTIPLE SPATIAL SCALES

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Abstract. Survival of fledgling songbirds can be influenced by habitat characteristics at multiple spatial scales, and identifying the relative influence of habitat characteristics at the micro (immediately surrounding fledglings) and meso (level of stand or cover type) scales is important for management and conservation planning. We modeled survival of fledgling Ovenbirds (*Seiurus aurocapilla*) in managed forest in north-central Minnesota by using micro-scale and meso-scale habitat characteristics and nestlings' mass as explanatory variables. Meso-scale variables (e.g., use of logging roads and distance to cover types other than those used for nesting) better explained fledgling Ovenbirds' survival than did nestlings' mass or micro-scale variables, including ground cover, litter depth, vegetation density, and food availability. Crossing of logging roads had the strongest relationship with survival of fledgling Ovenbirds: survival of fledglings that crossed roads was 50% lower during the first 8 days after fledging and 33% lower 9–16 days after fledging than that of fledglings that did not cross roads. We conclude that although micro-scale habitat characteristics can influence fledgling Ovenbirds' survival, meso-scale characteristics have a much stronger effect. We believe nestlings' mass had little influence on survival because mass may be a poor indicator of body condition, and regardless of condition most predation occurs before fledglings are capable of eluding predators. Because of the association between logging roads and fledglings' reduced survival, we suggest that reclamation of abandoned logging roads, a process underway on many federal lands, could have a positive effect on populations of ground-dwelling forest birds in managed forests.

Key words: fledgling, habitat, management, Seiurus aurocapilla, *songbird, survival*.

Supervivencia de Volantones de *Seiurus aurocapilla*: Influencia de las Características del Hábitat a Múltiples Escalas Espaciales

Resumen. La supervivencia de los volantones de las aves canoras puede estar influenciada por las características del hábitat a múltiples escalas espaciales, e identificar la influencia relativa de las características del hábitat a las escalas micro (alrededor de los volantones) y meso (a nivel de rodal o tipo de cobertura) es importante para la gestión de manejo y conservación. Modelamos la supervivencia de los volantones de *Seiurus aurocapilla* en bosques manejados en el centro y norte de Minnesota usando las características del hábitat a la micro y la meso escala y la masa del pichón como variables exploratorias. Las variables de la meso escala (e.g., uso de caminos madereros y distancia a los tipos de cobertura distintos de los usados para anidar) explicaron la supervivencia de los volantones de *S. aurocapilla* mejor que la masa de los pichones o las variables de la micro escala, incluyendo la cobertura del suelo, la profundidad de la hojarasca, la densidad de la vegetación y la disponibilidad de alimentos. El cruce de caminos madereros presentó la relación más fuerte con la supervivencia de los volantones de *S. aurocapilla*: la supervivencia de los volantones que atravesaron caminos fue 50% más baja durante los primeros ocho días luego del emplumamiento y 33% más baja 9–16 días luego del emplumamiento que la de los volantones que no cruzaron caminos. Concluimos que aunque las características del hábitat de la micro escala pueden influenciar la supervivencia de los volantones de *S. aurocapilla*, las características de la meso escala tienen un efecto mucho mayor. Creemos que la masa de los pichones tiene poca influencia en la supervivencia debido a que la masa sería un indicador mediocre de la condición corporal, e independientemente de la condición, la mayoría de la depredación se presenta antes de que los volantones sean capaces de eludir a los depredadores. Debido a la asociación entre los caminos madereros y la supervivencia reducida de los volantones, sugerimos que la recuperación de los caminos madereros abandonados, un proceso en marcha en muchos bosques federales, podría tener un efecto positivo en las poblaciones de aves que viven a nivel del suelo en los bosques manejados.

