

Seasonal productivity in a population of migratory songbirds: why nest data are not enough

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Abstract. Population models for many animals are limited by a lack of information regarding juvenile survival. In particular, studies of songbird reproductive output typically terminate with the success or failure of nests, despite the fact that adults spend the rest of the reproductive season rearing dependent fledglings. Unless fledgling survival does not vary, or varies consistently with nest productivity, conclusions about population dynamics based solely on nest data may be misleading. During 2007 and 2008, we monitored nests and used radio telemetry to monitor fledgling survival for a population of Ovenbirds (*Seiurus aurocapilla*) in a managed-forest landscape in north-central Minnesota, USA. In addition to estimating nest and fledgling survival, we modeled growth for population segments partitioned by proximity to edges of non-nesting cover types (regenerating clearcuts). Nest survival was significantly lower, but fledgling survival was significantly higher, in 2007 than in 2008. Despite higher nest productivity in 2008, seasonal productivity (number of young surviving to independence per breeding female) was higher in 2007. Proximity to clearcut edge did not affect nest productivity. However, fledglings from nests near regenerating sapling-dominated clearcuts (7–20 years since harvest) had higher daily survival (0.992 ± 0.005) than those from nests in interior forest (0.978 ± 0.006), which in turn had higher daily survival than fledglings from nests near shrub-dominated clearcuts (≤ 6 years since harvest; 0.927 ± 0.030) in 2007, with a similar but statistically non-significant trend in 2008. Our population growth models predicted growth rates that differed by 2–39% ($\bar{x} = 25\%$) from simpler models in which we replaced our estimates of first-year survival with one-half adult annual survival (an estimate commonly used in songbird population growth models). We conclude that nest productivity is an inadequate measure of songbird seasonal productivity, and that results based exclusively on nest data can yield misleading conclusions about population growth and clearcut edge effects. We suggest that direct estimates of juvenile survival could provide more accurate information for the management and conservation of many animal taxa.

Key words: migratory songbirds; Minnesota; nesting; Ovenbird; post-fledging; productivity; *Seiurus aurocapilla*.

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INTRODUCTION

Identifying factors that influence population growth is an integral goal in ecology with wide ranging implications for wildlife management

and conservation (Caughley 1977). A preponderance of research for many species is focused on population productivity, i.e., the number of young produced per breeding attempt. However, primarily due to logistical constraints, informa-

tion about survival of recently produced young is relatively rare. An extreme example is that of sea turtles (Cheloniidae and Dermochelyidae), for which the considerable challenges of monitoring nest productivity are dwarfed by the incredible difficulty of monitoring juvenile movements and survival in the open ocean during a period sometimes referred to as the lost year (Musick and Limpus 1997). Although the logistical constraints associated with studying juvenile survival in terrestrial systems are likely less than those for marine species, the juvenile life stage remains a relatively poorly understood period for many groups, including some bears (*Ursus* spp.; Miller et al. 2003), box turtles (Emydidae; Converse 1999), ducks (Anatidae; Amundson 2010), and songbirds (Passeriformes; Anders et al. 1997), to name a few. Studies in which the juvenile life stage has been investigated indicate that juvenile survival may be the most influential parameter in the growth of many populations (e.g., Gaillard et al. 1998, Amundson 2010), exemplifying the potential importance of expanding studies of reproductive ecology to include the juvenile life stage.

Songbird population ecology is an area of research potentially limited by the lack of information about juvenile survival (Anders et al. 1997). Reproductive output of songbird populations is traditionally measured with nest success, defined as the probability of a single nesting attempt producing at least one fledgling. Since Mayfield (1961, 1975) described an exposure method for estimating daily survival, increasingly robust statistical methods have been developed to accurately estimate nest success (reviewed by Johnson 2007). Murray (2000) demonstrated that nesting life-history characteristics can affect how nest success translates to nest productivity, or the mean number of fledglings produced per female within a nesting season. Making one or more nesting attempts following a failed attempt (re-nesting) and successfully fledging more than one brood in a season (multi-brooding) can compensate for low nest success (Murray 2000, Thompson et al. 2001). In addition, variation in the number of fledglings produced per successful nest can offset variation in nest success. For example, Flaspohler et al. (2001a) found that Ovenbird (*Seiurus aurocapilla*) nest success was lower near clearcut

edges than in interior mature forest, but because clutch size was higher near clearcut edges, nest productivity was similar between the two locations. Therefore, nest productivity is more appropriate than nest success for estimating songbird reproductive output during the nesting period (i.e., from first egg laid to fledge).

Although the nesting period is obviously an essential part of songbird reproduction, the dependent post-fledging period (i.e., after young fledge but before independence from adult care) can be as long as or longer than the nesting period (Ricklefs 1968). However, because songbirds are relatively quiet and mobile during the post-fledging period compared to the nesting period, it is difficult to monitor survival and habitat use of individual fledglings or family groups once they leave the nest. This difficulty has resulted in a lack of information about post-fledging survival and habitat use for most songbird populations (Anders et al. 1997). In the rare case that fledgling locations are predictable (e.g., Cactus Wrens [*Campylorhynchus brunneicapillus*] return nightly to roost in nests during the post-fledging period), apparent fledgling survival is low during the first few days after fledging (Ricklefs 1968), suggesting that variation in fledgling survival is likely important to seasonal productivity (i.e., mean number of fledglings raised to independence per breeding female).

