



RESEARCH ARTICLE

Postharvest regeneration, sciurid abundance, and postfledging survival and movements in an Ovenbird population

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ABSTRACT

Several studies have emphasized the importance of postfledging survival when estimating avian population growth rates, yet high variation exists in reported estimates. Mechanisms influencing postfledging survival also remain poorly understood. The influences of local habitat quality and landscape context on postfledging movements also remain largely undocumented. We measured daily postfledging survival and movements in Ovenbirds (*Seiurus aurocapilla*) in selection cut plots (30–40% basal area removal) and controls. Specifically, we tested predictions from the “concealment” hypothesis (higher survival/shorter movements with increased fledgling concealment), “body condition” hypothesis (higher survival/longer movements with increased body mass), and “predator abundance” hypothesis (higher survival/shorter movements when predator abundance is low) by monitoring fledgling survival ($n = 55$) and movements ($n = 41$) during the first 2 weeks postfledging. Fledglings were monitored over 2 breeding seasons in 5 pairs of experimental plots, 25 ha each (1 control and 1 treated plot per pair), located in mature hardwood stands. We found support for an effect of predator abundance on survival (i.e. effects of plot-level abundance of red squirrels and year). Models including habitat variables or body mass received weak support. A positive trend for effect of body mass on movement between successive locations was found but no evidence for an effect of predator abundance or habitat variables. These findings indicate that spatiotemporal variation in predator abundance was a key factor determining daily postfledging survival rate in this Ovenbird population; however, predator abundance did not influence movement rate, suggesting that fledgling Ovenbirds were unable to respond to predation risk.

Keywords: dispersal, habitat alteration, juvenile survival, predation risk, trophic cascades

Regeneración tras la tala, abundancia de sciúridos, movimientos y supervivencia tras abandono del nido en una población de *Seiurus aurocapillus*

RESUMEN

Diversos estudios han destacado la importancia de la supervivencia tras abandono del nido, al estimarse las tasas de crecimiento de poblaciones de aves. Sin embargo, existe una gran variación en las estimaciones reportadas, y los mecanismos que influyen en la supervivencia tras abandono del nido son pobremente comprendidos. Las influencias de la calidad del hábitat local y las condiciones paisajísticas en los movimientos tras abandono del nido, también siguen siendo en gran medida poco estudiadas. Medimos los movimientos y la supervivencia diaria tras el abandono del nido de *Seiurus aurocapillus* en parcelas de corte seleccionadas (remoción del área basal de 30–40%) y los controles. Específicamente, probamos las predicciones de la hipótesis de “ocultamiento” (mayor supervivencia/movimientos más cortos con mayor ocultación de volantones), la hipótesis de “condición corporal” (mayor supervivencia/movimientos más largos con una mayor masa corporal), y la hipótesis de “abundancia de depredadores” (mayor supervivencia/movimientos más cortos con menor abundancia de depredadores) estudiando la supervivencia de volantones ($n = 55$) y los movimientos ($n = 41$) durante las primeras dos semanas tras abandonar el nido. Estudiamos los volantones en cinco pares de parcelas de 25 ha (1 control y 1 estudiada), durante dos épocas reproductivas en bosques de maderas duras. Encontramos un efecto significativo en la supervivencia por la abundancia de depredadores (es decir, los efectos de la abundancia de ardillas rojas y el año a nivel de parcelas). Hubo poca evidencia en los modelos que incorporaron variables de hábitat o la masa corporal. Existió una tendencia por el efecto positivo de la masa corporal en los movimientos entre ubicaciones sucesivas, pero no encontramos evidencia de la abundancia de depredadores o de las variables del hábitat. Estos resultados indican que la variación espacio-temporal en la abundancia de depredadores fue un factor clave que determina la tasa de supervivencia diaria tras el abandono del nido en esta población de *Seiurus aurocapillus*. Sin embargo, la abundancia de depredadores no influyó en el grado de movimientos, lo que sugiere que los volantones de *Seiurus aurocapillus* tienen una limitada capacidad o incentivos para reducir el riesgo de depredación.

Palabras clave: movimientos, influencias de la calidad del hábitat local, supervivencia tras abandono del nido, riesgo de depredación

INTRODUCTION

Postfledging survival is an important aspect of songbird demography (Anders and Marshall 2005). Recent studies have documented juvenile survival rates during the first few weeks postfledging for many forest songbird species, and a wide range of survival estimates has been reported (e.g., 0.19–0.77; Powell et al. 2000, Fink 2003, Rush and Stutchbury 2008, Vitz and Rodewald 2011). Sources of this variation are not well understood but likely include species-specific life history and behavior, geographical location, methods, sample size, and environmental variability. For a given species, variation in postfledging survival has mainly been attributed to (1) concealment procured in vegetation, (2) predator abundance, and (3) body condition of fledglings.

