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RESEARCH ARTICLE

## Contrasting patterns of nest survival and postfledging survival in Ovenbirds and Acadian Flycatchers in Missouri forest fragments

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### ABSTRACT

We can improve our ability to assess population viability and forecast population growth under different scenarios by understanding factors that limit population parameters in each stage of the annual cycle. Postfledging mortality rates may be as variable as nest survival across regions and fragmentation gradients, although factors that negatively impact nest survival may affect postfledging individuals in different ways. We examined nest and postfledging survival of Ovenbirds (*Seiurus aurocapilla*) and Acadian Flycatchers (*Empidonax virescens*) in mature forest fragments in central Missouri. We used an information-theoretic approach to determine support for effects of factors intrinsic to the individual or nest site, temporal factors, local vegetation characteristics, and distance to edge on survival in both stages. We also examined the effect of incorporating the resulting survival estimates on population growth. In both species, survival increased from nest to postfledging stages (Ovenbirds:  $0.27 \pm 0.06$  to  $0.50 \pm 0.09$ ; Acadian Flycatcher  $0.30 \pm 0.03$  to  $0.89 \pm 0.11$ ). Age was by far the best predictor of survival in postfledging birds, with the majority of mortalities occurring in the first week out of the nest. We did not find support for survival tradeoffs of habitat used by nesting or postfledging birds. Acadian Flycatcher nest and postfledging survival were both related to variables associated with mature forest. Ovenbird nest survival was most affected by habitat characteristics associated with core mature forest, although postfledging survival may have improved near non-forest edges. We replaced an arbitrary estimate of juvenile survival (half of adult survival) with an estimate incorporating empirical postfledging survival estimates. With these revised parameters, Acadian Flycatcher population growth was more affected (13–26% increase in lambda) than Ovenbird population growth (3–6% change). Our results illustrate that species occupying similar nesting habitat do not necessarily face the same risks during the postfledging period.

**Keywords:** postfledging survival, nest success, population growth, *Seiurus aurocapilla*, radio-telemetry, *Empidonax virescens*

### Patrones contrastantes de supervivencia de los nidos y de los juveniles de *Seiurus aurocapilla* y *Empidonax virescens* en fragmentos de bosque en Missouri

#### RESUMEN

Comprendiendo los factores que limitan los parámetros poblacionales en cada etapa del ciclo anual, podemos mejorar nuestra habilidad de determinar la viabilidad de las poblaciones y de predecir su crecimiento bajo diferentes escenarios. Las tasas de mortalidad posterior al emplumamiento pueden ser tan variables como la supervivencia de los nidos a través de diferentes regiones y gradientes de fragmentación, y los factores que tienen un impacto negativo en la supervivencia de los nidos pueden afectar de diferentes maneras a los individuos después de dejar el nido. Examinamos la supervivencia de los nidos y de los jóvenes de *Seiurus aurocapilla* y *Empidonax virescens* en fragmentos de bosque maduro en el centro de Missouri. Usamos una aproximación de teoría de la información para determinar los efectos sobre la supervivencia en ambas etapas de factores intrínsecos del individuo o del sitio de anidación, factores temporales, características de la vegetación local y la distancia al borde. También examinamos el efecto de incorporar los estimados de supervivencia resultantes en el crecimiento poblacional. En ambas especies la supervivencia se incrementó desde el nido hasta las etapas posteriores al emplumamiento (*S. aurocapilla*:  $0.27 \pm 0.06$  a  $0.50 \pm 0.09$ ; *E. virescens*:  $0.30 \pm 0.03$  a  $0.89 \pm 0.11$ ). La edad fue sin duda el mejor predictor de la supervivencia en las aves juveniles; la mayoría de las muertes ocurrieron en la primera semana por fuera del nido. No encontramos sustento para la evidencia de compromisos sobre la supervivencia impuestos por el hábitat usado por la aves anidantes o los juveniles. La supervivencia de los nidos y de los jóvenes de *E. virescens* estuvo relacionada con variables asociadas con los bosques maduros. La supervivencia de los nidos de *S. aurocapilla* se vio más afectada por las características del hábitat asociadas con el centro de los bosques maduros, aunque la supervivencia de los jóvenes podría ser mayor cerca de los bordes del bosque. Reemplazamos un estimado arbitrario de la supervivencia de los jóvenes (la mitad de la

supervivencia de los adultos) con un valor que incorpora los estimados empíricos de la supervivencia fuera del nido. Con la revisión de estos parámetros, el crecimiento poblacional de *E. virescens* se vio más afectado (incremento en  $\lambda$  de 13 a 26%) que el crecimiento poblacional de *S. aurocapilla* (cambio de 3 a 6%). Nuestros resultados ilustran que las especies que ocupan hábitats de anidación similares no necesariamente enfrentan los mismos riesgos durante el periodo posterior al emplumamiento.

**Palabras clave:** crecimiento poblacional, *Empidonax virescens*, éxito de los nidos, *Seiurus aurocapilla*, supervivencia posterior al emplumamiento, telemetría de radio

## INTRODUCTION

Understanding what factors contribute to population declines in long-distance migrant songbirds is challenging, as populations could be limited during migration, on the breeding grounds, or on the wintering grounds (Faaborg et al. 2010, Marra et al. 2015, Runge et al. 2015, Rushing et al. 2016). This is further complicated because the majority of Neotropical migrant songbirds do not return to their natal area, making annual juvenile survival, an important vital rate affecting populations, difficult to measure (Anders and Marshall 2005). Nesting and postfledging are the 2 distinct juvenile life stages that occur on the breeding grounds, but we have a much better understanding of factors affecting survival during nesting than during postfledging (Cox et al. 2014). We can improve our ability to assess population viability and forecast population growth under different scenarios with a better understanding of the factors that limit population parameters in each stage of the annual cycle.

The effect of local habitat features on survival in each life stage is especially interesting to conservation biologists, as direct action improving survival can be taken through land management. Habitat requirements often change from the nesting to the postfledging period (Faaborg et al. 2010), and factors that negatively impact nest survival may or may not be as important in the postfledging period (Streby et al. 2014). Adults can lead mobile juveniles during the postfledging stage to areas that maximize their survival by minimizing predation risk while maximizing food acquisition. Effects of habitat features on nest success are regularly investigated at a variety of scales (reviewed in Martin 1993, Burhans and Thompson 1998, Thompson 2007). An increasing number of studies have explored habitat feature effects on postfledging survival, although the majority have been univariate tests that have not compared survival for nests and juveniles from the same populations (reviewed in Cox et al. 2014).

The Ovenbird (*Seiurus aurocapilla*) and the Acadian Flycatcher (*Empidonax virescens*) are Neotropical migrant songbirds that nest in similar habitats within large tracts of mature deciduous forests across eastern North America. Both species are area-dependent and sensitive to fragmentation but have very different nesting and foraging strategies (Whitehead and Taylor 2002, Porneluzi et al. 2011). Ovenbirds are ground-foraging and ground-nesting birds while Acadian Flycatchers

forage beneath the canopy in the open air and build nests in the lower canopy. Fledged Ovenbird young are initially unable to fly. In contrast, Acadian Flycatcher juveniles are typically able to make short flights at fledging. Postfledging juvenile Ovenbirds (during dependent and independent stages) use areas of dense ground cover, such as clear-cuts or second-growth forest in both contiguous forest and forest fragments (Lowther 1993, King et al. 2006, Porneluzi et al. 2011, Vitz and Rodewald 2011, Streby and Andersen 2012, Burke 2013). There is less information available for the habitat associations of postfledging Acadian Flycatchers. Ausprey and Rodewald (2011) found that postfledging survival was not strongly related to urbanism or forest edge. These changes in habitat use may suggest that habitat value may differ between the nesting and postfledging periods.