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INTRODUCTION

Many species of songbirds that breed in North America have experienced apparent long-term population declines (Peterjohn and Sauer 1994), highlighting the importance of demographic studies that focus on identifying the factors that influence population dynamics. For most songbirds, nest success remains the most commonly estimated measure of reproductive output, and mapping of breeding territories often provides the only information available about a species' habitat associations. However, studies of fledglings' survival and habitat use can improve estimates of reproductive success (Anders et al. 1997, Streby and Andersen 2011), characterizations of species' habitat relationships (King et al. 2006), and estimates of rates of songbirds' population growth (Streby and Andersen 2011).

Although several studies have demonstrated that for many songbirds habitat use during the post-fledging period differs from that during nesting (e.g., Anders et al. 1998, Pagen et al. 2000, Marshall et al. 2003), few studies have directly related habitat characteristics to fledglings' survival. King et al. (2006) found that fledgling Ovenbirds (*Seiurus aurocapilla*) used areas with denser vegetation more than those with sparser vegetation and that fledglings' survival increased with density of vegetation used. Despite sometimes lower nest success near edges of early-successional habitat (Manolis et al. 2002), which can be at least partly offset by larger clutch sizes (Flaspohler et al. 2001), Ovenbirds may continue to nest near regenerating clearcuts to facilitate their common use of those stands after fledging (Streby et al. 2011). Vitz and Rodewald (2011) also found a relationship between survival of fledgling Ovenbirds and density of vegetation used, but they reported that fledglings' relative condition was a better predictor of their survival. At a the scale of a stand of forest, survival of fledgling Ovenbirds is relatively low in or near recent clearcuts and along logging roads, moderate in core mature forest, and relatively high in or near forested wetlands and mid-successional stands dominated by saplings (Streby 2010). However, these studies have typically only investigated one of those two scales: either the micro scale, at which habitat characteristics (e.g., litter depth, food availability, vegetation density, and ground cover) are sampled within a few meters of fledglings' locations, or the meso scale, at which habitat characteristics are measured at the level of the forest stand (e.g., cover type, patch size, and distance to edge). Despite the importance of understanding fledgings' habitat associations at multiple spatial scales (Mitchell et al. 2010), to our knowledge, no study has compared the relative influence of habitat characteristics at multiple scales on fledgling songbirds' survival.

For habitat management to enhance population growth, it is necessary to understand which habitat characteristics most strongly affect survival and productivity. Our objective was to determine the relative importance of micro- and meso-scale habitat characteristics on survival of fledgling Ovenbirds (Table 1). Ovenbirds nest in mature forest but commonly use other types of cover after fledging (e.g., Marshall et al. 2003, Vitz and Rodewald 2006, Streby et al. 2011). Fledgling songbirds are most vulnerable to predation in the few days immediately after leaving the nest (Ricklefs 1968, Anders et al. 1997, Berkeley et al. 2007), and fledgling Ovenbirds are primarily dependent on food collected by adults elsewhere (often >100 m away) and brought to the fledglings (H. M. Streby, pers. obs.). Therefore, among micro-scale variables, we expected food availability to have little influence on fledglings' survival but ground cover and lateral cover by understory vegetation to be positively related to survival of the young soon after fledging. We expected food availability to increase in relative importance as older fledglings started to feed themselves and may have required less

TABLE 1. Relative importance of variables for explaining survival of fledgling Ovenbirds during the first 16 days after fledging in managed forests of north-central Minnesota. Relative is quantified as the cumulative Akaike weight (*w*) of all models including each variable (each variable was included in five candidate models).

Variable	Definition	*w* (days 1–8)	*w* (days 9–16)
Meso scale	Variables measured at the stand level		
RDX	Road crossing: whether the fledgling crossed a logging road	0.85	0.57
DLSC	Distance to cover type associated with low fledgling survival	0.40	0.24
DHSC	Distance to cover type associated with high fledging survival	0.30	0.32
Micro scale	Variables measured at specific locations of fledglings		
LITDEP	Litter depth	0.09	0.09
LATCOV	Lateral cover or vegetation density	0.09	0.16
GVEG	Percent ground cover by vegetation	0.09	0.09
GWOOD	Percent ground cover by woody debris	0.04	0.05
LITINV	Invertebrate abundance in ground litter	0.03	0.08
PITINV	Invertebrate activity sampled using pitfall trap	0.03	0.04
Condition	Index of relative fledgling condition		
NMASS	Mass of nestling at time of transmitter attachment	0.06	0.06