Higher juvenile survival has been reported in areas with dense ground cover, leading some authors to suggest that concealment from predators is crucial (hereafter “concealment hypothesis;” King et al. 2006, Vitz and Rodewald 2011). Other studies, however, have reported no differences in postfledging survival between control plots and plots altered by harvest treatments resulting in denser shrub cover (Moore et al. 2010, Eng et al. 2011). This lack of consistency suggests that vegetation cover may interact with the predator species assemblage or other factors (e.g., food abundance) in different regions. Evidence also exists for important annual variation in postfledging survival, linked to fluctuations in predator abundance (“predator abundance hypothesis;” Schmidt et al. 2008, Streby and Anderson 2011). Finally, body condition may be an important predictor of postfledging survival (“body condition hypothesis;” Mitchell et al. 2011, Vitz and Rodewald 2011). Fledglings in better condition should be able to sustain flight earlier, thus shortening the critical stage of low mobility when they are most vulnerable to predators (Naef-Daenzer et al. 2001). Although a growing body of evidence supports these factors, their relative importance in the same system has rarely been tested. Without simultaneously testing these alternative hypotheses, our ability to realistically predict how fledgling survival is influenced by environmental variation, and therefore its contribution to per capita productivity and population dynamics, will remain limited.

Juvenile survival is often estimated as a population level rate, but choices made by individuals ultimately determine whether they survive. In forest ecosystems, studies on different species have shown that fledglings from mature forests often disperse to early seral forests or to other patches with a dense shrub cover during the postfledging

period (Vitz and Rodewald 2006, Streby et al. 2011a, Chandler et al. 2012). Dense cover may reduce predation risk and should offer similar benefits to adults that are molting and less mobile (Anders et al. 1998, Vega Rivera et al. 1999, Pagen et al. 2000, Bayne and Hobson 2001). Shrubby cover may also provide access to food sources that are less abundant in more open understories (Vitz and Rodewald 2007, Streby et al. 2011b, Chandler et al. 2012).

Although the apparent convergence of postfledging movements toward areas with a dense shrub cover has been shown in several studies, how far and when fledglings move to such patches is still unknown. Another key uncertainty (but see Vitz and Rodewald 2010, Streby and Anderson 2013a) is whether fledglings originating from habitat with sparse shrub cover have higher movement rates, and whether these movements are directed toward dense vegetation relative to young fledged in areas with denser shrub cover. The body condition of nestlings has also been shown to be positively correlated with postfledging movement rate (Naef-Daenzer and Gruebler 2008, Vitz and Rodewald 2010), and although a similar positive relationship would be expected in response to predator abundance, to our knowledge this prediction remains untested.

In this study our goal was to address gaps in our understanding of postfledging ecology. Specifically, we tested predictions from the concealment, body condition, and predator abundance hypotheses to determine which factor or combination of factors best explained postfledging survival and movement in an Ovenbird (*Seiurus aurocapilla*) population from an intensively managed forest landscape. The Ovenbird is a songbird generally associated with closed-canopy deciduous forest with a relatively sparse understory (Porneluzi et al. 2011). The study was conducted during 2 breeding seasons in plots treated 4 and 5 years earlier through selection harvesting, and in control plots. Shrub cover was denser in treated plots than in controls (22.8% and 32.1% for the fourth and fifth year postharvest, respectively; Haché et al. 2013a). Hence, according to the concealment hypothesis, we predicted higher postfledging survival and lower movement rates in treated plots than in controls. Because food density was higher in controls than in treated plots during the fourth year postharvest (by 10–60%, depending on invertebrate taxa; Haché et al. 2013b), we predicted higher postfledging survival/longer movements in controls than in treated plots, in accordance with the body condition hypothesis. Alternatively, individuals in good body condition may exhibit low movement rates if they fledged from an area of high food abundance, while individuals in poor

body condition might exhibit higher movement rates as they search for areas of high food abundance. Finally, based on the predator abundance hypothesis, we predicted that spatial and temporal variation in predator abundance would be a better predictor of postfledging survival/movement rates than concealment from the vegetation or body condition of fledglings.

METHODS

Study Area

The study was conducted in a forest owned by J. D. Irving Ltd. (Black Brook District) located in northwestern New Brunswick, Canada (47°23'N, 67°40'W). The study area is dominated by spruce plantations (37%) and forest stands characteristic of the Acadian region such as shade-tolerant hardwoods (25%), spruce-fir (20%), and mixed-wood stands (18%; Etheridge et al. 2006). The Black Brook District is considered one of the most intensively managed forest landscapes in Canada (Montigny and MacLean 2005). Hardwood stands are generally managed through partial harvesting. Among the different silvicultural prescriptions (e.g., strip-cutting, patch-cutting, shelterwood), selection harvesting has been the most frequently used method since the early 1980s. The creation of skid trails removes ~20% of the basal area (sum of the cross-sectional area at breast height [1.3 m] of all trees within a study plot), and an additional 10–20% is selectively harvested within the remaining forest strips. Skid trails are ~5 m wide and 20 m apart (see figure 2 in Haché and Villard 2010 for an aerial photo).