Both adults and fledglings of many songbirds use non-nesting areas during the post-fledging period (Pagen et al. 2000, Marshall et al. 2003). Furthermore, habitat characteristics in areas used during the post-fledging period can influence fledgling survival (e.g., King et al. 2006), suggesting that information about fledgling survival and habitat use are necessary for understanding songbird population dynamics. For more than a decade, advancements in microtechnology have made radio telemetry an available method for monitoring fledgling songbird movements and survival (Anders et al. 1997, Cohen and Lindell 2004, King et al. 2006). However, fledgling survival for most species is unstudied. Therefore, nest success, or sometimes nest productivity, remains as the reproductive parameter used to model population growth (e.g., Podolsky et al. 2007), determine source-sink dynamics (e.g., Donovan et al. 1995), compare habitat quality

(e.g., Weinberg and Roth 1998), and identify effects of human activities on songbird populations (e.g., Manolis et al. 2002). Furthermore, despite the advantages of nest productivity over nest success as a measure of reproductive output, nest success remains the most commonly reported comparative estimate of this important parameter (Thompson et al. 2001). Generally, when songbird nest success is low, habitat quality is described as low (e.g., Trine 1998). When nest success is low near edges of non-nesting habitat, edges are described as negatively affecting population growth (e.g., King et al. 1996). When birds nest at high densities and nest success is low, the area is presumed to be an ecological trap (e.g., Purcell and Verner 1998). Conversely, when nest success relates positively to density, density has been purported to be a useful indicator of population productivity (e.g., Perot and Villard 2009).

Models of songbird population growth rely primarily on nest data and usually include fledgling survival within a broader estimate of first-year survival (e.g., Donovan et al. 1995, Podolsky et al. 2007). Although these models are stochastic, mean first-year survival is usually assumed to be one-half of adult annual survival (Ricklefs 1973, Temple and Cary 1988). That estimate is derived from return rates of first-year birds with some assumption of natal philopatry. However, natal philopatry in migrant songbirds is generally low and poorly understood (Schlossberg 2009). Models including that estimate of first-year survival (one-half of adult annual survival) have been used to infer regional population growth and source-sink dynamics (e.g., Donovan et al. 1995, Porneluzi and Faaborg 1999, Podolsky et al. 2007). However, conclusions based on those models require the assumption that fledgling survival is either constant or varies consistently in direction and magnitude with nest productivity. If fledgling mortality is high and varies inconsistently with nest productivity, conclusions about seasonal productivity based solely on nest success or nest productivity will be misleading.

We studied a population of Ovenbirds in a managed, forested landscape in north-central Minnesota, USA, and investigated the relative contribution of nest productivity and fledgling survival to seasonal productivity over 2 years. In

addition, we tested the hypothesis that non-mature forest edges have similar effects on nest productivity and fledgling survival. Ovenbird nest success is sometimes lower near clearcut edges (Manolis et al. 2002, King et al. 1996), but that effect can be offset by increased brood size near edges (Flaspohler et al. 2001a). Ovenbird fledglings frequently use mature-forest edges and non-nesting cover types (Vitz and Rodewald 2007), and vegetation density can influence Ovenbird fledgling survival (King et al. 2006). We expected that clearcut edges may negatively influence nest productivity in our study, but that they may positively influence fledgling survival. In addition, we modeled growth for our Ovenbird population using our estimates of nest productivity and fledgling survival. We compared our models to simpler models in which we removed estimates of fledgling survival and assumed that first-year survival was one-half of adult survival. We expected that population growth estimates from our models would differ considerably from estimates from simpler models.

METHODS

Study species

Ovenbirds (see Plate 1) winter throughout Central America, southern Mexico, many Caribbean islands, and southern Florida, and breed in mature forests throughout eastern and north-central North America (Van Horn and Donovan 1994). Female Ovenbirds build distinctive dome-shaped nests on the forest floor, and likely due to high nesting densities and the relative ease of monitoring ground nests, Ovenbird nesting ecology is well studied among songbirds (Van Horn and Donovan 1994). Ovenbirds often re-nest after initial nest failure, but successfully fledge only one brood per year. Ovenbird nest success is highly sensitive to edges of agricultural fields and other types of anthropogenic development (Burke and Nol 2000). The effects of edges created by forest harvest (i.e., clearcuts) in predominantly forested areas are less clear, but nest success is at least sometimes negatively related to clearcut edges (e.g., Manolis et al. 2000, King et al. 2006). However, as with most songbirds, little is known about survival and habitat use of Ovenbirds during the post-fledg-

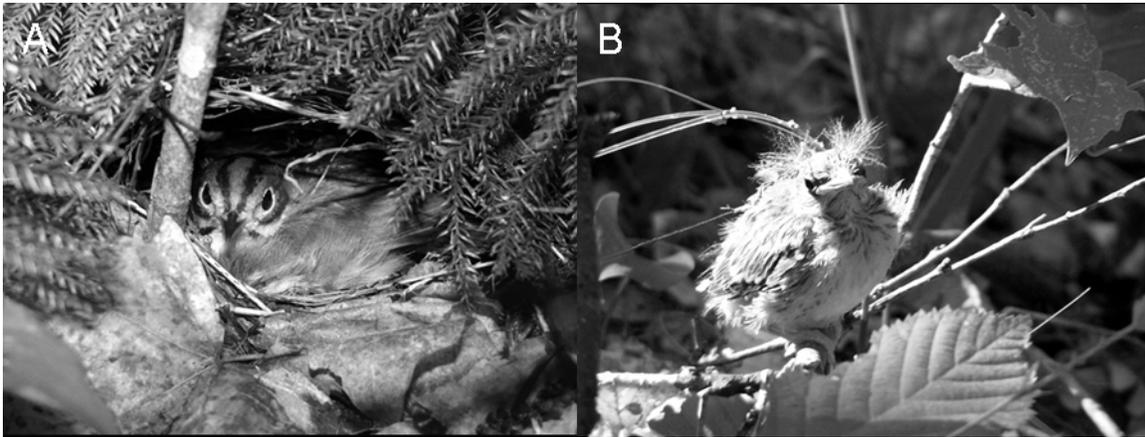


Plate 1. Ovenbirds are ground-nesting (A) migratory songbirds for which nesting ecology is relatively well studied among songbirds. However, as is the case with most songbirds, Ovenbird fledgling (B) survival and habitat use are not well understood. Photo credits: (A) H. M. Streby and (B) S. M. Peterson.

ing period (King et al. 2006).