concealment. However, most mortality of fledgling songbirds is from predation and not starvation (Sullivan 1989, Anders et al. 1997, Cohen and Lindell 2004, King et al. 2006, Streby and Andersen 2011), and densities of mammalian and avian predators vary at spatial scales broader than a fledgling's specific location, suggesting that predation might be more strongly associated with meso-scale habitat characteristics regardless of a fledgling's age. Furthermore, an individual's condition can have a larger influence than micro-scale habitat characteristics on survival of fledgling Ovenbirds (Vitz and Rodewald 2011). Therefore, we expected meso-scale habitat characteristics and nestling condition to explain fledgling survival better than micro-scale habitat characteristics.

METHODS

STUDY AREA

We studied fledgling Ovenbirds at two sites in north-central Minnesota in the Chippewa National Forest, which is located in the transition zone from northern hardwood to northern conifer forest. It is actively managed for improvement of forest ecosystems and water quality and for sustainable timber harvest and recreation. Both study sites, separated by 25 km and encompassing ~4 km^2 each, were characterized by extensive mature forest interspersed with forested wetlands, tamarack (*Larix laricina*) bogs, lakes, and regenerating clearcuts ranging from 2 to 20 years since harvest. In the study area, Ovenbirds nest in mature forest consisting primarily of sugar maple (*Acer saccharum*), American basswood (*Tilia americana*), red pine (*Pinus resinosa*), paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), big-tooth aspen (*P. grandidentata*), and red maple (*A. rubrum*), with a patchy understory of sugar maple, red maple, and hazel (*Corylus* spp.).

NEST MONITORING AND RADIO TELEMETRY

We used radio telemetry to monitor the habitat use and survival of fledgling Ovenbirds from nests we monitored during the breeding seasons of 2007 and 2008. We searched for and located nests in 16 10-ha plots around points we randomly selected in a geographical information system (GIS) within stands of mature forest. Of these plots, 12 were adjacent to one or two regenerating clearcuts and extended 250–510 m from the clearcuts' edges, four were >250 m from a clearcut, and eight of the plots were adjacent to at least one other such plot. We monitored nests at 4-day intervals and made more frequent visits during egg laying and days of expected hatching to help predict the date of fledging. We took different paths to and from nests during subsequent visits, and we sometimes (~10% of observations) observed nests remotely with binoculars to reduce disturbance of nest sites.

On the seventh day of the nestling stage (one to two days before the date of expected fledging), we removed nestlings and carried them in a soft cloth bag ≥10 m from the nest. We weighed each nestling to the nearest 0.1 g, banded it with a standard aluminum U.S. Geological Survey leg band, and attached a radio transmitter to one or two nestlings from each nest. We attached transmitters with a figure-8 harness design for passerines modified from Rappole and Tipton (1991). The mass of the transmitter and harness (0.67 g) equaled 4.3–4.9% of the nestling's mass at the time of attachment, less as birds developed, and 3.2% of adults' mass. We returned the brood to the nest ≤15 min after removal. We then used ground-based and sometimes aerial telemetry and located fledglings daily from 12 June to 11 August. During ground-based telemetry, we first used triangulation to estimate the location of each fledgling, then confirmed the location visually and ascertained survival or mortality by approaching the source of telemetry signals on foot. When fledglings moved beyond the range of ground-based telemetry, either under their own power or by being carried off by a wide-ranging predator, we located them from the air by standard aerial telemetry procedures (Mech 1983). We recorded the location of each nest and fledgling with a handheld GPS unit (100 points averaged, estimated error <10 m) and noted the cover type (see categories below) of the occupied stand. Within the first 16 days after fledging we ascertainted the mortality or survival of each fledgling each day (i.e., no transmitter signals were lost). For a detailed description of predator identification, see Streby and Andersen (2011).