Experimental Design and Data Collection

In 2006, we selected 5 pairs of experimental plots (25 ha each; 1 treated plot and 1 control per pair) to measure the demographic response of the Ovenbird to selection harvesting. All plots were located within northern hardwood stands dominated by sugar maple (*Acer saccharum*). These plots have not been disturbed for at least 30 years and were dominated by trees 120–150 years old. Paired plots were located 3–6 km apart, and the mean distance between pairs of plots was 23.8 km (± 9.1 SD). Plots from a pair had to be close enough to avoid plot-specific landscape effects, yet far enough to avoid an influence of treatment effects on controls. Selection harvesting was applied to each treated plot and to a ~50 m band around each plot during winter 2006–2007. This study was based on data collected during the fourth (2010) and fifth (2011) years postharvest. See Haché and Villard (2010) for further details on the experimental design.

When nestlings were 6–7 days old, 1 (2010 and 2011) or 2 (2011) individuals per brood were weighed to the nearest 0.1 g and fitted with a ~0.5 g (0.48–0.52 g) radio-transmitter (BD-2N, Holohil Systems). In 2011, 2 individ-

uals per brood were monitored to increase sample size. We used nestling body mass as a proxy for body condition. Studies have often used ratios or residual indices, but body mass alone can provide a reasonable, easily measured estimate of fat content (Labocha and Hayes 2012) and may be more appropriate than unverified indices (Schamber et al. 2009).

Transmitters were fitted using the harness technique developed by Hallworth et al. (2009). We relocated each fledgling every 2 days after fledging to determine its status (dead or alive) until day 14 and record its GPS location. Visual contact was required to determine the fate of each individual. To avoid disturbing family groups, we returned to each location later in the season (in July) to quantify microhabitat characteristics. Specifically, we measured litter depth and estimated shrub cover at all locations where fledglings were relocated, as well as 10 m north, southeast, and southwest of each location. We measured litter depth down to the mineral soil (to the nearest 0.5 mm) and estimated shrub cover (0.1–1.3 m high within a 2.5 m radius) using a semiquantitative scale (0–10, 10–25, 25–50, 50–75, 75–90, and 90–100%). For each individual, we measured the distance between locations for every 2-day interval and between the nest and the location of each individual on day 14 using ArcGIS 10. Fledglings were monitored during the “dependent period” when adult care is provided (~24 days in Minnesota; Streby and Anderson 2013a). By day 14, fledglings can sustain flight over relatively long distances (>10 m; S. Haché, M.-A. Villard, and E. M. Bayne personal observation).

In 2010, Haché et al. (2013b) estimated the density of Coleoptera, Gastropoda, and total invertebrates at 60 locations per study plot by counting for 3 minutes all litter invertebrates (≥ 2 mm) detected within a 0.2×1.0 m quadrat. Our current study also included the density of Lepidoptera larvae because softer food items represent a high proportion of the diet of fledglings (Streby et al. 2013). The 3 other groups of invertebrates are important items in the diet of adults, if not fledglings (Stenger 1958, Holmes and Robinson 1988, Pabian and Brittingham 2011, Streby et al. 2013), and they should at least influence the ability of adults to care for their young (via adult body condition) and, consequently, postfledging survival and movement. Due to logistical constraints, invertebrate sampling took place in only 4 pairs of study plots. Shrub cover and litter depth were estimated at 400 locations in 4 treated plots and 2 controls using the same approach described above to generate plot-level estimates (Haché et al. 2013a). We had to limit the number of study plots due to logistical constraints. Lastly, in 2010 and 2011, Villard et al. (2012) estimated the relative abundance of 2 important predators on nests and fledglings: eastern chipmunk (*Tamias striatus*; King et al. 2006, Schmidt et al. 2008) and red squirrel (*Tamiasciurus hudsonicus*; Ball et al.

2009). Relative abundances of these predators were expressed as the mean number of detections per plot on the basis of 8 spot mapping visits during the Ovenbird's breeding season.

Statistical Analyses

To determine the relative importance of different habitat characteristics and spatiotemporal variation in abundance of predators on daily postfledging survival, we compared the importance of 10 a priori models using Akaike's information-theoretic approach for model selection. Daily postfledging survival estimates were calculated using logistic-exposure models with a random effect (Shaffer 2004). To produce these models, we used the PROC NLMIXED procedure in SAS 9.2 (SAS Institute 2008). We accounted for our hierarchical experimental design by considering study plots ("Plot") as a random effect. To our knowledge, all studies measuring postfledging survival have shown important effects of number of days since fledging on survival rates, with most mortality occurring within the first 4 days and being negligible after 10 days. Consequently, all models presented include "Age" as a fixed effect (2, 4, 6, . . . , and 14 days). A model with Age as the only predictor was considered our null model because we were only interested in knowing whether models including the predictors of interest (i.e. Year, Abundance of eastern chipmunks, Abundance of red squirrels, Treatment, Litter depth, and Shrub cover) better explained variation in survival than a model including Age as single predictor. A model with both variables measured at individual locations (i.e. Litter depth + Shrub cover) was used to compare the relative importance of microhabitat; however, individuals found dead might have been carried by a predator, and these locations may not reflect where predation occurred. Because most mortality occurred during the first 4 days postfledging when little movement was observed, we used values of shrub cover and litter depth from the previous visit. Similar models were also generated using vegetation measurements from locations where young were found dead, and both approaches yielded qualitatively similar results; hence, we only reported the former models. Another model including plot-level abundances of both predators was considered as an "Abundance of rodent predators" model. Lastly, a model comprising all predictors was included as our full model. All 10 a priori models were run with and without a squared term for Age to determine whether a nonlinear relationship would better predict daily postfledging survival rate. Models without the squared term provided a better fit to the data, so we present results from these models.