We examined nest and postfledging survival of Ovenbirds and Acadian Flycatchers in Missouri forest fragments from 2012 to 2015. We used an information-theoretic approach (Burnham and Anderson 2002) to determine support for effects of intrinsic, temporal, edge, and local vegetation factors on survival in both the nesting and postfledging stages. We were especially interested in determining if the effects of habitat features on survival changed between nesting and postfledging. We predicted similar species-level responses to temporal factors, likely due to changes in predator community activity (Thompson 2007) and similar responses to intrinsic factors, such as mass at fledging (Naef-Daenzer et al. 2001). We expected divergent species responses to local vegetation features due to differences in nest-site selection, foraging strategies, and development level at fledging. We conducted extensive habitat sampling to test the prediction that Ovenbirds have lower nest survival and higher postfledging survival in closer proximity to areas with more developed understory. We predicted that Acadian Flycatchers have higher survival near areas with more canopy structure and less understory structure. We used these survival parameter estimates in a simple projection model to illustrate the sensitivity of population growth to postfledging survival.

## METHODS

### Study Sites

We conducted our study from 2012 to 2015 on 3 sites within a transitional zone between central hardwood forest and

grassland in Boone, Randolph, and Howard counties in Central Missouri. Our study sites were the Thomas S. Baskett Wildlife Research and Education Center (38.73°N, 92.2°W; 890 ha) in 2012–2015; Rudolf Bennitt State Conservation Area (39.13°N, 92.25°W; 1146 ha) in 2013–2015; and Three Creeks Conservation Area (38.21°N, 92.28°W; 575 ha) in 2014–2015; hereafter Baskett, Bennitt, and Three Creeks, respectively. Study sites consisted of mixed-hardwood forest interspersed with successional red cedar (*Juniperus virginiana*) stands. Sawtimber density and snag density are similar across the 3 study sites ( $P > 0.1$ ). All sites are situated within a matrix of forest patches, old-fields, pasture, and cropland. Acadian Flycatchers nested at all 3 sites and Ovenbirds nested at Bennitt and Baskett; in 2012, however, we only monitored Ovenbirds at Baskett.

### Study Species

Breeding Bird Survey (BBS) data from 1966 to 2013 indicate that Ovenbird and Acadian Flycatcher populations have remained relatively stable nationwide (Sauer et al. 2014). Ovenbirds arrive the final week of April in our region, initiate breeding in early May, and generally stop nesting in late July. Ovenbirds will renest after nest failure but do not attempt a second clutch after successfully fledging young. Acadian Flycatchers typically initiate and continue nesting in central Missouri later than Ovenbirds, nesting from mid-May through mid-August (J. M. A. Jenkins personal observation). Acadian Flycatchers will renest after nest failure and sometimes initiate a second clutch after successfully breeding; 28% of females in our study region fledged a second brood when monitored into September in 2007–2009 (Hirsch-Jacobson 2011). Ovenbird clutches range from 2 to 5 eggs, and have a 12–13 day incubation period, with juveniles fledging ~8 days after hatching (Porneluzi et al. 2011). Fledged Ovenbird young are unable to fly for the first 3–4 days out of the nest and are kept apart from siblings, camouflaged among the leaves and groundcover, and fed by adults. After 4 days the young become increasingly mobile and vocal, remaining mainly on the ground or low vegetation in semi-dependent family groups for 20–30 days (J. M. A. Jenkins personal observation). Acadian Flycatcher clutches typically contain 2 or 3 eggs, have a 13–15 day incubation period, and fledge 13–14 days after hatching (Whitehead and Taylor 2002). Unlike Ovenbird juveniles, Acadian Flycatcher young remain in close association with siblings throughout the dependent period, often perching “snuggled” together in the canopy (Mumford 1964). Juveniles remain partially dependent upon parents for 18–24 days postfledging (J. M. A. Jenkins personal observation).

### Nest Monitoring and Radio Telemetry

We found nests from mid-May to mid-August each year by systematically searching appropriate habitat in study areas

and observing adult behaviors. We monitored nests every 3–5 days, more frequently near hatching and fledging periods, recording the nest stage, number of eggs, nestlings, and occurrence of Brown-headed Cowbird (*Molothrus ater*; hereafter cowbird) parasitism (Martin and Geupel 1993). On the day before projected fledging, we captured all available nestlings and recorded nestling mass ( $\pm 0.1$ g). We supplemented Ovenbird nest captures with opportunistically hand-caught non-volant fledged juveniles (1–2 days out of the nest). We attached unique combinations of 3 colored leg bands and a standard aluminum U.S. Geological Survey leg band to all captured Ovenbirds and attached radio transmitters to 1 or 2 (rarely 3) individuals per brood. All Acadian Flycatcher nestlings received a standard aluminum U.S. Geological Survey band and one juvenile per nest received a single colored leg band and a radio transmitter. Transmitters were attached using a leg-loop harness made with flexible cording (Rappole and Tipton 1991). In 2012, transmitters weighed 0.55 grams, were 3.5–5% of Ovenbird juvenile mass at time of attachment, and had an expected battery life of 22 days (model A1015, Advanced Telemetry Systems (ATS), Itasca, Minnesota, USA). In 2013–2015, transmitters weighed 0.3 g, were 1.8–2.8% of Ovenbird mass and 2.3–3.3% of Acadian Flycatcher mass at time of attachment, and had an expected battery life of 44, 29, and 44 days depending on the model (2013 and 2015: model A2414, ATS; 2014: model PicoPip Ag337, Biotrack, Wareham, Dorset, UK).

We located birds daily or nearly daily by homing using handheld receivers (model R410, ATS, and model R1000, Communication Specialists, Orange, California, USA) and handheld directional antennas (Yagi 3-element and H-Type, ATS). We observed radio-tagged birds for as long as possible without disturbing the individual, usually for 5–20 min. We recorded locations of nests and juveniles in Universal Transverse Mercator (UTM) coordinates with handheld GPS units (GPS error < 10 m). We recorded the coordinates of the location where we first sighted the individual, or if we flushed them, of the area where they resumed normal activity. We assumed our presence did not alter their habitat use. We relocated individuals until the transmitter signal was no longer detectable (transmitter battery failure or dispersal out of study area) or until we determined mortality. We assigned a cause to mortality events when possible. We assumed that an individual was dead if (1) the body or pieces of marked bird were found; (2) the transmitter was found with juvenile feathers or body parts; (3) the transmitter signal was lost, the bird was <14 days postfledging, and we resighted marked siblings or adults near the last location; (4) the damaged or digested radio was found near last location and bird was <4 days postfledge; or (5) we tracked signal to snake body or to same location in hollow tree for >3 days (assumed predation by snake or other). If a signal was lost after 15 days postfledging, we searched

for the signal across the study area and surrounding forest patches on foot, by truck, or by helicopter. If the signal was still lost at the end of the potential battery life, we censored it after the last actual observation because we could not distinguish long-distance movement from mortality.