Study area

We collected data during May–August 2007 and 2008 in the Chippewa National Forest (CNF) in north-central Minnesota, USA. The CNF encompasses approximately 600,000 ha of Cass and Itasca Counties in the transition zone from northern hardwood to boreal forest, and includes mature mixed northern hardwood-conifer forest stands interspersed with lakes, marshes, forested wetlands, and regenerating clearcut stands (9–15-ha even-aged stands of primarily aspen [*Populus* spp.] with remnant mature oak [*Quercus* spp.] and white pine [*Pinus strobus*] trees and occasional large snags on our sites) of various seral stages. Mature forest stands at our sites ranged from mostly coniferous to mostly deciduous and were primarily composed of red pine (*Pinus resinosa*), sugar maple (*Acer sacharum*), American basswood (*Tilia americana*), aspen, birch (*Betula* spp.), white pine, and northern white-cedar (*Thuja occidentalis*). Forested wetland stands were primarily composed of tamarack (*Larix laricina*), black ash (*Fraxinus nigra*), and alder (*Alnus* spp.). We monitored nests on 16 randomly established 10-ha plots in mature upland forest stands in the Suomi Hills and Cutfoot Sioux areas of the CNF. Of the study plots, 12 were adjacent to one or two regenerating clearcuts, and extended 250–510 m from clearcut edges, and four were entirely >250 m from clearcut edges. We assigned regenerating

clearcuts in our study to categories based on vegetation structure, as either shrub-dominated (young clearcuts; primarily shrubs and saplings <3 m in height; ≤ 6 years since harvest) or sapling-dominated (old clearcuts; primarily aspen 4–15 m in height; 7–20 years since harvest). We divided regenerating-forest stands into these two categories because they represent two structurally and ecologically distinct cover types. Although there is variation depending on many biotic and abiotic factors, regenerating forest stands in our study area transition 5–7 years after harvest from primarily low dense shrubby vegetation to fast growing tree saplings (usually aspen). Before and after this transition, regenerating stands differ considerably in plant-species composition, canopy height, vegetation density, fruit abundance, invertebrate biomass, and in their use by forest-nesting birds (Streby 2010).

Data collection

We monitored Ovenbird nests following procedures modified from Martin and Geupel (1993) and used in previous studies of forest-nesting birds in north-central Minnesota (Manolis 1996, Perry 1998). Starting 15 May, we intensively searched each plot every 4 days, and located nests by combining systematic searching and observations of adult behavior (e.g., singing males, flushing females, and females carrying nesting material). We recorded each nest location with a handheld GPS unit (100 points averaged)

and marked the area with flagging tape 2–5 m in a random direction from the nest. During nest monitoring, we approached nests from various directions and continued walking past nests to avoid attracting predators with dead-end paths (Martin and Geupel 1993). We visited each nest at 4-day intervals, and more frequently when we expected transition between nest stages (i.e., laying or hatching), to help predict fledge dates. When expected transitions between nest stages were not imminent and when nest positions allowed (~10% of observations), we monitored nests from >5 m using binoculars. During each nest visit, we recorded the status of nest contents (i.e., number of eggs, number of nestlings, and estimated age of nestlings) until nestlings were one or two days from fledging.

We attached radio transmitters to nestlings one or two days prior to estimated date of fledging. To minimize the chance of attracting predators to nest sites, we attached transmitters only when we could see or hear no common nest predators (e.g., eastern chipmunk [*Tamias striatus*] and red squirrel [*Tamiasciurus hudsonicus*]) nearby. We extracted all nestlings and carried them in soft cloth bags 10–15 m from the nest, where we weighed and banded them using standard aluminum U.S. Geological Survey legbands. We attached radio transmitters (0.67 g including harness) to ≥ 1 nestling from each nest using a figure-eight harness design (Rappole and Tipton 1991) and then replaced nestlings in the nest. Transmitters were 4.3–4.9% of nestling body mass at time of attachment. We used the fates of radio-marked juveniles to determine fates of nests found empty on or near the expected fledge date because nest condition can be a misleading indicator of nest fate (Streby 2010).

Radio telemetry

We used radio telemetry to monitor fledglings following procedures modified from Anders et al. (1998) and Vega Rivera et al. (1998). We located and monitored survival of radio-marked fledglings from 12 June to 11 August via ground-based telemetry. We used triangulation to estimate the location of each fledgling and approached estimated locations and attained visual confirmation of survival or mortality. When fledglings moved beyond the range of our ground-tracking capabilities, either indepen-

dently or when carried by predators, we relocated them from the air using standard aerial telemetry techniques (Mech 1983). Once a bird was relocated from the air, we determined its specific location and survival status using ground-based telemetry. We considered fledglings independent from adult care when we no longer observed adult attendance during >20 minutes of observation on two consecutive days. We used GIS software to measure distances between nests and fledgling locations, between consecutive fledgling locations, and between fledgling locations and nearest edges of shrub-dominated and sapling-dominated clearcuts using a forest cover-type layer provided by the U.S. Forest Service.

Predator identification

We did not directly observe any nest predation events during this study. We used condition and location of recovered fledglings and transmitters to identify predators. We identified a predator as an owl when a transmitter and corresponding legband were recovered entangled in an owl pellet (Streby et al. 2008). We identified a predator as a hawk when a transmitter was recovered in a pile of plucked feathers, when a transmitter was located in a hawk nest, or in one case when a transmitter was tracked directly to a flying Broad-winged Hawk (*Buteo platypterus*). We identified a predator as a small mammal when a dead fledgling was found cached underground or in a chipmunk burrow, when a transmitter and banded leg were found on a stump or low conifer branch commonly occupied by feeding chipmunks or red squirrels, or when a fledgling was found to have been chewed open and had its brain or entrails eaten.