Villard et al. (2012) detected a significant Year effect (2006–2011) on both rodent predators, but no significant Treatment effect. In this study we present results from

multiple comparison analyses testing for a Year effect (2010 vs. 2011) on the abundance of eastern chipmunks, red squirrels, and both rodent predators. Haché et al. (2013b) tested for effects of Treatment, Year, and Year \times Treatment interaction effects on density of Coleoptera, Gastropoda, and total invertebrates. Similarly, we used a generalized linear mixed effect model (GLMM) with a negative binomial distribution to test for a Treatment effect on density of Lepidoptera larvae (with Plot as a random effect). We used a chi-square test to determine whether fledglings originating from the same brood could be considered independent sampling units by comparing the number of events where only one individual died, both individuals died, and both lived, to the number expected by chance alone.

We tested the effects of the same predictors (i.e. 10 a priori models) on the distance between successive locations using linear mixed models (LMM; fledglings [FID] nested within Plot was used as a random effect for this and other models described). Because age has been identified as important factor influencing fledgling movement (Vitz and Rodewald 2010, Streby and Anderson 2013a), the model containing Age as the only predictor was considered our null model. Again, because the distance over which predators can travel with their prey is unknown, only distances among locations where individuals were found alive were used. The same statistical approach was applied to determine Treatment, Year, and Treatment \times Year interaction effects on the distance between locations of individuals on day 14 and the nest from which they fledged. We used an LMM to test for Treatment, Year, and Treatment \times Year interaction effects on body condition; to test whether body condition was a reliable predictor of the number of days a fledgling would live; and to predict the distance between successive locations. We applied a logarithmic transformation to distance between successive locations to meet the assumptions of normality and equal variances. LMM and GLMM were generated using the PROC MIXED and PROC GLIMMIX procedures, respectively, in SAS. We report mean values \pm 95% CI.

RESULTS

Transmitters were fitted on 65 nestlings from 49 nests. Reliable data from the entire period (until death or when individuals reached 14 days) were obtained for 55 fledglings. Transmitter failure or loss of harness (8 individuals) and uncertain predation outcomes (2 individuals; fledglings from the same brood found dead within 1 m of their undisturbed nest) explain the discrepancy in sample size; however, observations made prior to transmitter loss were used in the analyses (4 individuals). In 16 cases, 2 nestlings from the same brood were fitted with a

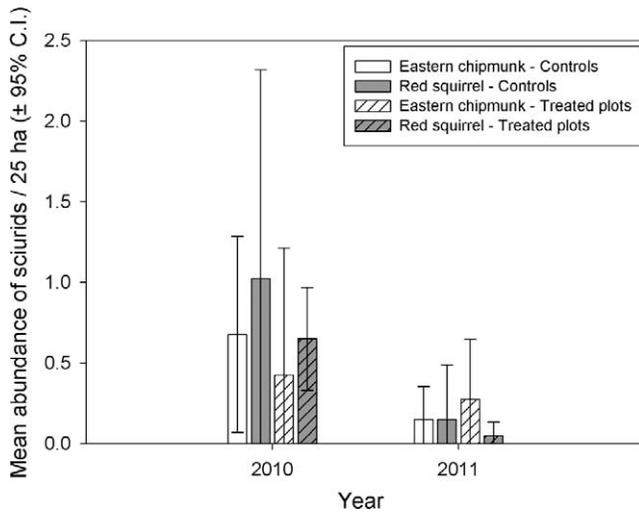


FIGURE 1. Mean abundance ($\pm 95\%$ CI) of eastern chipmunks and red squirrels in plots treated by selection harvesting and controls during the 2 years of the study, 2010–2011.

transmitter. In 5 instances, only 1 of the 2 individuals was found dead. Only twice were both young from the same nest found dead at the same visit. In 6 instances, siblings were found >100 m apart after 4 or 6 days. Thus, nestlings represented independent sampling units ($\chi^2_2 = 2.5$, $p = 0.29$).

We found 70% (21/30) of dead fledglings cached in shallow depressions in mineral soil covered by leaf litter. In one instance, remains were found in an eastern chipmunk burrow, and twice they were found on the top of conifer snags with no evidence of feathers having been plucked (i.e. raptor or corvid predation unlikely), suggesting predation by red squirrel or another small mammal. If this assumption is correct, then raptors or corvids were

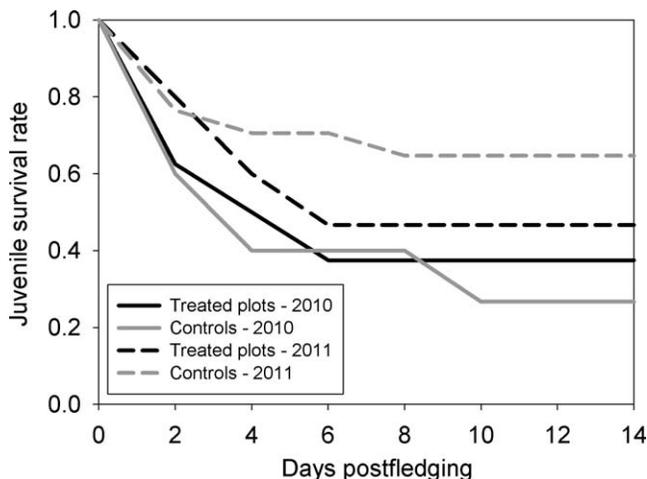


FIGURE 2. Cumulative postfledging survival rates of Ovenbirds as a function of Treatment for both 2010 and 2011.