### Vegetation Sampling

After family groups left the area, we sampled habitat structure at each nest and for at least half of fledgling locations. We used vegetation variables from the previous location for juvenile mortality events when a body was either not found or was found far from the family group, reasoning that the transmitter had been moved by a predator or scavenger. We estimated nest height to the nearest 0.5 m and estimated the percent of nest concealed by vegetation at nest height, 1 m from the nest in each cardinal direction, from above, and below (flycatchers only). We calculated canopy cover at each use point (nest or juvenile location) using the average of 4 spherical densiometer readings (1 in each cardinal direction). We averaged litter depth measurements taken at the central point and 2 m from the central point in each cardinal direction. We estimated percent green groundcover, live herbaceous or woody vegetation >0.3 m high, within an 11.3-m diameter circle. We estimated shrub density by counting woody stems <3 cm in diameter, at ~1.3 m above ground, along two 22.6 m transects in cardinal directions, bisecting the use point and converted this count to density of stems per hectare (stems ha<sup>-1</sup>). We measured the diameter at breast height (DBH) of all stems >3 cm DBH in a 10-factor basal area wedge plot and recorded trees as deciduous, coniferous (primarily cedars), or dead trees (snags). We calculated total basal area (BA) of all live trees and stem densities per hectare of saplings (3.0–12.5 cm DBH), pole timber (12.5–27.5 cm DBH), sawtimber (>27.5 cm DBH), and snags greater than 12.5 cm DBH (West 2009). We estimated understory foliage density using the average of 4 density board (0.3 m wide × 2.0 m tall) measurements taken from 11.3 m in each cardinal direction from the central point. Density board measurements were divided into 3 regions: low (0–0.3 m), mid (0.3–1.0 m), and high (1–2 m). We also created an overall groundcover metric by multiplying the low foliage density board measure with the percent green groundcover for each sample plot. We calculated distance to nearest non-forest edge for each nest and juvenile location remotely in ArcGIS (ESRI 2012) using the 30 m resolution Missouri 2005 Land Use Land Cover Database refined using aerial photos of field sites (<http://msdis.missouri.edu/>; USDA-FSA Aerial Photography Field Office). Non-forest edge included all forest boundaries adjacent to ponds, roads, power line cuts, and other non-forest land uses that were visible from aerial photos; however, trails

and non-improved roads with full canopy coverage were not considered edge.

### Survival Analysis

We used the logistic exposure method to estimate daily survival and relationships with covariates for both nests and postfledging juveniles (Shaffer 2004, Shaffer and Thompson 2007; GENMOD Procedure, SAS Institute, Cary, North Carolina, USA). Because we monitored multiple Ovenbird juveniles from the same brood, we adjusted standard errors for repeated measures using generalized estimating equations by identifying brood as the subject (SAS Institute 2008; Schreiber et al. 2016). We used an information-theoretic approach (Burnham and Anderson 2002) to determine support for effects of temporal, intrinsic, local vegetation (understory and tree level) covariates and distance to non-forest edge on survival. We first tested a priori nest and postfledging survival models within 4 subcategories to determine which were most supported and used these in the final additive model set. The temporal models for both juveniles and nests included a categorical effect of year (0–4 for Ovenbirds and 0–3 for Acadian Flycatchers), ordinal date, ordinal date<sup>2</sup>, ordinal date<sup>3</sup>, a categorical variable of 2-seasons, a categorical variable of 3-seasons, and additive models of year and the other variables. Nest temporal model sets also included the categorical variable nest stage (lay, incubation, and nestling) and additive models of nest stage with other temporal variables. We created categorical variables representing seasonal intervals using the 50<sup>th</sup> percentile of fledging dates to create 2 intervals and the 33<sup>rd</sup> and 66<sup>th</sup> percentile to create 3 intervals for each species. The intrinsic models for juveniles included mass at fledging, number fledged per brood, and their additive combination. The intrinsic models for nests included nest height (flycatchers only), cowbird nest parasitism status, nest concealment, and their combination. Vegetation models included all singular and additive combinations of groundcover, shrub density, litter depth, understory foliage density, sapling density, pole timber density, sawtimber density, total basal area ha<sup>-1</sup>, and canopy cover. If distance to non-forest edge outperformed the null model, it was included in the final additive model set. We normalized all continuous variables before conducting analysis.

Each subcategory model-set was compared to a null model and evaluated using Akaike's Information Criterion adjusted for small sample sizes (AIC<sub>c</sub>). The nest survival null model included intercept and a fixed effect of site. The postfledging survival null model included intercept, site, and age (days since fledging). We included site as a categorical fixed effect in all models to account for any variation due to differences in predator communities or landscape effects between our study locations. We include

a fixed effect of age (days out of the nest) in all postfledging models because juveniles are most vulnerable immediately after leaving the nest (Anders et al. 1997, Brown and Roth 2004, Vitz and Rodewald 2011, Streby and Andersen 2013). We considered subcategory models competitive and moved them to the final model set if a model  $AIC_c$  was lower than the null model, was within 2  $AIC_c$  units of the best model, and did not differ from more supported models only by the addition of uninformative parameters (Arnold 2010). If there were competitive models that described the same aspect of a hypothesis (such as 2-seasons vs. 3-seasons), only the top model was carried forward. Final model sets included all singular and additive combinations of the top subcategory models.

We estimated daily nest and daily postfledging survival for each species with the most-supported model or model-averaged coefficients and predictions when more than one model was competitive in the final model suite (Burnham and Anderson 2002). We present daily survival predictions for each covariate holding all other continuous factors at their means and categorical values at their observed frequencies. We calculated nest period survival for Ovenbirds based on a 25-day nesting cycle (4 lay days, 12 incubation days, and 8 nestling days). For Acadian Flycatchers we used a 30-day nesting cycle (2 lay days, 14 incubation days, 14 nestling days). Overall postfledging period survival rates were created using cumulative survival for the postfledging period: 1–23 days postfledging for Ovenbirds and 1–20 days postfledging for Acadian Flycatchers, based on the mean number of days juveniles were dependent upon parents (Jenkins 2016).

### Population Growth Models

We used a simple population growth model to illustrate the potential utility of incorporating empirical postfledging survival estimates into annual juvenile survival:  $\lambda = P_A + P_j\beta$ , where  $\lambda$  is the population growth rate,  $P_A$  is the annual survival of adult females,  $P_j$  is the annual survival of juveniles, and  $\beta$  is the number of fledged juvenile females produced annually (Pulliam 1988). A population is stable if  $\lambda = 1$ . We calculated  $\beta$  using  $\frac{1}{2} Y_N \times (1 - (1 - P_N)^n)$ , where  $P_N$  is nest success,  $n$  is number of nest attempts, and  $Y_N$  is the mean number of young produced per fledged brood (Anders and Marshall 2005). We assumed a 50:50 sex ratio of fledglings. We did not consider the potential for double brooding in Acadian Flycatchers, or movement between populations in our models. Historically, when empirical estimates of juvenile survival are unknown, first year survival has been arbitrarily designated based on adult survival, typically as half of adult survival (Ricklefs 1973, Greenburg 1980, Temple and Cary 1988). When postfledging survival is known,  $P_j$  can be written as  $P_{PF} \times P_W$ , where  $P_{PF}$  is postfledging period survival and  $P_W$  is overwinter survival.