MICRO-SCALE VARIABLES

We sampled vegetation characteristics and invertebrate abundance and activity at fledglings' locations every fourth day, starting with the first day after fledglings left a nest. We centered a 1-m-radius plot on each location, within which we visually estimated percent ground cover (below 0.25 m) by vegetation and by woody debris. In addition, we measured litter depth by pushing a ruler through the litter to the humus layer at three locations within each plot and used the mean of those measurements for analysis. We estimated vegetation density, or lateral cover, around each of these plots by a profile-board method modified from MacArthur and MacArthur (1961). We divided a 2 × 0.25-m board into eight 0.25 × 0.25-m squares and painted the squares alternately orange and white. One observer held the board vertically at a fledgling's location (or 2 m from the location if the fledgling did not move upon our arrival) while a second observer viewed the board from a distance of 10 m in a randomly selected direction and estimated the percent of each square obscured by vegetation (random directions were selected consecutively from a list generated by computer). We then turned the board 90° to the right and repeated the process. We used the mean of the 16 estimates (eight from each direction) as a single estimate of lateral cover around each location.

The Ovenbird is insectivorous and forages primarily on the ground, secondarily in shrubs and ground vegetation (Porneluzi et al. 2011). We measured the abundance and activity of ground invertebrates by two methods at each fledgling-location plot. We used dry mass of invertebrates collected from litter samples as an estimate of invertebrates' micro-scale abundance and dry mass of invertebrates captured in pitfall traps as an estimate of their micro-scale activity. From each fledgling-location plot, we collected a litter sample covering 0.25 m² down to the humus layer. We sifted through litter samples immediately after collecting them, removed all visible invertebrates, and stored them in 50% ethanol solution. Second, we sampled the activity of ground invertebrate in each plot with a pitfall trap. For each pitfall trap, we used a 473-mL plastic cup, with ~50 mL of 50% ethanol solution, buried such that the top of the cup was flush with the ground surface. We deployed each pitfall trap immediately after observing a fledgling, collected the trap's contents after 24 hr, and stored them in a 50% ethanol solution. We counted and identified invertebrates from each leaf-litter and pitfall-trap sample, dried each sample for 24 hr in a drying oven, and measured its dry mass to within 0.0001 g.

To reduce disturbance around nests, we did not record micro-scale data at nest locations within the 24 hr preceding fledging. However, many mortalities of fledglings (34% of predation) occurred within the first 24 hr after fledging, and we could not exclude those fledglings from survival analysis. Therefore, for those fledglings that died in the first 24 hr after leaving their nest, we used micro-scale habitat data collected from the location of the mortality or from a random location <25 m from the nest if a predator carried the fledgling away (e.g., if we found the transmitter in a hawk nest).

MESO-SCALE VARIABLES

At each location of a fledgling, we recorded the cover type (mature forest, forested wetland, logging road, young regenerating clearcut, or older regenerating clearcut) and the distance between the location and each type of non-nesting cover (other than mature forest). We defined shrub-dominated stands ≤6 years since harvest as young regenerating clearcuts and sapling-dominated stands 7–20 years since harvest as older regenerating clearcuts. In this region regenerating clearcuts tend to transition from dominated by shrubs (primarily *Rubus*, *Salix*, and *Corylus*) to dominated by fast-growing aspen saplings ~5–7 years after harvest. We defined forested wetlands as all stands of forest in which the ground was ephemerally or permanently covered with water (e.g., black ash [*Fraxinus nigra*] stands, tamarack bogs, and alder [*Alnus* spp.] thickets). We grouped older regenerating clearcuts and forested wetlands as high-survival cover types, young regenerating clearcuts and logging roads as low-survival cover types (Streby 2010). We used GIS software to measure the minimum distance between each location of a fledgling and the edge of the nearest stand of high-survival and low-survival cover. We recorded distance to edge as zero if a fledgling was at the edge of or in non-nesting cover. Because we tracked many individuals on opposite sides of logging roads on consecutive days, our method of observing fledglings once per day likely underestimated fledglings' use of logging roads. Therefore, we created a binomial meso-scale variable (road crossing), in which we used daily locations to determine if a fledgling crossed a logging road. We assigned a fledgling a value of 1 if we recorded it within a 4-day interval on opposite sides of a logging road, a value of 0 if not.