TABLE 1. Number of nestlings fitted with a radio transmitter and postfledging observations (dead or alive) for each study plot and both years of the study, 2010 and 2011. For 4 nestlings, data were available prior to transmitter loss.

Study plot	Study plot pair	Treatment	# of nestlings (2010/2011)	# of observations (2010/2011)
A	1	Selection cut	0/4	0/7
B	1	Control	3/3	16/9
C	2	Selection cut	3/4	10/28
D	2	Control	5/2	11/14
E	3	Selection cut	3/2	9/14
F	3	Control	4/10	11/50
G	4	Selection cut	2/6	4/16
H	4	control	1/4	7/16
I	5	Selection cut	1/0	7/0
J	5	Control	2/0	2/0
Total			24/35	77/154

responsible for 20% (6/30) of mortalities. No evidence for a Treatment effect on sciurid abundance was found (Villard et al. 2012), but abundance varied widely between years: eastern chipmunk and red squirrel abundances were 8.3 and 2.5 times higher, respectively, in 2010 than in 2011 (Figure 1). Only a trend for Year effect was found on the abundance of eastern chipmunk ($t_{40} = 1.9$, $p = 0.07$), however, and it was only statistically significant when abundances of both rodent predators were pooled ($t_{40} = 2.4$, $p = 0.02$; red squirrel: $t_{40} = 1.2$, $p = 0.25$).

Of the 55 fledglings whose fate was known, 45.5% (25/55) were still alive on day 14 and 60% (18/30) of the cases of mortality occurred during the first two days postfledging, and the other 12 cases occurred between days 2 and 10 (Figure 2). For the fledglings with known fates and those whose transmitters lasted beyond day 2, we recorded 231 events (dead or alive based on visual contact; Table 1). The model explaining variation in daily postfledging survival rate with the lowest AIC value was Age + Abundance of red squirrels (Plot; Table 2; Figure 3A). Another model (Age + Abundance of red squirrels + Abundance of eastern chipmunks [Plot]) had a $\Delta\text{AIC} < 2.0$, suggesting competition among top models; however, little evidence suggested that eastern chipmunk was an important variable because the ΔAIC for this model was equivalent to the penalty associated with adding this extra parameter to our best-ranked model. Although it had a relatively large ΔAIC (4.08), the Age + Year (Plot) model performed better than the null model ($\Delta\text{AIC} = 6.31$; Figure 3B). Support was weak for the 6 other candidate models.

Body weight did not differ significantly between years (13.5 ± 0.7 g [$n = 20$] and 14.3 ± 0.7 g [$n = 30$] in 2010, and 2011, respectively; $F_{1,36} = 3.5$, $P = 0.07$), and there were no Treatment or Treatment \times Year interaction effects ($P > 0.37$ for each). In 2010, densities of Coleoptera, Gastropoda, and total invertebrates were 1.1, 1.6, and 1.4 times higher, respectively, in controls than in treated plots

TABLE 2. Results from 10 a priori models used to generate daily postfledging survival estimates from 231 observations of Ovenbirds ($n = 59$) in northwestern New Brunswick, Canada. Models are ranked from the lowest to the highest Akaike's information criterion (AIC) values. K is the number of parameters, Dev is the deviance, Δ AIC is the AIC value relative to the top-ranked model, W is model weight, RESQ is abundance of red squirrels, and EACH is abundance of eastern chipmunks. Note that all models included Plot as a random effect.

Model description	K	Dev	AIC	Δ AIC	W
Age + RESQ (Plot)	4	137.3	145.3	0	0.55
Age + RESQ + EACH (Plot)	5	137.1	147.1	1.88	0.22
Age + Year (Plot)	4	141.3	149.3	4.08	0.07
Age (Plot)	3	145.6	151.6	6.31	0.02
Age + Treat + Year + Lit + Shrub + RESQ + EACH (Plot)	9	134.2	152.2	6.96	0.02
Age + Lit (Plot)	4	144.6	152.6	7.34	0.01
Age + Shrub (Plot)	4	144.8	152.8	7.58	0.01
Age + Treat (Plot)	4	145.4	153.4	8.12	0.01
Age + EACH (Plot)	4	145.5	153.5	8.26	0.01
Age + Lit + Shrub (Plot)	5	144.0	154.0	8.71	0.01

(Haché et al. 2013b); however, no Treatment effect was found on the density of Lepidoptera larvae (treated plots = 0.20 ± 0.07 , controls = 0.16 ± 0.05 , $F_{1,472} = 0.31$, $p = 0.576$), and there was no evidence that nestling body