Unfortunately,  $P_W$  is unknown for the majority of migratory species, including our study species. Nonbreeding season studies of other migratory birds, including Black-throated Blue Warblers (*Setophaga caerulescens*), American Redstarts, (*S. ruticilla*), and Barn Swallows (*Hirundo rustica*), have found equal survival rates for nonbreeding adult and juvenile migratory birds (Marra and Holmes 2001, Sillett and Holmes 2002, Gruebler et al. 2014). However, inexperience may reduce juvenile survival during migration (e.g., Opper et al. 2015), and juvenile birds may be excluded from high-quality wintering habitat, increasing mortality (Sherry and Holmes 1996, Marra and Holmes 2001). We assumed that  $P_{PF} < P_W$  and modeled 2 conservative scenarios for  $P_W$ : where  $P_W = P_A$  and where  $P_W = \frac{3}{4} P_A$ . We compared lambda from postfledge inclusive models and a model produced using the generic juvenile survival value of half of adult annual survival, keeping all other model components stable. We used our calculated fecundity values and an adult annual survival rate of 0.62 for both species—0.62 is the mean of all published adult survival rates for Ovenbirds and is also commonly used for other small migratory passerines (Temple and Cary 1988, Donovan et al. 1995). There are no good estimates of annual survival for *Empidonax* flycatchers. We present all summary variables as means  $\pm$  standard errors (SE).

## RESULTS

### Ovenbird Survival

We monitored 94 Ovenbird nests every  $2.8 \pm 0.06$  days for a total of 308 observations. Thirty-nine Ovenbird nests successfully fledged a mean of  $2.86 \pm 0.05$  young weighing  $14.52 \pm 0.06$  g at time of capture. Predation was the primary cause of nest failure, accounting for 90% of all nest failures. Fifty-three percent of Ovenbird nests were parasitized by cowbirds. Of these 50 parasitized nests, 19 successfully fledged at least 1 Ovenbird. Most nests were first observed after the lay stage (Ovenbirds: 8% lay, 51% incubation, and 41% nestling). Fledging date for Ovenbirds ranged from May 26 to July 15. Ovenbird nests were  $69.24 \pm 2.08\%$  visually concealed. Two Ovenbird nests failed due to adult mortality at the nest.

We attached transmitters to 50 Ovenbird fledglings from 36 known nests (7 from 3 nests in 2012, 11 from 6 nests in 2013, 17 from 14 nests in 2014, and 15 from 13 nests in 2015). An additional 12 non-volant fledged Ovenbirds were opportunistically captured and radio-tagged postfledging (1–2 days postfledge). Four Ovenbird transmitters fell off before radio failure (harness strap failure) and were censored after the last color-band observation (day 1, day 3, day 8, day 19). We recorded 29 Ovenbird mortalities (6 in 2012, 6 in 2013, 9 in 2014, and 8 in 2015). All recorded mortalities occurred in the first 10

**TABLE 1.** Arithmetic mean values ( $\pm$  SE) of vegetation from all locations used by Acadian Flycatcher nests ( $n = 264$ ) and juvenile locations ( $n = 442$ ), and Ovenbird nests ( $n = 94$ ) and juvenile locations ( $n = 556$ ), in Boone County, Missouri, from 2012 to 2015.  $F$  and  $P$  values are given for generalized linear model with fixed effect of site and stage (nest vs. postfledge). Degrees of freedom (df) for the difference between nesting and postfledging Ovenbird and Acadian Flycatcher models was 1 and 657 and 1 and 702, respectively.

	Acadian Flycatcher nests	Acadian Flycatcher juveniles	$F$	$P$	Ovenbird nests	Ovenbird juveniles	$F$	$P$
Canopy cover	94.97 $\pm$ 0.28	95.87 $\pm$ 0.21	4.08	0.04	94.93 $\pm$ 0.38	93.37 $\pm$ 0.41	2.53	0.11
Foliage density (0–2 m)	42.81 $\pm$ 2.45	36.46 $\pm$ 1.74	0.00	0.97	58.88 $\pm$ 3.83	71.97 $\pm$ 2.18	15.08	< 0.001
Leaf litter depth	1.75 $\pm$ 0.08	1.8 $\pm$ 0.06	0.28	0.60	2.63 $\pm$ 0.12	2.03 $\pm$ 0.06	14.45	< 0.001
Shrub density	1252 $\pm$ 97	982 $\pm$ 71	0.28	0.60	1677 $\pm$ 184	2363 $\pm$ 113	12.99	< 0.001
Groundcover	621 $\pm$ 37	507 $\pm$ 25	1.28	0.26	844 $\pm$ 54	982 $\pm$ 26	8.04	0.005
Live tree stems ha <sup>-1</sup>	975 $\pm$ 51	1278 $\pm$ 56	10.77	0.001	959 $\pm$ 104	1263 $\pm$ 49	4.79	0.03
Pole timber stems ha <sup>-1</sup>	155 $\pm$ 9	189 $\pm$ 9	3.48	0.06	194 $\pm$ 23	206 $\pm$ 10	0.03	0.87
Sapling stems ha <sup>-1</sup>	714 $\pm$ 51	778 $\pm$ 43	0.45	0.50	653 $\pm$ 105	731 $\pm$ 38	0.31	0.58
Sawtimber stems ha <sup>-1</sup>	106 $\pm$ 4	115 $\pm$ 3	3.77	0.05	112 $\pm$ 6	106 $\pm$ 3	0.57	0.45
Snag stems ha <sup>-1</sup>	29.35 $\pm$ 3.02	27.78 $\pm$ 2.76	0.11	0.74	22.53 $\pm$ 4.75	29.04 $\pm$ 2.72	0.89	0.35
Basal area ha <sup>-1</sup>	54.26 $\pm$ 1.15	59.59 $\pm$ 1.00	8.55	0.004	55.11 $\pm$ 1.88	54 $\pm$ 0.85	0.53	0.47
Distance to edge (m)	149 $\pm$ 6	141 $\pm$ 5	1.09	< 0.001	168 $\pm$ 11	132 $\pm$ 5	8.44	0.004

days of the postfledging period, with 13 individuals that died before the first relocation. Three individuals from one nest were killed in a weather event on day one and were censored from the analysis. All other Ovenbird mortalities were categorized as predation. Multiple siblings in a brood were depredated in 2 cases, but none of the sibling mortalities took place on the same day. We observed postfledging Ovenbirds for 1–49 days for a total of 669 observations. We were able to sample vegetation at 556 of those observed locations. Birds that survived the study period with radios intact were monitored for  $30.13 \pm 1.26$  days (min = 23 days). Ovenbird nests and juvenile locations differed in mean understory foliage density, litter depth, shrub density, groundcover, overall tree density, and distance from non-forest edge (Table 1).

We had an effective sample size of 754 days for Ovenbird nest survival models and 856 days for Ovenbird postfledging survival models. We model averaged 2 of 22 additive nest survival models, including the covariates site, 3-season, sawtimber density, and snag density (Table 2 and Figure 1). Of the model-averaged covariates, sawtimber density and 3-seasons did not include zero in their 95% confidence intervals (Appendix Table 5 and Figure 1). We model averaged 5 of 8 additive Ovenbird postfledging survival models, including the covariates site, mass, age, sapling density, basal area ha<sup>-1</sup>, and distance to edge (Table 2 and Figure 2). Age was the only model-averaged effect with a 95% confidence interval that did not overlap zero (Appendix Table 6 and Figure 2). Uninformative parameters from supported models not included in model averaging included groundcover ( $\beta = -0.27$ ) and foliage density ( $\beta = -0.35$ ). Daily nest survival was lowest for nests that fledged early in the season (Figure 1A). Daily nest survival decreased as sawtimber density increased (Figure 1C). Overall nest period (25 days) and postfledging period

(0–23 days) survival for Ovenbirds was  $0.27 \pm 0.06$  and  $0.50 \pm 0.09$ , respectively.