STATISTICAL ANALYSIS

First, we tested for correlations between explanatory variables. We expected litter depth to have a significant positive correlation with abundance and activity of invertebrates because those variables are commonly reported as highly correlated (e.g., Haskell 2000). In addition, we expected a strong correlation between proximity to low-survival cover and our road-crossing variable. Because regenerating clearcuts are typically associated with logging roads, it is reasonable to expect that fledglings closer to young regenerating clearcuts and logging roads were more likely to cross logging roads than fledglings farther from those cover types.

We used the logistic exposure method (Shaffer 2004) to model fledglings' survival with one intrinsic (nestling mass) and nine extrinsic (meso- and micro-scale habitat measurements) explanatory variables (Table 1), and fitted models with proc nlmixed (SAS Institute 2008). All models included a random effect for nest plot (the 16 plots) to account for potential non-independence among fledglings originating from nearby nests. The logistic exposure method was designed to estimate daily survival of nests monitored at intervals and to examine the explanatory value of categorical and continuous variables on variation in daily survival of nests. This method is therefore convenient and appropriate for the analysis of data about fledgling survival recorded similarly. We used survival (i.e., whether a fledgling survived a 4-day interval) as the response variable and nestlings' mass (on day 7 of the nestling stage) and the meso- and micro-scale habitat data we recorded on the first day of each interval as explanatory variables. Our objective was to compare the relative importance of each variable for explaining survival of fledgling Ovenbirds. Therefore, we included each variable in the same number of candidate models and compared the cumulative weights of models including each variable (Burnham and Anderseon 2002:167–169, Arnold 2010). We used Akaike's information criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002) to rank models. Although they are not necessary for comparing variables' relative importance, we developed candidate models based on biologically relevant combinations of our variables, producing 22 models (including a null model) with each variable included in 5 models (Table 2). Throughout, we present estimates of fledglings' survival as values ± SE.

RESULTS

We attached transmitters to fledgling Ovenbirds from 91 successful nests. We removed from analysis birds that slipped out

TABLE 2. Candidate models for explaining survival of fledgling Ovenbirds from 1 to 8 and from 9 to 16 days after fledging in managed forests of north-central Minnesota. Each model also included a random effect for nest plot (not shown). Candidate models were developed primarily to ensure that each variable was in the same number of models so that the relative importance of these variables could be compared by cumulative Akaike weight and secondarily to include biologically relevant combinations of variables. Models are listed in order of complexity, not ranked. See Table 1 for definitions of variables.

Model no.	Model	K
1	S_{CONSTANT}	2
2	S_{DLSC}	3
3	S_{DHSC}	3
4	S_{RDX}	3
5	S_{LATCOV}	3
6	S_{LITDEP}	3
7	S_{NMASS}	3
8	$S_{\mathrm{DLSC+DHSC}}$	4
9	$S_{\mathrm{DLSC+RDX}}$	4
10	$S_{\mathrm{DHSC+RDX}}$	4
11	$S_{\mathrm{GVEG+GWOOD}}$	4
12	$S_{\mathrm{LITINV+PITINV}}$	4
13	$S_{\mathrm{DLSC+DHSC+RDX}}$	5
14	$S_{\mathrm{LATCOV+GVEG+LITINV}}$	5
15	$S_{\mathrm{LATCOV+LITINV+PITINV}}$	5
16	$S_{\mathrm{GVEG+GWOOD+NMASS}}$	5
17	$S_{\mathrm{LATCOV+PITINV+NMASS}}$	5
18	$S_{\mathrm{LITDEP+GVEG+NMASS}}$	5
19	$S_{\mathrm{LITDEP+GWOOD+PITINV}}$	5
20	$S_{\mathrm{LATCOV+LITDEP+GVEG+GWOOD}}$	6
21	$S_{\mathrm{DLSC+GVEG+GWOOD+NMASS}}$	6
22	$S_{\mathrm{DHSC+RDX+LITDEP+GWOOD+PITINV}}$	7