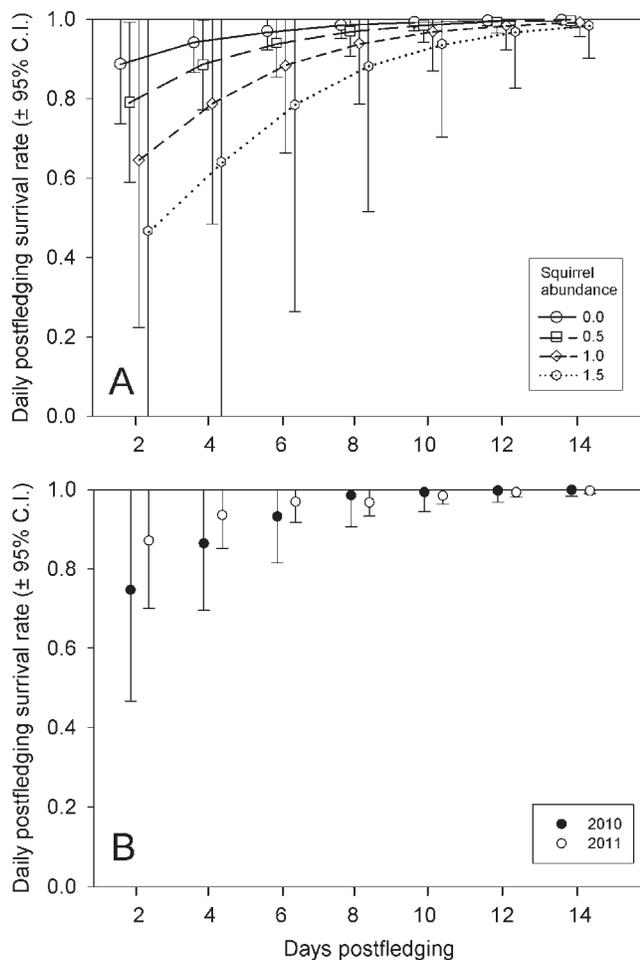


FIGURE 3. Predicted daily postfledging survival estimates in Ovenbirds as a function of Age and (A) Abundance of red squirrels (mean number of detections per visit) or (B) Year.

condition was a reliable predictor of fledgling survival ($n = 50$, $F_{1,38} = 1.3$, $P = 0.26$).

We recorded 199 distances among successive locations (2-day intervals) occupied by fledglings. The model explaining variation in movement between subsequent locations with the lowest AIC value was Age (Plot[FID]; Table 3). The Δ AIC for the second best-ranked model was 4.7, suggesting little support for effects of habitat variables (Figure 4) and abundance of predators; however, a trend was noted for a positive effect of body condition on movement between subsequent locations ($F_{1,142} = 3.9$, $P = 0.05$).

In control plots, the mean distance between nests from which fledglings were radio-tracked, and the closest stand with dense ground cover (i.e. plantation <10 years old or recently harvested hardwood stand <10 years post-harvest) was only $284.6 \text{ m} \pm 44.0$. Nonetheless, only 3 individuals moved away from the stand in which they fledged, and they moved into >10-year-old plantations or a coniferous riparian area with open ground cover.

Although some movements covered relatively long distances (maximum 355 m), fledglings generally remained in the vicinity of their nest during the first 2 weeks postfledging. Mean distances between the nest and location on day 14 were $138.5 \text{ m} \pm 53.4$ in treated plots ($n = 10$) and $212.2 \text{ m} \pm 125.7$ in controls ($n = 15$), but no Treatment effect was found on total distance moved ($F_{1,17} = 1.0$, $P = 0.34$).

DISCUSSION

Our data provide strong support for the predator abundance hypothesis to explain variation in fledgling survival. Postfledging movement rate, however, was not influenced by habitat variables, predator abundance, or body condition. The 3 best-ranked models suggest that spatiotemporal variation in abundance of sciurid predators

TABLE 3. Results from 10 a priori models testing for effects on the distance between subsequent locations ($n = 199$) from 41 Ovenbirds in northwestern New Brunswick, Canada. Only distances from individuals found alive have been used in these analyses. Models are ranked from the lowest to the highest Akaike's information criterion (AIC) values. K is the number of parameters, Dev is the deviance, Δ AIC is the AIC value relative to the top-ranked model, W is model weight, RESQ is abundance of red squirrels, and EACH is abundance of eastern chipmunks. Note that all models included fledgling ID nested within Plot as a random effect.