### Acadian Flycatcher Survival

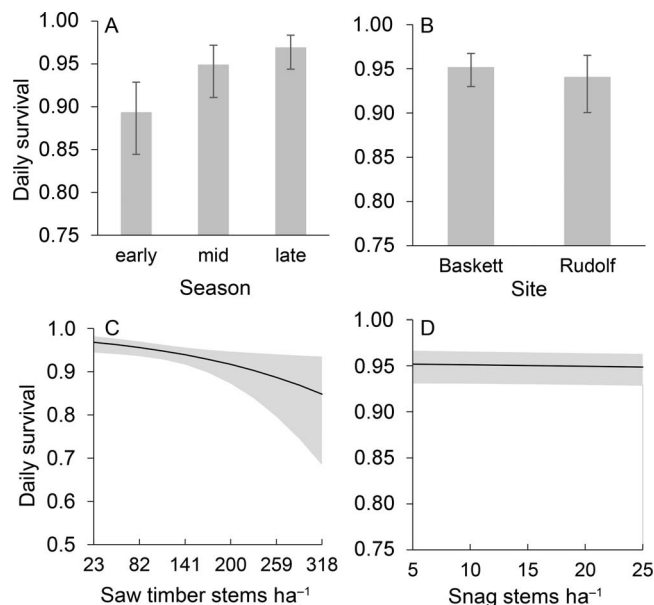
We monitored 264 Acadian Flycatcher nests every  $3.56 \pm 0.04$  days for a total of 1,258 observations. Eighty Acadian Flycatcher nests successfully fledged a mean of  $2.39 \pm 0.03$  young weighing  $11.36 \pm 0.04$  g at time of capture. Predation was the primary cause of nest failure, accounting for 90% of all nest failures. Thirteen percent of Acadian Flycatcher nests were parasitized by cowbirds. No parasitized Acadian Flycatcher nests successfully fledged young. The majority of nests were first observed after the lay stage (3% lay, 53% incubation, and 42% nestling). Acadian Flycatcher nests were between 1.25 and 15 ( $5.98 \pm 0.17$ ) meters high and were  $44.14 \pm 1.19\%$  visually concealed. Acadian Flycatchers fledging dates ranged from June 12 to August 5.

We deployed radio transmitters on 45 Acadian Flycatcher fledglings (11 in 2013, 13 in 2014, and 21 in 2015). We observed Acadian Flycatchers for 1–46 days for a total of 541 observations. We sampled vegetation at 442 juvenile Acadian Flycatcher locations. Birds that survived the study period with radios intact were monitored for  $27.11 \pm 1.57$  days (min = 15 days). The majority of juvenile observations came from Baskett (77%), with 7% from Rudolf and 16% from Three Creeks. Five transmitters fell off before radio failure (harness strap failure) and were censored after the last color-band observation (3 at 1-day and 2 at 2-days postfledging). We recorded 10 Acadian Flycatcher mortality events; all but one occurred before independence from parents (1 in 2013, 3 in 2014, and 6 in 2015). Seven birds died before the first relocation. One carcass was found 2 days postfledging, undamaged but wet after a severe storm. The other 9 mortalities were classified as depredation.

**TABLE 2.** Summary of model-selection results from the best-ranked additive candidate models of top a priori intrinsic, temporal, edge, and vegetation subcategory models explaining survival of Ovenbird nests and postfledging juveniles in central Missouri, 2012–2015. Null models are also included for comparison. Models are ranked according to Akaike’s Information Criterion adjusted for small sample sizes ( $\Delta AIC_c$ ). Models with a lower  $AIC_c$  have more substantial support. Number of parameters ( $K$ ) in each model includes the intercept, site and each additional explanatory variable. Deviance (Dev) and Akaike’s model weights ( $w_i$ ) are also shown.

Model	Dev	$K$	$\Delta AIC_c^*$	$w_i$
<b>Ovenbird nests</b>				
Site + 3-Seasons + Sawtimber + Snag	240.70	6	0.00	0.13
Site + 3-Seasons + Sawtimber	243.45	5	0.72	0.09
Site + 3-Seasons + Sawtimber + Snag + Canopy Cover	240.43	7	1.77	0.05
Null (Site)	264.89	2	11.75	< 0.01
<b>Ovenbird postfledging juveniles</b>				
Age + Site + Edge + Mass	158.40	5	0.00	0.10
Age + Site + Edge	160.63	4	0.21	0.09
Age + Site + Edge + Mass + Foliage Density	157.27	6	0.89	0.07
Age + Site + Mass	161.35	4	0.93	0.06
Age + Site + Edge + Mass + Groundcover	157.62	6	0.93	0.06
Age + Site + Edge + Foliage Density	159.34	5	0.94	0.05
Age + Site + Edge + Sapling + Basal Area	157.62	6	1.25	0.05
Age + Site + Edge + Groundcover	159.79	5	1.38	0.05
Age + Site + Edge + Sapling + Basal Area + Mass	155.81	7	1.47	0.05
Age + Site + Mass + Basal Area + Sapling	157.98	6	1.61	0.05
Age + Site + Sapling + Basal Area	160.07	5	1.67	0.04
Age + Site + Mass + Groundcover	160.19	5	1.78	0.04
Null (Age + Site)	164.25	3	1.80	0.04

\*The lowest  $AIC_c$  value was 252.8 for Ovenbird nests and 168.47 for juveniles.



**FIGURE 1.** Predictions of the best-supported models showing the effects of season (A), site (B), sawtimber density (C), and snag density (D) on daily survival of Ovenbird nests in Missouri, 2012–2015. Estimates are provided for the range of effects sampled while holding other variables at their mean or observed frequency. Error bars (A and B) and shaded areas (C and D) represent 95% confidence intervals.

Acadian Flycatcher nests and juvenile locations differed in mean canopy cover, total tree density, and total basal area (Table 1).

The effective sample sizes for Acadian Flycatchers were 4,002 days for nesting and 695 days for postfledging. There were 24 models in the final nest model set and 88 models in the final postfledging model set. Two models were model averaged to create final nest survival estimates, containing the covariates site, stage, 3-season, and understory foliage density (Table 3 and Figure 3). The nest covariates season and stage had 95% confidence intervals that did not overlap zero (Appendix Table 7 and Figure 3). There were 2 postfledging models that were supported in the final postfledging model selection set; however, only the top model was used for estimates because sawtimber density was included within estimates of total tree density (Table 3). There was a negative effect of tree density ( $\beta = -0.75$ ) in the top model, which corresponded to a positive effect of sawtimber density ( $\beta = 0.78$ ) in the collinear model. The model postfledging covariates for age and tree density had confidence intervals that did not overlap zero (Appendix Table 8 and Figure 4). Nest and postfledging survival was lowest early in the season (Figure 3A and Figure 4A). Daily nest survival decreased with increasing understory foliage density (Figure 3D) while daily postfledging survival was negatively related with tree stem density (Figure 4C). Overall nest period (30 days) and postfledging period (1–20 days)



**TABLE 3.** Summary of model-selection results from the best-ranked additive candidate models of top a priori intrinsic, temporal, and vegetation subcategory models explaining survival of Acadian Flycatcher nests and postfledging juveniles in central Missouri, 2013–2015. Null models are included for comparison. Models are ranked according to Akaike's Information Criterion adjusted for small sample sizes ( $\Delta AIC_c$ ). Models with a lower  $AIC_c$  have more substantial support. Number of parameters ( $K$ ) in each model includes the intercept, site, and each additional explanatory variable. Deviance (Dev) and Akaike's model weights ( $w_i$ ) are also shown.