Statistical analysis

We used PROC GENMOD (SAS Institute 2008) to fit logistic exposure models (Shaffer 2004) to Ovenbird nest and fledgling survival data. Logistic exposure models are generalized linear models that allow for the inclusion of continuous and categorical explanatory variables, with a modified link function that allows for varying lengths of intervals between observations of nests or animals. For each period (nesting and post-fledging), we compared 16 candidate models including a constant survival model and all

combinations of four explanatory variables: year (*YEAR*), nest initiation date (*NESTIN*), distance to shrub-dominated clearcut (*DYC*), and distance to sapling-dominated clearcut (*DOC*). We used Akaike's Information Criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2002) to rank candidate models. We considered the best-supported model and all models with ΔAIC_c values < 2.0 to be competing models. We used the cumulative Akaike weights (w ; Burnham and Anderson 2002) of all models that included a given variable to identify the relative value of that variable for explaining variation in fledgling survival.

Because nest infestation by bird blow flies (*Trypocalliphora braueri*) apparently does not affect Ovenbird nest productivity but can significantly lower fledgling survival (Streby et al. 2009), we included infested nests ($n = 7$) but excluded fledglings ($n = 8$) from those nests from survival analysis. We compared daily survival rates of nests and fledglings between years and among population segments using Z-tests (Johnson 1979). From each brood for which we tracked multiple fledglings, we included one randomly selected fledgling in estimates of survival (67% of siblings had the same fate as those we included in analysis) to avoid pseudoreplication (Hurlbert 1984). However, because no two siblings were depredated by the same predator group (i.e., mammals or raptors), we included all fledglings when comparing predation by predator group. We compared fledgling predation by raptors and small mammals between years with χ^2 tests of independence.

Density of nesting songbirds can vary considerably among years in response to various factors including weather conditions (Yackel Adams et al. 2006). In female-based population models, productivity is typically expressed by the number of female offspring produced per adult female. However, if density of adult females differs considerably among years, overall population productivity can differ even if per-female productivity is similar. Weather conditions differed considerably between the two years of our study, as 2007 had temperatures and precipitation near spring means for the previous decade, and 2008 was one of the warmest and driest springs on record (NCDC, <http://www.ncdc.noaa.gov>). Therefore, we investigated whether nesting female Ovenbird density differed in our

study population between 2007 and 2008. Ovenbird populations are usually female limited (i.e., there are almost always fewer females than males; Habib et al. 2007) with pairing success of males ranging from 0% to nearly 100% (Van Horn et al. 1995, Bayne and Hobson 2001). Therefore, even a census of singing males likely does not reflect density of nesting females in an Ovenbird population. For example, a count of 100 male Ovenbirds, with no knowledge of pairing success, could represent 0–100 nesting pairs. Because females are the reproductive unit of interest in our models of population growth, we used the number of nests we found per hour of searching as an index of nesting female Ovenbird density in our study population to be compared between years. Because female Ovenbirds renest after initial nest failures, including nests initiated late in the season could affect this index of nesting female density if years differ in nest success and thus differ in renesting rates. Therefore, we included in this analysis only nests found during the first 20 days after the first nest was initiated each year, the period in which we estimated all first nests were initiated. Because detectability of nests may vary in areas that differ in vegetation density, we did not compare nesting female density among areas within each year.

Population modeling

We modeled growth for three segments of our Ovenbird population partitioned based on proximity of nests to clearcut edges. Although edge effects on nests success can extend 300 m or more into mature forest stands (e.g., Manolis et al. 2000, Flaspohler et al. 2001b), our preliminary models of nest and fledgling survival using the logistic exposure method with distance-to-edge as a continuous explanatory variable indicated an apparent inflection point at ~ 100 m from clearcut edge (H. M. Streby and D. E. Andersen, *unpublished data*). This distance (100 m) is consistent with studies of the most common predators of ground nests in northern-hardwood forests (Fenske-Crawford and Niemi 1997), eastern chipmunk and red squirrel, for which abundance is highest within 100 m of clearcut edges (King et al. 1998). Therefore, we modeled growth for three segments of our Ovenbird population based on nest location: (1) ≤ 100 m

from shrub-dominated clearcuts, (2) ≤ 100 m from sapling-dominated clearcuts, and (3) > 100 m from any clearcut edge. We refer to these population segments as near shrub-dominated clearcut, near sapling-dominated clearcut, and interior forest, respectively.

We built female-based stochastic population models in Excel (use of trade names does not imply endorsement by either the U.S. Geological Survey or the University of Minnesota) spreadsheets for each year and segment of the sampled Ovenbird population. We built 12 models: one for the entire study population for each of the 2 years and both years combined (three models), and one for each of the three population segments for each of the 2 years and both years combined (nine models). We ran 1000 iterations of each model and we allowed each parameter to vary randomly within 1 SD (unless otherwise noted) of the estimated mean for that parameter. All of the models were structurally identical and included adult annual survival (from Podolsky et al. 2007), nest productivity, dependent fledgling survival, independent fledgling survival (our estimates), and non-breeding season survival (calculated using our estimates and adult annual survival from Podolsky et al. 2007). We compared our models to simpler models identical to our models for all parameters except that for the simpler models we replaced our estimates of independent fledgling survival and non-breeding survival with a common estimate of first-year survival for forest-nesting songbirds equal to one-half of adult annual survival.

Model parameterization

We estimated nest success for each population segment from regression coefficients of a logistic exposure model (Shaffer 2004) that included a year and population segment interaction term. We used the same method to estimate survival for dependent fledglings (S_{DF}) originating from nests within each population segment. We used a single estimate for survival of independent (from adult care) fledglings (S_{IF}) because nest location (within a stand) is likely not relevant to survival once fledglings are capable of independently moving > 1 km per day.