Model description	K	Dev	AIC	Δ AIC	W
Age (Plot[FID])	4	141.4	149.4	0.0	0.79
Age + RESQ (Plot[FID])	5	144.1	154.1	4.7	0.07
Age + Treat (Plot[FID])	5	144.7	154.7	5.3	0.06
Age + Year (Plot[FID])	5	145.0	155.0	5.6	0.05
Age + EACH (Plot[FID])	5	145.9	155.9	6.5	0.03
Age + RESQ + EACH (Plot[FID])	6	148.6	160.6	11.2	0.00
Age + Shrub (Plot[FID])	5	151.4	161.4	12.0	0.00
Age + Lit (Plot[FID])	5	151.8	161.8	12.4	0.00
Age + Lit + Shrub (Plot[FID])	6	161.7	173.7	24.3	0.00
Age + Treat + Year + Lit + Shrub + RESQ + EACH (Plot[FID])	10	174.5	194.5	45.1	0.00

was a key factor influencing fledgling survival. Only plot-level abundance of red squirrels had an important predictive effect, however; the model with plot-level abundance of eastern chipmunks as the single predictor received poor support. The third best-ranked model only included a year effect. Daily survival rate in year _{x} was inversely related to the abundance of both red squirrels and eastern chipmunks which, again, is consistent with the predator abundance hypothesis. Although shrub cover was significantly denser in treated plots than in controls in both years, there was no evidence for an effect of selection harvesting on postfledging survival or movement, and hence no support for the concealment hypothesis. The absence of treatment-specific variation in body mass prevented us from experimentally testing the body condition hypothesis; however, there was no evidence that body condition influenced postfledging survival or movements.

Unlike effects of concealment in vegetation and body condition, the influence of predator abundance on postfledging survival and movements has rarely been tested, and therefore the relative influence of concealment versus predator abundance remains poorly understood. Perceived predation risk induces antipredation responses (site selection and foraging behavior) that can substantially reduce the number of young fledged (Zanette et al. 2011). Our results provide no evidence that movement rate of fledgling Ovenbirds was altered by the abundance of rodent predators, but we cannot rule out the possibility that altered adult behavior (e.g., foraging behavior) resulted in fledglings being disproportionately more vulnerable to predation in areas of high rodent density.

A seasonal decline in the postfledging survival of Great Tits and Coal Tits (*Parus major* and *P. ater*, respectively) has been attributed to higher abundance of predators later in the season (Naef-Daenzer et al. 2001). Fisher and Davis

(2011) and Vitz and Rodewald (2011) have also suggested that spatial variation in predator abundance could be an important predictor of postfledging survival, but to our knowledge only Schmidt et al. (2008) have explicitly tested effects of predator abundance on postfledging survival in songbirds. They found that survival rate of juvenile Wood Thrushes (*Hylocichla mustelina*) was higher in years with intermediate rodent abundance, a relationship they interpreted as a functional response of raptors to changes in rodent abundance. The same rodent-raptor interaction was also proposed to explain the year effects observed on Ovenbird postfledging survival by Streby and Anderson (2011).

In this study, most predation on fledglings was associated with rodents (24/30), especially during the first

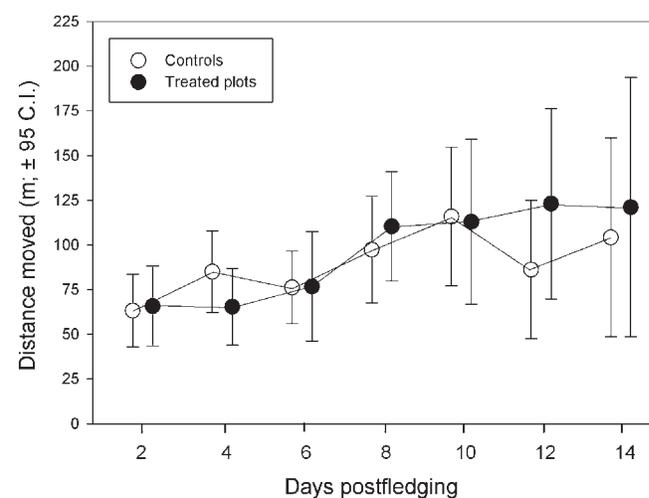


FIGURE 4. Movements of juvenile Ovenbirds during the first 2 weeks postfledging in treated plots and controls. For example, a value recorded at day 4 is the distance between locations occupied on days 2 and 4.

4 days when the fledglings cannot sustain flight. Of the 6 predation cases attributed to raptors or corvids, 3 occurred between day 4 and 10. Some fledglings with transmitter failures might have been preyed upon by raptors and carried outside the range of our receivers, whereas others might have died from disease or exposure and subsequently been scavenged by rodents. Nonetheless, in 63% (24/38) of all instances of mortality or transmitter failure, carcasses were found in shallow depressions in mineral soil covered by leaf litter, in a chipmunk burrow, or depredated without evidence of plucked feathers, suggesting that rodents and other small mammals were the prominent predators of fledglings in this study.

Rodent abundance in 2010 was high but may have been insufficient to generate a shift in raptor diet toward a higher proportion of rodents. For example, we detected 4.3 times more eastern chipmunks and 3.4 times more red squirrels in the same study plots in 2007 than in 2010 (Villard et al. 2012). Forest-specialist raptors might also be present at lower densities in our study area as a result of intensive forest management (Olsen et al. 2006, Vanderwel et al. 2009, Harrower et al. 2010). Concealment might also be more important for fledgling survival and movement when density of raptors (visual predators) is high and olfactory predators such as rodents (Rangen et al. 2000, Colombelli-Négré and Kleindorfer 2009) are kept at low densities.