Model	Dev	$K$	$\Delta AIC_c^*$	$w_i$
<b>Acadian Flycatcher nests</b>				
Site + Stage + 3-Seasons + Foliage Density	1013.73	8	0.00	0.19
Site + Stage + 3-Seasons + Foliage Density + Litter	1012.04	9	0.32	0.17
Site + Stage + 3-Seasons + Foliage Density + Nest Height	1013.11	9	1.39	0.10
Site + Stage + 3-Seasons	1017.22	7	1.48	0.09
Site + Stage + 3-Seasons + Foliage Density + Parasite	1013.27	9	1.55	0.09
Site + Stage + 3-Seasons + Foliage Density + Litter + Parasite	1011.51	10	1.80	0.08
Site + Stage + 3-Seasons + Foliage Density + Litter + Nest Height	1011.62	10	1.91	0.08
Null (Site)	1043.11	3	19.35	<0.01
<b>Acadian Flycatcher postfledging juveniles</b>				
Age + Site + Litter + Ordinal Date <sup>3</sup> + Mass + Tree Density	56.63	10	0.00	0.15
Age + Site + Litter + Ordinal Date <sup>3</sup> + Mass + Tree Density + Total Basal Area	54.90	11	0.34	0.13
Age + Site + Litter + Ordinal Date <sup>3</sup> + Mass + Sawtimber	58.44	10	1.81	0.06
Null (Age + Site)	74.97	4	6.08	<0.01

\* The lowest  $AIC_c$  value was 1029.76 for Ovenbird nests and 76.95 for juveniles.

# Models with covariate polynomials also included all lower levels.

survival of Acadian Flycatchers was  $0.30 \pm 0.03$  and  $0.89 \pm 0.11$ , respectively.

### Population Growth

Population growth models using the arbitrary juvenile survival estimate of  $\frac{1}{2} P_A$  projected populations in decline for both species (Table 4). Acadian Flycatcher models incorporating empirical postfledging period survival with either high or conservative winter survival predicted either a 26% or 13% increase in lambda, respectively, above the arbitrary estimate (Table 4). The effect of incorporating empirical postfledging survival estimates was not as great for Ovenbird population growth estimates. The model incorporating Ovenbird postfledge survival with high winter survival projected a 3% higher growth rate compared to the arbitrary estimate and the model incorporating Ovenbird postfledge survival with conservative winter survival pro-

jected a 5% lower growth rate compared to the arbitrary estimate (Table 4).

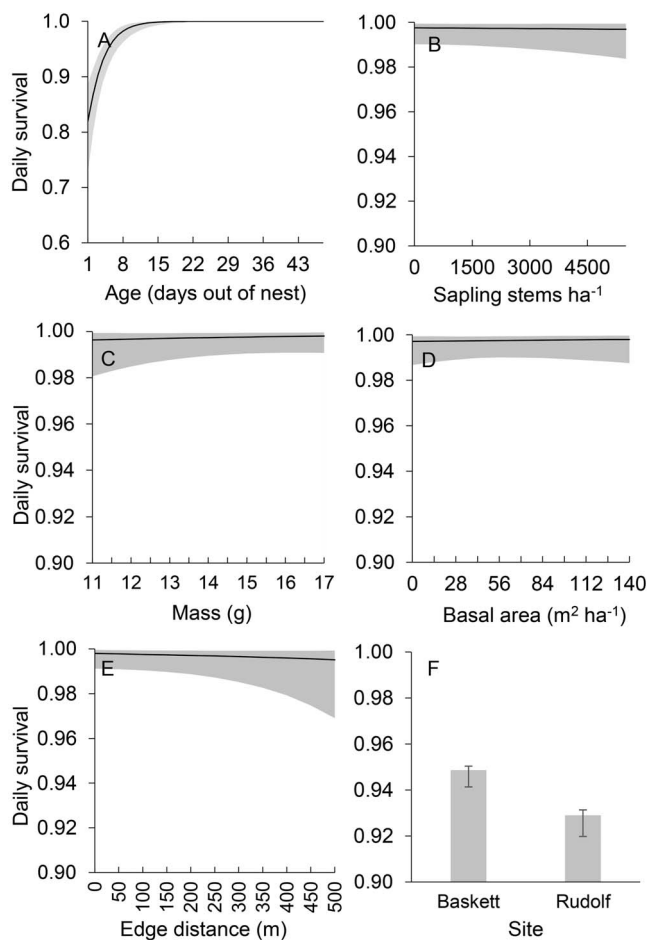
### DISCUSSION

We did not find any clear support for tradeoffs in the effects of local habitat characteristics on survival of nests vs. fledglings for either of our species. Acadian Flycatcher nest and postfledging survival were both related to variables associated with mature forest; low understory foliage density was related to higher nest survival (Figure 3D) and low overall tree density (with more big trees) and high litter depths were related to higher postfledging survival (Figure 4C, 4D). Contrary to our results, survival of postfledging Acadian Flycatchers in Ohio riparian forests was positively associated with tree density, negatively associated with large trees, and positively associated with small trees (Vitz and Rodewald 2011). This difference

**TABLE 4.** Population growth estimates ( $\lambda$ ) and model parameter values for Missouri forest fragment populations from 2012 to 2015 including annual survival rates for adults ( $P_A$ ) and juveniles ( $P_J$ ), juvenile postfledging period survival ( $P_{PF}$ ) and overwinter survival ( $P_W$ ), nest success ( $P_N$ ), mean number of nest attempts ( $n$ ), and mean number of fledglings per fledged brood ( $Y_N$ ).

	$\lambda$	$P_A$	$P_J$	$\beta$	$P_{PF}$	$P_W^*$	$P_N$	$n$	$Y_N$
<b>Ovenbirds</b>									
Empirical, $P_W = P_A$	0.92	0.62	0.34	0.88	0.50	0.67	0.27	3	2.9
Empirical, $P_W < P_A$	0.84	0.62	0.25	0.88	0.50	0.50	0.27	3	2.9
Arbitrary, $P_J = \frac{1}{2} P_A$	0.89	0.62	0.31	0.88	-	-	0.27	3	2.9
<b>Acadian Flycatchers</b>									
Empirical, $P_W = P_A$	1.09	0.62	0.60	0.79	0.89	0.67	0.30	3	2.4
Empirical, $P_W < P_A$	0.97	0.62	0.45	0.79	0.89	0.50	0.30	3	2.4
Arbitrary, $P_J = \frac{1}{2} P_A$	0.87	0.62	0.31	0.79	-	-	0.30	3	2.4

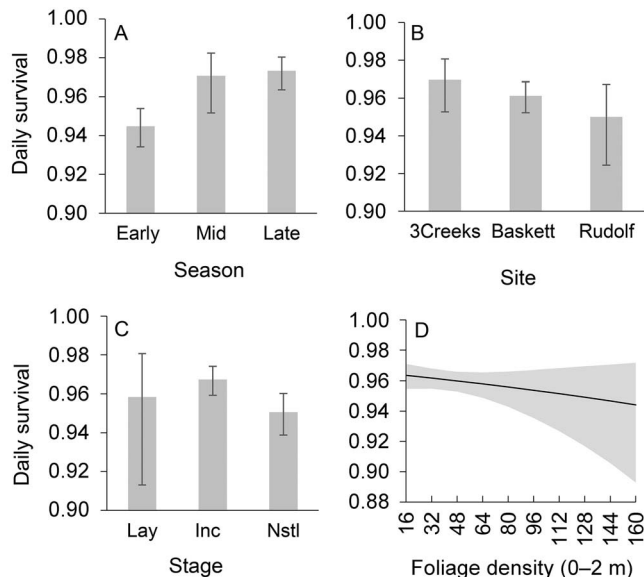
\* We used a 10-month period of adult survival since juveniles spent  $\sim 2$  months in the nest and postfledging.