We used nest initiation dates (date of first egg laid) and nest failure dates in our sample and estimated probabilities of re-nesting in our study

population. Because we intensively searched all sites starting before first nests were initiated, and because $> 50\%$ of nests were found during nest building or egg laying, we are confident that there were not considerable differences in the initiation dates of first nests among sites or years during this study. The range of initiation dates for nests we observed was 47 days, with nests initiated from Julian dates 137–183 (we refer to date 137 as day one of the nesting season hereafter). Ovenbirds in this population have a mean nesting period of 24 days (from first egg laid to fledge), take 4–9 ($\bar{x} = 7$) days to build a nest after failure, and then 2–3 days to lay the first egg, or initiate a subsequent nest attempt (H. M. Streby and D. E. Andersen, *unpublished data*).

We visually assessed a frequency distribution of the initiation dates of nests we monitored and observed a distinct peak in the first 20 days of the nesting season. We assumed that all females initiated a first nesting attempt within that 20-day period. Therefore, we estimated that first nesting attempts occurred during days 1–43 of the nesting season (a nest initiated on day 20, if successful, would succeed on day 43). Because birds in this population take ~ 10 days between failure and initiation of a subsequent nesting attempt, we assumed that nesting attempts that failed after day 37 (10% of first nesting attempts we observed) did not have time to re-nest. Again because birds take ~ 10 days to initiate a subsequent nest after failure, we assumed that birds initiated first re-nesting attempts during days 11–47, second re-nesting attempts during days 22–47, and third re-nesting attempts during days 33–47. We then calculated the percent of nests we observed that were initiated during each of those periods and that failed after day 37 (too late to re-nest) and estimated the probability of a female re-nesting after each failed attempt in our population. From those calculations, our model assumed that 90% of females that fail during a first nesting attempt re-nest ($R_1 = 0.90$), 60% that fail during a second nesting attempt re-nest ($R_2 = 0.60$), and 30% that fail during a third nesting attempt re-nest ($R_3 = 0.30$). Although Ovenbirds can re-nest four or more times (Hann 1937) and can rarely successfully fledge two broods (Podolsky et al. 2007), we determined that the length of the nesting season in our study area likely precluded more than three re-nesting

attempts or double-brooding.

We observed evidence of adult female mortality (i.e., adult feathers or other remains) associated with three (3.5%) nest failures. We included probability of female survival during failed nesting attempts ($S_{FF} = 0.965$) as a fixed value when computing nest productivity. Because we found no effect of nest initiation date on nest success, we considered nest success constant throughout the nesting season. For each population segment, we computed nest productivity for initial nesting attempts (P_{N0}), and first (P_{N1}), second (P_{N2}), and third (P_{N3}) re-nesting attempts as,

$$P_{N0} = NS,$$

$$P_{N1} = (1 - P_{N0})(S_{FF})(R_1)(NS),$$

$$P_{N2} = (1 - P_{N0} - P_{N1})(S_{FF})(R_2)(NS),$$

$$P_{N3} = (1 - P_{N0} - P_{N1} - P_{N2})(S_{FF})(R_3)(NS),$$

where NS = nest success, S_{FF} = female survival, and R = re-nesting probability.

Within each model iteration, we computed fecundity (F ; mean number of female young fledged per female) for each population segment as,

$$F = (P_{N0} + P_{N1} + P_{N2} + P_{N3})(0.5)(B),$$

where B = fledged brood (i.e., mean number of fledglings produced per successful nest, for which we observed no variation with nest initiation date [$R^2 < 0.01$, $P = 0.96$]). Because we allowed our estimates of nest success (NS) and fledged brood (B) each to vary randomly within 1 SD, each calculation of fecundity (F) included variation from both of those parameters.

We used 0.633 (95% CI = 0.545–0.721) as annual adult female Ovenbird survival (S_A ; Podolsky et al. 2007). Podolsky et al. (2007) did not report SD for their estimate of S_A , so we allowed that parameter to vary randomly within the reported 95% CI in our models. We acknowledge that SD is a measure of the variability in the population, whereas a 95% CI is derived from SE, which describes the precision of the estimate. However, the 95% CI from Podolsky et al. (2007) was the best available approximation of range for S_A .

We computed first-year survival (S_{FY}) as,

$$S_{FY} = (S_{DF})(S_{IF})(S_{NB}),$$

where S_{NB} is survival during the 9-month non-breeding season, $S_A(0.75)$. This derivation of S_{NB} assumes constant adult survival within a year. Although survival likely varies among the breeding and winter seasons and spring and fall migration, sufficient estimates to better inform our model are not currently available for nearly all populations of migratory songbirds (Sherry and Holmes 1995).

We computed the intrinsic rate of growth (λ) from models of both years combined, each year, and each population segment as,

$$\lambda = N_{t+1}/N_t$$

where

$$N_{t+1} = (N_t)(F)(S_{FY}) + (N_t)(S_A),$$

and N_t was arbitrarily set at 1000 for each model iteration.

We determined the amount of uncertainty in our estimates of λ by performing 1000 stochastic iterations of each model. For each of our models, we calculated the geometric mean λ from the 1000 iterations (Pulliam 1996) and calculated 95% confidence intervals (Sokal and Rohlf 1981:421). For comparison to models excluding direct estimates of fledgling survival, we replicated each of our models replacing values of S_{FY} with 0.317, or one-half of S_A , as per many previous songbird population growth models (e.g., Donovan et al. 1995, Porneluzi and Faaborg 1999). In addition, we calculated the coefficient of determination (r^2) from linear regressions of the parameter values and lambdas from each of the 1000 iterations to explore how uncertainty in each parameter related to the population growth rate.

RESULTS

We monitored 184 Ovenbird nests (90 in 2007 and 94 in 2008), of which 91 (49%) succeeded, 86 (47%) failed, and seven (4%) had uncertain fates. Nest construction took 4–9 days ($\bar{x} = 7.0$), clutch sizes ranged from one to six eggs ($\bar{x} = 4.8$), and fledged broods ranged from one to six fledglings ($\bar{x} = 4.2$). During the first 20 days of nest searching, we found 72 nests during 454 searching-hours in 2007 (0.16 nests/hour) and 74 nests during 470 searching-hours in 2008 (0.16 nests/hour). Based on our per-unit-effort index, density

of nesting females was nearly identical between years ($\chi^2 = 0.001$, $df = 1$, $P = 0.97$).