of their harness <24 hr after fledging (n = 8) and birds that died in association with blow fly infection (n = 8; Streby et al. 2009) or of apparent starvation because of having a Brown-headed Cowbird (*Molothrus ater*) as a brood mate (n = 1; Peterson et al. 2011), mortalities that were unrelated to use of post-fledging habitat. After those birds were removed from the sample, only 10 broods remained with >1 sibling marked. Siblings in doubly marked broods occupied the same cover type during 84% of days tracked, moved similar daily distances, and 64% of siblings experienced similar fates. Therefore, we randomly selected one fledgling from each doubly marked brood to avoid pseudoreplication (Hurlbert 1984). We included the remaining 74 fledglings from 74 nests in analysis. Because 94.6% of all mortalities (including multiply marked broods and blowfly-infected fledglings) of fledgling Ovenbirds we observed occurred during the first 16 days after fledging, we limited our survival analysis to those 16 days. Furthermore, fledgling Ovenbirds transition from primarily hopping along the ground and low vegetation and relying entirely on their parents for food to flying short distances and occasionally gathering their own food approximately 5–8 days after fledging (H. M. Streby and D. E. Andersen, unpubl. data). Therefore, because a fledgling's ability to elude a predator and gather food appeared to transition during that period, we modeled fledglings' survival for post-fledging days 1–8 and 9–16 separately.

We recorded 545 daily locations for the 74 fledglings and recorded habitat data for 187 of those locations. There were no significant correlations between any of our explanatory variables. Of particular interest was the lack of correlation between litter depth and invertebrate abundance ($r^2 < 0.01$, $n = 175$, $P = 0.48$), between litter depth and invertebrate activity ($r^2 < 0.01$, $n = 175$, $P = 0.34$), and between road crossing and proximity to low-survival cover ($r^2 < 0.01$, $n = 175$, $P = 0.98$).

Fledglings' survival during the first 8 days after fledging was best explained by the model including only the road-crossing variable (all models also included a random effect for nest plot). Fledglings that crossed a logging road at least once in the first 8 days (n = 38) were twice as likely to be depredated (daily survival = 0.87 ± 0.03) during that period than fledglings for which there was no evidence of crossing a logging road (n = 36, daily survival = 0.95 ± 0.02; Fig. 1A). Cumulative weights indicated that road crossing was the strongest meso-scale predictor of fledglings' survival (w = 0.85), followed by proximity to low-survival cover (w = 0.40), which had a negative effect on survival, and proximity to high-survival cover (w = 0.30), which had a positive effect on survival. Nestlings' mass and the micro-scale habitat variables each had cumulative weights ≤0.09 (Table 1), and the best-performing model that included any of those variables performed only slightly better than the constant-survival model.

Fledglings' survival 9–16 days after fledging was also best explained by the model that included only the road-crossing variable. During that period, fledglings that crossed a logging road at least once were 33% less likely to survive (daily survival = 0.94 ± 0.02) through day 16 than fledglings that did not cross a road (daily survival = 0.99 ± 0.01; Fig. 1B). Cumulative weights indicated that road crossing was the strongest (w = 0.57) meso-scale predictor of fledglings' survival, followed by proximity to high-survival cover (w = 0.32), which had a positive effect on survival, and proximity to low-survival cover (w = 0.24), which had a negative effect on survival during days 9–16. Nestlings' mass and the micro-scale habitat variable each had cumulative weights ≤0.16 (Table 1).