**FIGURE 2.** Predictions of the best-supported models showing the effects of age (A), sapling density (B), mass (C), basal area (D), distance to non-forest edge (E), and site (F) on daily survival of postfledging Ovenbirds in Missouri, 2012–2015. Estimates are provided for the range of effects sampled while holding other variables at their mean or observed frequency. Shaded areas (A–E) and error bars (F) represent 95% confidence intervals.

may be due to structural differences between urban riparian corridors and mature forest fragments with distinct canopy layers. We observed Acadian Flycatcher family groups utilizing both mid- and high-canopy areas for foraging. We observed independent postfledging Acadian Flycatchers utilizing areas with high tree densities, such as forest edge areas or cedar patches, although these observations took place after all of our recorded mortality events.

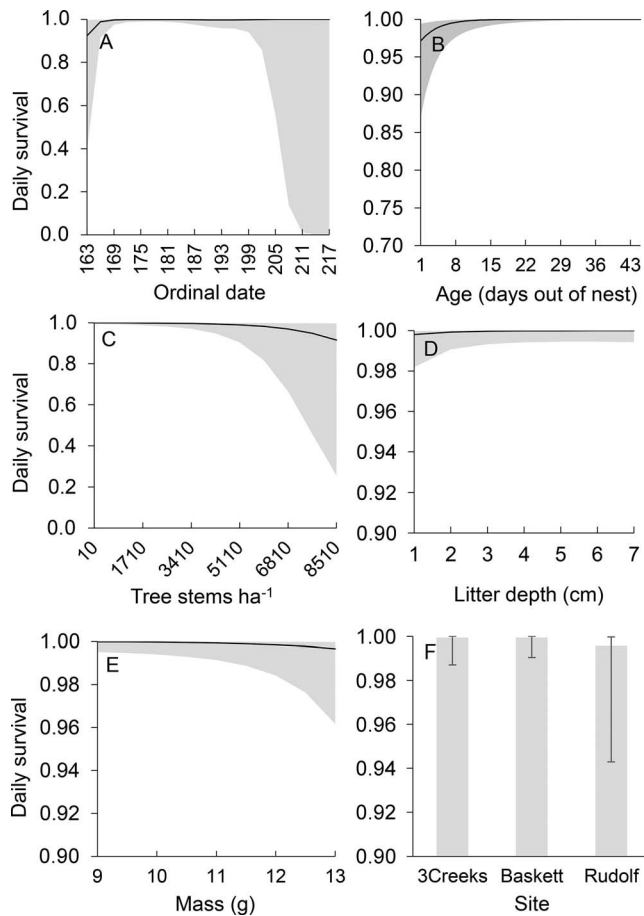
Contrary to our prediction, we did not find support for habitat survival tradeoffs for Ovenbirds. Ovenbird nest survival was most affected by habitat characteristics associated with core mature forest areas; low sawtimber density was related to higher nest survival. However, our top postfledging survival model did not have any habitat covariates without zero in their 95% confidence intervals.



**FIGURE 3.** Predictions of the best-supported models showing the model averaged effects of season (A), site (B), nest stage (C), and understory foliage density (D) on daily survival of Acadian Flycatcher nests in Missouri, 2013–2015. Estimates are provided for the range of effects sampled while holding other variables at their mean or observed frequencies. Error bars (A–C) and shaded area (D) represent 95% confidence intervals.

Postfledging studies in harvested and contiguous mature forest found strong effects of understory density on Ovenbird postfledging survival (King et al. 2006, Vitz and Rodewald 2011). We did find that Ovenbird postfledging daily movements decreased once individuals located dense understory vegetation, and we found that postfledging Ovenbird resource selection was positively affected by understory foliage density (Jenkins 2016). The importance of understory cover to survival may increase when there is a limited supply of dense cover near nest sites; the distribution of understory structure in our fragmented sites (edges, power line cuts, trails, roads, and creeks) may not be sparse enough to negatively affect postfledging survival.

Landscape-level habitat features, such as percent forest cover or extent of fragmentation, may affect nesting and postfledging survival through changes in predator community distribution and abundance (Dijak and Thompson 2000, Cox et al. 2012). Rates of nest parasitism and nest predation of mature-forest-nesting birds often increase near forest edges, especially when areas are fragmented (Hahn and Hatfield 1995, Donovan et al. 1997, Flaspohler et al. 2001). We did not observe a trend of reduced survival near edges with our multivariate models of nest survival or postfledging survival. Distance to edge was only included in the top model for Ovenbird postfledging survival with a mean negative effect, suggesting potentially higher post-



**FIGURE 4.** Predictions of the best supported models showing the effects of season (A), age (B), tree density (C), litter depth (D), mass (E), and site (F) on daily survival of postfledging Acadian Flycatchers in Missouri, 2013–2015. Shaded areas (A–E) and error bars (F) represent 95% confidence intervals.

fledging survival near forest edges. However, the 95% confidence interval overlapped zero. Postfledging Spotted Towhee (*Pipilo maculatus*) nest success was higher and postfledging survival was lower near forest edges (Shipley et al. 2013), suggesting a need to consider species and breeding stages individually when considering edge effects. Postfledging survival does not always change in the same manner as nest success over fragmentation gradients. Wood Thrush (*Hylocichla mustelina*) postfledging survival in Missouri was higher in forest fragments surrounded by agriculture (mainly pastures) than in contiguous mature forest, directly contrasting the trend in nest survival (Fink 2003). However, Hooded Warbler (*Setophaga citrina*) postfledging survival did not differ between large and small forest fragments in Pennsylvania, although nest success declined with fragment size (Rush and Stutchbury 2008). We may not have found effects of edge or percent forest cover on survival because our study sites were essentially in a single landscape context, and strong

fragmentation effects have generally been found when a wide range of fragmentation and forest cover are studied (Thompson 2007). There is a need for further investigation of postfledging survival in fragmented forest.

Temporal factors such as season (early summer vs. late summer) are usually interpreted as proxy indicators for changes in predator behavior, food availability, or weather (Thompson 2007). Overall, there was a positive relationship between survival and season for both nests and postfledging birds in our study. Nest survival for both species was lowest early and higher later. Acadian Flycatcher juveniles that fledged later in the season also had higher daily survival probabilities. We did not find a strong seasonal effect on postfledging Ovenbird survival, although we began nest searching after Ovenbird spring arrival, so we may have missed some early nest attempts. Ovenbirds finished attempting nests earlier (mid-July) than Acadian Flycatchers (September). If any seasonal effects were present, they may have been overpowered by the strong relationship of Ovenbird age and survival.