We monitored 109 fledglings from the 91 nests known to be successful. Transmitters fell off of 11 birds <48 hr after fledging, and we therefore did not include those birds in survival estimates. We removed from the sample fledglings that died associated with blow fly infection ($n = 8$; Streby et al. 2009) and one fledgling that died of apparent starvation that was a brood mate of a Brown-headed Cowbird (*Molothrus ater*). To avoid pseudoreplication within the remaining 89 fledglings, we randomly selected one fledgling from each brood for which we monitored multiple siblings. Therefore, we included 74 fledglings from 74 nests in survival analysis and population modeling. Based on observations of adult activity, we estimated that fledglings were independent of adult care ~25 days after fledging. Forty-eight of the fledglings we monitored were depredated during the 24-day dependent post-fledging period. We monitored the remaining 26 fledglings for 1–24 days ($\bar{x} = 12.5$) after independence from adult care.

Logistic exposure models indicated that year effects explained the most variation in both daily survival of nests and fledgling daily survival. The *YEAR* variable was included in the best-supported model for each period and was the only variable included in all competing models. Cumulative weights for nest survival models including each variable were: year (*YEAR*) = 0.65, distance to sapling-dominated clearcut (*DOC*) = 0.43, distance to shrub-dominated clearcut (*DYC*) = 0.34, and nest initiation date (*NESTIN*) = 0.23. Cumulative weights for fledgling survival models including each variable were; *YEAR* = 0.57, *NESTIN* = 0.23, *DOC* = 0.20, and *DYC* = 0.21.

Nest daily survival was significantly lower in 2007 than 2008 ($z = 5.858$, $P < 0.001$), whereas fledgling daily survival was significantly higher in 2007 than 2008 ($z = 3.683$, $P < 0.001$; Fig. 1). Seasonal productivity was significantly higher in 2007 than 2008 ($z = 4.70$, $P < 0.001$). Nest daily survival was not significantly different among population segments within 2007 or 2008 (Table 1). However, our two models of nest survival with the lowest AIC_c ($S_{YEAR+DOC}$, $\Delta AIC_c = 0$, and $S_{YEAR+DYC}$, $\Delta AIC_c = 0.01$) each included an effect of distance to clearcut edge, indicating a positive

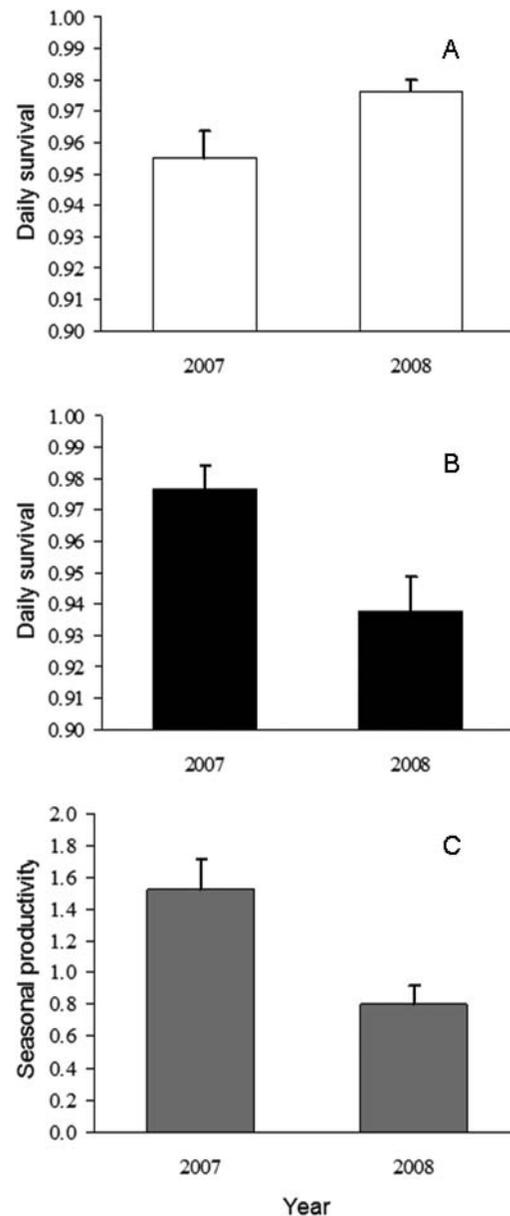


Fig. 1. Daily survival of Ovenbird nests (A) and fledglings (B), and seasonal productivity (fledglings raised to independence per nesting female; C) during 2007 and 2008 in the Chippewa National Forest, Minnesota, USA. Error bars depict SE, all three are significantly different between years.

influence of sapling-dominated clearcut edges and a negative influence of shrub-dominated clearcut edges on nest survival. Fledgling daily survival from nests near sapling-dominated

Table 1. Fledged brood size and daily survival for nests and fledglings (\pm SE) for Ovenbirds nesting ≤ 100 m from shrub-dominated clearcuts ≤ 6 years since harvest (Near YCC), nesting ≤ 100 m from sapling-dominated clearcuts 7–20 years since harvest (Near OCC), and nesting > 100 m from any clearcut edge (Int. Forest) in the Chippewa National Forest, Minnesota, USA.