DISCUSSION

Micro-scale habitat characteristics, such as vegetation density and ground cover, can influence survival of fledgling Ovenbirds (King et al. 2006, Vitz and Rodewald 2011). If we had limited our analysis to micro-scale variables we would

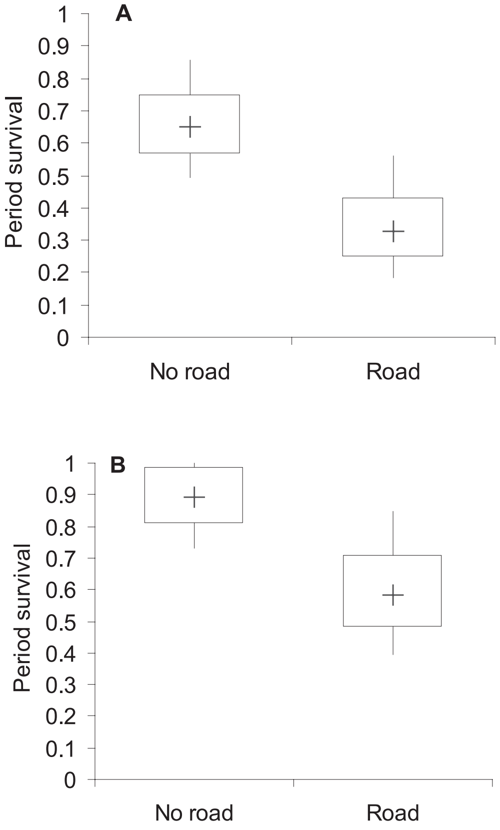

FIGURE 1. Estimated probabilities of survival over 8 days (daily survival^8) of fledgling Ovenbirds that crossed at least one logging road (Road) or did not cross a logging road (No Road) during (A) days 1–8 after fledging, and (B) days 9–16 after fledging, during 2007 and 2008 in the Chippewa National Forest, Minnesota. Plus signs, boxes, and whiskers represent mean, SE, and 95% CI, respectively.

have obtained similar results, with vegetation density or lateral cover around fledglings best explaining their survival 9–16 days after fledging. However, we found that the relationships of meso-scale characteristics to fledglings' survival are much stronger than those of micro-scale characteristics. In a later analysis of 21 additional models we investigated interaction effects between the meso- and micro-scale variables and found no improvement upon competing models. Our results might be explained by the densities of predators varying at spatial scales much broader than a fledgling's location. Fledglings' survival is likely strongly associated with predators' density because the primary predator-avoidance strategy of young fledgling Ovenbirds is holding still, the effectiveness of which is likely strongly related to predator density. Therefore, within an area of given predator density, fledglings' survival may vary with their use of habitat at the micro scale, but that variation is small in comparison to variation in survival among broader areas or cover types used by fledglings. We found fledglings' use of logging roads and proximity to nonnesting cover were more strongly related to survival than were any of the micro-scale variables or nestling mass. Crossing a logging road or being close to a logging road or young clearcut were each negatively related to survival, whereas being close to or using older regenerating clearcuts or forested wetlands was positively related to survival. Our finding that logging roads were the habitat feature with the strongest relationship to fledglings' survival is especially important because neither we (unpubl. data) nor King and DeGraaf (2002) found an apparent relationship of logging roads to the Ovenbird's nest productivity. This result exemplifies the importance of including the post-fledging period in any assessment of the effects of habitat characteristics on songbirds' population productivity.

We expected our variables of road crossing and proximity to low-survival cover to be strongly correlated, but we found no relationship between them. Many birds fledged from nests ≤5 m from logging roads but moved away from the roads in the first few days after fledging, apparently without crossing them. Therefore, our results suggest that although the use of mature forest near young regenerating clearcuts and logging roads was negatively related to survival of fledgling Ovenbirds, the specific use of logging roads by fledglings presented a separate and greater risk of mortality. This may be because hawks (*Buteo* spp. and *Accipiter* spp.) regularly course logging roads throughout our study sites (Streby 2010), and a fledgling Ovenbird is probably in the greatest danger of detection by a road-coursing hawk only when the fledgling is in the open space of the road. Indeed, during our study, raptors accounted for up to 50% of annual predation on fledglings (Streby and Andersen 2011), and of 12 fledglings we observed on or within 2 m of roads, we tracked 4 to hawk nests the following day (Streby 2010). The negative relationship between use of logging roads and fledglings' survival may have been underestimated because we used the crossing of roads as our indicator of road use, and any bird that was depredated the first time it used a road would not have been recognized as using a road in our analysis unless the transmitter was recovered across that road. Therefore, our estimate of the effect of road use on fledglings' survival is likely conservative.