Although a year effect on fledgling survival is consistent with an effect of annual variation in predator abundance, annual variation in other biotic or abiotic factors could also be invoked. For example, drought intensity had a strong negative effect on postfledging survival in Lark Buntings (*Calamospiza melanocorys*; Yackel Adams et al. 2006); however, no major change occurred in food density in control plots from 2006 to 2011 (Haché et al. 2013b) and, according to a local weather station, no substantial variation in mean temperature (17.3 vs. 16.5°C) or total precipitation (142.9 vs. 144.5 mm) in June and July 2010 versus 2011 (Environment Canada 2012). Also, the observed pattern might have been influenced by density-dependent effects on predation risk through apparent competition. Density of Ovenbird males was lower in treated plots than in controls in 2010 but was similar in 2011, with no evidence for a year effect (Haché et al. 2013b). In the same study plots, 4 bird species had higher densities in 2011 than 2010, but 4 other species showed no year effect (Haché et al. 2013a). Except for the Ovenbird, however, we do not know whether these changes in density are correlated with the number of young fledged. Future studies should investigate the relative importance of density-dependence (conspecifics and heterospecifics) on fledgling survival.

Plot-level abundance of red squirrels, but not that of eastern chipmunks, had an important effect on Ovenbird

postfledging survival, irrespective of year. This was unexpected because eastern chipmunk detections were 20% higher than those of red squirrel, and the chipmunk is a known predator of fledglings (King et al. 2006, Schmidt et al. 2008). In the same study area, Poulin and Villard (2011) showed a negative relationship between daily nest survival rate of Brown Creepers (*Certhia americana*) and the proportion of cone-producing spruce plantations within a 2 km radius of the study plots. They suggested that spruce cone production may increase local abundance of red squirrels and, in turn, affect nest survival in years of low cone crops. In our study, higher plot-level abundance of red squirrels was found in plots located near older plantations or coniferous riparian areas (S. Haché and M.-A. Villard personal observation); hence, landscape structure may influence Ovenbird fitness (see also Burke and Nol 2000). Vitz and Rodewald (2011) mentioned that regional variation in predator abundance could explain the wide differences in postfledging survival reported among studies for a given species. Based on our results, spatial variation in predator abundance may also affect postfledging survival over relatively fine spatial scales.

Previous studies on songbird postfledging survival within partially harvested northern hardwood forests also did not report evidence for harvesting effects (Moore et al. 2010, Eng et al. 2011). Spatial heterogeneity in shrub cover within old, untreated northern hardwood forests (gap-phase dynamics; Runkle 1985) may provide sufficient concealment against visual predators. Similarly, movements seemed unaltered by postharvest regeneration in our plots (see also Berkely et al. 2007, Vitz and Rodewald 2010). Movements of fledglings from controls were not directed toward harvested areas or young plantations, as was predicted based on previous studies (Vitz and Rodewald 2006, Streby et al. 2011a, but see Chandler et al. 2012); however, the peak in capture rate of hatch-year Ovenbirds in Minnesota clearcuts occurred around the second week of August (Streby et al. 2011a), whereas our monitoring ended during the last week of July. Hence, we cannot rule out the importance of early seral forest stands for juvenile Ovenbirds later in the season (see also Streby and Anderson 2012).

In our study area, the forestry company uses herbicides to control deciduous regeneration shortly after planting spruce, which reduces the amount and diversity of food (fruits and invertebrates) available to songbirds and, consequently, may reduce the attractiveness of this habitat to songbirds hatched in nearby hardwood stands. An experimental reduction of food abundance in recent clearcuts (5–12 years old) lowered the frequency of occurrence of mature-forest birds (Major and Desrochers 2012). Streby and Anderson (2013a, 2013b) found that Ovenbird postfledging survival rate was lower in young

clearcuts and when crossing roads than in older sapling-dominated clearcuts (but see Vitz and Rodewald 2013). In our study, the 3 individuals that moved outside their natal stand went into old coniferous stands after crossing a road, but limited sample size prevents us from making strong inferences.

A positive effect of body mass on songbird juvenile survival has often been reported (e.g., Perrins 1965, Nur 1984, Naef-Daenzer et al. 2001, Suedkamp Wells et al. 2007, Mitchell et al. 2011), but many other studies reported no relationship (e.g., Anders et al. 1997, Hovick et al. 2011, Rivers et al. 2012, Streby and Anderson 2013b). In our study, the selection harvest treatment did not influence nestling body mass shortly before fledging, and although movements tended to increase with body mass, no significant relationship was found between body mass and postfledging survival, irrespective of the treatment.

Postfledging survival is an important component of songbird demography, and this critical part of their life cycle must be incorporated in population growth and viability analyses. Our results indicate that for the Ovenbird, a species typically associated with closed-canopy deciduous forest with a relatively open understory, moderate habitat alteration through selection harvesting may not influence survival or movements of fledglings. Effects of spatiotemporal variation in predator abundance on postfledging and nestling survival rates differ, emphasizing the importance of stage-specific survival estimates (Schmidt et al. 2008, Streby and Anderson 2011). Future studies should explore effects of landscape configuration on juvenile survival and address the complex relationships between yearly variations in predator abundance and associated trophic cascades (Yang 2004, Schmidt et al. 2008, Schmidt and Ostfeld 2008). Such information about spatiotemporal variation in predation risk during the postfledging period is needed to accurately model songbird population dynamics.

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