Population segment	Year	Nest exposure days	Nest daily survival	Fledged brood size	Fledgling exposure days	Fledgling daily survival
Near YCC	2007–2008	441	0.968 \pm 0.009	4.33 \pm 0.19	104	0.933 \pm 0.023
Near OCC	2007–2008	596	0.969 \pm 0.007	4.25 \pm 0.22	229	0.969 \pm 0.011
Int. Forest	2007–2008	1604	0.966 \pm 0.004	4.19 \pm 0.15	563	0.956 \pm 0.008
Near YCC	2007	267	0.958 \pm 0.013	4.29 \pm 0.29	63	0.927 \pm 0.030
Near OCC	2007	210	0.971 \pm 0.011	4.33 \pm 0.49	108	0.992 \pm 0.005
Int. Forest	2007	671	0.948 \pm 0.012	3.83 \pm 0.32	293	0.978 \pm 0.006
Near YCC	2008	174	0.982 \pm 0.012	4.38 \pm 0.26	41	0.937 \pm 0.026
Near OCC	2008	386	0.969 \pm 0.010	4.21 \pm 0.24	121	0.944 \pm 0.021
Int. Forest	2008	933	0.978 \pm 0.005	4.36 \pm 0.15	270	0.936 \pm 0.013

clearcuts and nests near shrub-dominated clearcuts was significantly higher ($z = 2.259$, $P < 0.025$) and lower ($z = 10.397$, $P < 0.001$), respectively, than that of fledglings from nests in interior mature forest in 2007. There was a similar trend in fledgling survival among population segments in 2008, but differences were not statistically significant (Table 1).

Population growth models predicted that the entire study population had positive growth in 2007 ($\lambda = 1.07$, 95% CI = 1.03–1.10), negative growth in 2008 ($\lambda = 0.86$, 95% CI = 0.84–0.89), and negative growth for both years combined ($\lambda = 0.96$, 95% CI = 0.93–0.99; Table 2). For both

years combined, population growth derived for the population segment nesting near shrub-dominated clearcuts was negative ($\lambda = 0.80$, 95% CI = 0.77–0.83), for the segment nesting near sapling-dominated clearcuts was positive ($\lambda = 1.09$, 95% CI = 1.06–1.13), and for the segment nesting in interior forest was stationary, or may have been slight negative ($\lambda = 0.97$, 95% CI = 0.94–1.01). Using our models as standards, simpler models (without direct estimates of fledgling survival) produced predicted values of λ biased by 2–39% ($\bar{x} = 25\%$; Table 2). Population growth (λ) derived from simpler models was significantly different from λ derived from

Table 2. Population growth rates (λ) predicted by models including our direct estimates of fledgling survival (Fledgling model) and models including an estimate of constant first-year survival (Constant S_{FY} model) commonly used in previous songbird population models. Exposure days for nests and fledglings monitored, and differences in population growth rates ($\Delta\lambda$) are presented for the entire study population and population segments nesting ≤ 100 m from brush-dominated clearcuts ≤ 6 years since harvest (Near YCC), nesting ≤ 100 m from sapling-dominated clearcuts 7–20 years since harvest (Near OCC), and nesting > 100 m from any clearcut edge (Interior Forest) in the Chippewa National Forest, Minnesota, USA.

Population segment	Year	No. nests	Nest productivity	λ Fledgling model (95%CI)	λ Constant S_{FY} model (95%CI)	$\Delta\lambda$
Entire population	2007–2008	185	0.799	0.96 (0.93–0.99)	1.16 (1.12–1.19)	0.20*
Entire population	2007	90	0.653	1.07 (1.03–1.10)	1.05 (1.02–1.08)	0.02
Entire population	2008	95	0.897	0.86 (0.84–0.89)	1.23 (1.19–1.27)	0.37*
Near YCC	2007–2008	26	0.848	0.80 (0.77–0.83)	1.19 (1.15–1.23)	0.39*
Near OCC	2007–2008	43	0.797	1.09 (1.06–1.13)	1.19 (1.14–1.22)	0.10*
Interior forest	2007–2008	116	0.788	0.97 (0.94–1.01)	1.18 (1.14–1.21)	0.22*
Near YCC	2007	15	0.706	0.77 (0.75–0.79)	1.11 (1.08–1.14)	0.34*
Near OCC	2007	16	0.771	1.48 (1.41–1.54)	1.20 (1.15–1.24)	0.28*
Interior forest	2007	59	0.593	1.01 (0.98–1.04)	0.99 (0.96–1.01)	0.02
Near YCC	2008	11	0.963	0.88 (0.84–0.91)	1.28 (1.23–1.32)	0.40*
Near OCC	2008	27	0.815	0.88 (0.85–0.91)	1.17 (1.13–1.20)	0.29*
Interior forest	2008	57	0.913	0.87 (0.84–0.89)	1.26 (1.21–1.30)	0.39*

* Denotes a statistically significant difference in λ between our Fledgling model and the simpler Constant S_{FY} model at the 95% confidence level.

models that included fledgling survival for 10 of the 12 models we compared.

Coefficients of determination in our models indicated that variation in non-breeding survival explained the most variation in λ among the 1000 model iterations for each year, and both years combined. Among breeding-season parameters, coefficients of determination indicated that fledgling survival explained the most variation in λ . Mean coefficients of determination from models of the entire population for each year and both years combined were S_{NB} (0.50), S_{DF} (0.31), S_B (0.13), S_{IF} (0.04), NS (0.01), and B (0.01).

Most nest failures (90%) were caused by either predation or abandonment following partial predation. The remaining 10% of nest failures resulted from apparent abandonment (females may have abandoned the nest or may have been depredated). Most fledgling mortalities (95%) were caused by mammalian predators (61% of predation) and raptors (39% of predation). The remaining 5% of fledgling mortalities were caused by unknown predators or apparent starvation (i.e., dead fledgling found with no apparent injury and an empty stomach). Raptors accounted for a significantly higher percent of fledgling predation in 2008 (50%) than in 2007 (21%; $\chi^2 = 4.19$, $df = 1$, $P = 0.04$). Based on location and condition of recovered transmitters and fledglings, mammalian predators likely included eastern chipmunks and red squirrels, although other possible mammalian predators include all of those that depredate songbird nests in this region (see Fenske-Crawford and Niemi 1997). We identified Broad-winged Hawks, Red-tailed Hawks (*Buteo jamaicensis*), Sharp-shinned Hawks (*Accipiter striatus*), Cooper's Hawks (*A. cooperii*), and Barred Owls (*Strix varia*) as fledgling predators because we tracked transmitters to their nests (each hawk species), pellets near their nest (Barred Owl), or the actual predator (one Broad-winged Hawk).