The rate of survival of Ovenbird fledglings we observed was considerably lower than that reported in Ohio (Vitz and Rodewald 2010). It is unlikely that the lower survival we observed was due to the transmitters used in the two studies having different effects because our transmitters were 25% smaller and were fitted to birds of similar size by the same methods. Furthermore, transmitters nearly twice as large relative to body mass have been fitted to warblers with no discernable affects on activity (Neudorf and Pitcher 1997), suggesting that transmitters likely had little effect on birds in either study. It is possible that the difference in survival was due to natural variation, as survival of other fledgling songbirds has been reported as low as or lower than our estimate

(Berkeley et al. 2007, Rush and Stutchbury 2008) and as high as Vitz and Rodewald's estimate (Moore et al. 2010, Kershner et al. 2004). Some of the difference between our survival estimate and that of Vitz and Rodewald (2010) may be due to the timing of transmitter attachment. We attached transmitters to nestlings before they fledged, and we observed that 34% of mortalities occurred <24 hr after a fledging left its nest (Streby 2010). Dates of fledging are not perfectly predictable, and Vitz and Rodewald (2011) attached transmitters to some fledglings after they left the nest, which suggests that the greater survival they observed may have been because many of those birds had already survived part of or all of the day of greatest mortality of the post-fledging period.

We observed no relationship between nestlings' mass and fledglings' survival. This lack of a relationship may be explained by the fact that all fledgling Ovenbirds have limited flight capabilities in the first few days after fledging, and thus all fledglings are likely similarly susceptible to predation during that period regardless of their condition. In addition, we are skeptical of the reliability of mass, or any index that includes mass, as a measure of the condition of small nestling songbirds. Some nestlings (about one per nest) defecated while we were weighing them, reducing their mass by as much as 8% and demoting many of them from being one of the heaviest in the brood to one of the lightest. It is possible that much of the variation in mass of small songbird nestlings is caused by short-term variation in the contents of their digestive systems, limiting the utility of mass as a measure of their condition, but more study is needed.

Our finding that meso-scale habitat characteristics were more strongly associated with survival of fledgling Ovenbirds than were micro-scale habitat characteristics or nestlings' mass suggests that common forest-management practices (usually conducted at the stand level) have larger effects on survival of fledgling Ovenbirds than does natural, smaller-scale habitat heterogeneity. Because logging roads present areas of high predation for Ovenbird fledglings, they may have similar effects on other songbirds as well as game birds such as the American Woodcock (*Scolopax minor*) and Ruffed Grouse (*Bonasa umbellus*). This may be important to investigate, because habitat management for the Ruffed Grouse often includes creation and maintenance of trails (e.g., Berner and Gysel 1969). Logging roads, many of which extend for kilometers through mature forest, and some of which are not again used, are often slow to regenerate because the soil is compacted by logging machinery. Although the process is expensive, road removal is being used to reduce the effects of some of the nearly 900 000 km of roads on U.S. federal lands (Switalski et al. 2004). We suggest that in addition to the intended physical and ecological goals of road removal (e.g., erosion control and water quality), the process may enhance populations of ground-dwelling birds in managed forests. Road reclamation is probably not appropriate for areas logged in cycles where roads are reused every few years. However, when a site is logged for one or two decades and then not for several decades (as at our sites where stands are <20 and >60 years old), the potential ecological benefits of reclaiming and then reclearing roads deserve further investigation and consideration.

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