DISCUSSION

Our results demonstrated that annual differences in songbird nest productivity can be offset by differences in fledgling survival, and that the effects of clearcut edges on fledgling survival are not necessarily similar to their effects on nest productivity. Despite statistically significantly

higher Ovenbird nest productivity in 2008, seasonal productivity was statistically significantly higher in 2007 in our study in north-central Minnesota, USA. Furthermore, despite no significant effects of clearcut edges on nest productivity, shrub-dominated clearcut edges appeared to negatively affect fledgling survival, whereas sapling-dominated clearcut edges appeared to positively affect fledgling survival.

Our models indicated that our entire study population declined slightly over the two-year study period. Because growth of the interior-forest population segment was stationary, it is likely that the negative effect of shrub-dominated clearcut edges, specifically on fledgling survival, accounted for the overall population growth rate of <1 . Our study sites were selected partly based on the presence of considerable area of shrub-dominated clearcuts, and $\sim 7\%$ of our total study area was comprised by clearcuts ≤ 6 since harvest. The surrounding landscape (5-km radius) at each of our study sites included considerably less recent clearcut ($<3\%$). Therefore, we do not believe the slight negative population growth in our study area is necessarily evidence of a negative trend at larger spatial scales.

Predation was the primary cause of both nest failure and fledgling mortality during our study. Artificial ground nests in northern Minnesota forests are depredated primarily by mammals (Fenske-Crawford and Niemi 1997) and there was no evidence that Ovenbird nests were depredated by raptors in our study. To our knowledge, only two studies have used video cameras to identify predators of a total of 11 natural Ovenbird nests in northern hardwood or boreal forests (King and Degraaf 2006, Ball et al. 2009). Those predators included eastern chipmunk, red squirrel, red-backed vole (*Clethrionomys gapperi*), and unidentified small mammals. Although hawks, owls, and corvids were identified as predators of songbird nests in those studies, all predators of Ovenbird nests were identified as mammals (D. King and J. Ball, *personal communications*). Although avian predators likely depredate some Ovenbird nests, empirical evidence and our circumstantial evidence suggest that the proportion is quite small.

Although mammals were likely responsible for nearly all nest predation, raptors accounted for 39% of fledgling predation. Because raptors prey

on small mammals and songbirds, our annual differences in fledgling predation rates may be explained by prey-switching in the raptor community in response to relative local prey densities. Lower densities of small mammals following a relatively severe winter could result in reduced predation on ground-nesting songbird nests, shifting the relative availability of prey-types for raptors from small mammals to songbird fledglings. Because Ovenbird nest densities at our study sites were similar between 2007 and 2008, and nest productivity was significantly higher in 2008, fledgling density was likely significantly higher in 2008 than in 2007. In 2007, conditions the preceding winter were moderate, Ovenbird nest productivity was similar to that of past studies in this region (e.g., Manolis et al. 2000), and 3.8 times as many fledglings were depredated by small mammals than by raptors. Conversely, in 2008 conditions the preceding winter were relatively severe, Ovenbird nest productivity was significantly higher, and fledgling predation by mammals was 11% lower, whereas fledgling predation by raptors was 21% higher than in 2007.

Variation in estimates of population growth was most sensitive to variation in non-breeding survival and dependent-fledgling survival both between and within years of our study. Fledglings from nests near sapling-dominated clearcuts had higher survival than those from nests near shrub-dominated clearcuts or those in interior mature forest. These results demonstrate that edge effects are not limited to the nesting period, and that the proximity of nests to edges can have different effects on survival of nests and fledglings. Many fledglings from nests near sapling-dominated clearcuts used these clearcuts both before and after independence from adult care, and survival within those stands was relatively high (Streby 2010). Therefore, there is likely a reproductive benefit from nesting near sapling-dominated clearcuts in this population. In addition, proximity to areas associated with high fledgling survival may be an important factor in territory and nest-site selection for Ovenbirds. Selection of nest sites to optimize fledgling survival over nest survival (Hypothesis 4; Refsnider and Janzen 2010) may explain weak or absent correlations between songbird nest success and nesting habitat parameters observed

in many studies (see Martin 1993 for a review).

In summary, our results indicate that nest productivity can be a misleading indicator of seasonal productivity in Ovenbirds. We suspect that nest productivity may more accurately approximate seasonal productivity in species with longer nestling periods that produce more highly developed fledglings. However, if fledgling predators are different from nest predators, as appears to have been the case in our study, fledgling condition may not be a good predictor of differences in fledgling survival among species. In addition, we caution that nest productivity may more poorly approximate seasonal productivity in species for which multi-brooding is common. We conclude that studies of songbird productivity that do not include direct estimates of fledgling survival can produce misleading conclusions about seasonal productivity. Consequently, we suggest that many questions about songbird population dynamics, predator-prey relationships, and territory and nest-site selection based on nest data alone, may require revisiting.

Finally, it is important to consider the fact that all ecological research is limited by budget and logistical constraints, and that studying juvenile survival may be financially precluded in many cases. Based on our results, and those of other recent studies (Anders and Marshall 2005), fledgling songbird survival is generally lower and more variable than the values included in population models. We agree with Anders and Marshall (2005) that in the absence of fledgling survival data, population models should include lower and more variable values for first-year survival than in previous modeling efforts. However, our results demonstrate that fledgling survival can be relatively high in years (and in areas) that nest productivity is relatively low, and that population growth can be more sensitive to fledgling survival than to nest productivity. Therefore, we caution that although lowering guesses of juvenile survival will produce more conservative estimates of lambda, those estimates will not necessarily be more accurate. In general, we recommend that more resources be directed toward studies of young animals across taxa to investigate potential similar issues in other systems.

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