The average postfledging period survival was much lower for Ovenbirds than for Acadian Flycatchers. In general, the relationship of age (time out of the nest) and daily postfledging survival for both species fits the general pattern of low initial daily survival that stabilizes to high daily survival by independence from parental care, as discussed by Cox et al. (2014) in a review of 45 studies of 35 passerine species. We did not observe a second spike in mortality, reported in some studies, when birds became independent (Anders et al. 1997). Our observed difference in period survival is likely due to the difference in fledging age and, to a lesser degree, differences in postfledging foraging behavior between the 2 species. The longer nestlings remain in the nest, the larger (higher mass) and more resilient they are once fledged (Cox et al. 2014). Individuals in better condition are also more likely to attain sustained flight more quickly postfledging than individuals in poor condition, shortening their time of extreme vulnerability to predation (Naef-Daenzer et al. 2001). The effects of mass on survival is variable in postfledging studies; some report positive effects (Dhondt 1979, Naef-Daenzer et al. 2001, Dybala et al. 2013) and some report no effect (Anders et al. 1997, Streby and Andersen 2013, Haché et al. 2014). Initial body condition may be less important for species like flycatchers that are volant at fledging. Also, we should consider that while the effect of mass may represent lower body condition, it may also signify cases where birds fledged earlier than was ideal, either due to forced fledging by predators or our handling of nestlings.

Our nest period survival estimates (equivalent to period nest success) for both species are within the range of reported values in our region (Donovan et al. 1995, Hirsch-Jacobson 2011) and studies in other highly fragmented

areas (Donovan et al. 1995, Whitehead and Taylor 2002, Bakermans et al. 2012). The only other estimate for postfledging survival of Acadian Flycatchers is a period survival (22 day) of  $0.72 \pm 0.10$  in mature riparian forests within the urban matrix of central Ohio (Ausprey and Rodewald 2011). Postfledging period (21 days) survival was equally high for 2 other *Empidonax* flycatchers in New Mexico: 0.74 for Willow Flycatchers (*E. traillii*) and 0.88 for Dusky Flycatchers (*E. oberholseri*) (Vormwald et al. 2011). Other estimates of Ovenbird postfledging survival come from contiguous mature forest and actively harvested forests (clear cuts and selection cuts). To our knowledge; we are the first to estimate Ovenbird postfledging survival in stable (low disturbance) forest fragments surrounded by an agricultural matrix. Our period survival estimate of 0.50 (23 days) is moderate compared to higher survival in relatively undisturbed mature forests and lower survival reported in forests with active timber harvest. In contiguous forest of northern New Hampshire, Ovenbird postfledging period (21 days) survival was 0.68 (King et al. 2006). Survival was also high in a 70% forested landscape in Ohio: 0.70 for 21 days postfledging (Vitz and Rodewald 2011). Ovenbird postfledging survival was lower in harvested Minnesota mature forest (clear-cut regime): 0.42 for 22 days (Streby and Anderson 2011; period rate calculated by Cox et al. 2014). Ovenbird postfledging survival is lower in highly managed (harvested) forest in New Brunswick, Canada: 0.45 for 14 days (Haché et al. 2014). Variation in predator community distribution and abundance, known to affect nest survival, may be responsible for the large variation reported in Ovenbird postfledge survival rates (Dijak and Thompson 2000, Cox et al. 2014). For example, eastern chipmunks (*Tamias striatus*), one of the main nest and fledgling predators reported in New England (King et al 2006, Schmidt et al 2008, Haché et al 2014), are rare in our Missouri forest fragments, where snakes are the most common nest predator (Cox et al. 2012). Snakes were the only predators we were able to conclusively identify for postfledging Ovenbirds and Acadian Flycatchers. Hierarchical multi-scale models incorporating landscape effects (Thompson et al. 2002) specific to the postfledging period would help researchers understand the variation in survival observed across species' ranges.

Variation in Ovenbird postfledging survival across study regions and the variation between our study species highlights a need for expanding the number of species and landscapes where full breeding season (both nesting and postfledging) survival is investigated (Cox et al. 2014). Our results also illustrate that we should not assume that species occupying similar nesting habitat will have similar risk after fledging. We did not detect survival tradeoffs for habitat utilized in the nesting and postfledging periods, but the effects of vegetation on a postfledging

individual likely changes along with their behavior. Furthermore, the change in estimated population growth when we incorporated postfledging survival rates into juvenile survival was much more pronounced for Acadian Flycatchers than for Ovenbirds, suggesting that the importance of postfledging mortality to population models of forest breeding migratory songbirds varies among species. The addition of a postfledging component to nesting studies, even for just 2 weeks postfledging, would greatly improve our understanding of potential tradeoffs between the nesting and postfledging period associated with habitat or landscape (Cox et al. 2014; however, see Dybala et al. 2013).

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**Author contributions:** J. Jenkins led and worked on all aspects of this study; J. Faaborg and F. Thompson contributed to the conception and design of the study and writing the manuscript; F. Thompson assisted with data analysis.

## LITERATURE CITED

- Anders, A. D., D. C. Dearborn, J. Faaborg, and F. R. Thompson III (1997). Juvenile survival in a population of Neotropical migrant birds. *Conservation Biology* 11:698–707.
- Anders, A. D., and M. R. Marshall (2005). Increasing the accuracy of productivity and survival estimates in assessing landbird population status. *Conservation Biology* 19:66–74.
- Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *The Journal of Wildlife Management* 74:1175–1178.
- Ausprey, I. J., and A. D. Rodewald (2011). Postfledging survivorship and habitat selection across a rural-to-urban landscape gradient. *The Auk* 128:293–302.

- Bakermans, M. H., A. D. Rodewald, and A. C. Vitz (2012). Influence of forest structure on density and nest success of mature forest birds in managed landscapes. *The Journal of Wildlife Management* 76:1225–1234.
- Brown, W. P., and R. R. Roth (2004). Juvenile survival and recruitment of Wood Thrushes *Hylocichla mustelina* in a forest fragment. *Journal of Avian Biology* 35:316–326.
- Burhans, D. E., and F. R. Thompson III (1998). Effects of time and nest-site characteristics on concealment of songbird nests. *The Condor* 100:663–672.
- Burke, A. D. (2013). Mature forest-breeding bird use of early-successional habitat. M.A. thesis, University of Missouri, Columbia, MO, USA.
- Burnham, K. P., and D. R. Anderson (2002). *Model Selection and Multimodel Inference: A Practical Information Theoretic Approach*, second edition. Springer-Verlag, New York, NY, USA.
- Cox, W. A., F. R. Thompson III, A. S. Cox, and J. Faaborg (2014). Post-fledging survival in passerine birds and the value of post-fledging studies to conservation. *The Journal of Wildlife Management* 78:183–193.
- Cox, W. A., F. R. Thompson III, and J. Faaborg (2012). Landscape forest cover and edge effects on songbird nest predation vary by nest predator. *Landscape Ecology* 27:659–669.
- Dhondt, A. A. (1979). Summer dispersal and survival of juvenile Great Tits in southern Sweden. *Oecologia* 42:139–157.
- Dijak, W. D., and F. R. Thompson III (2000). Landscape and edge effects on the distribution of mammalian predators in Missouri. *The Journal of Wildlife Management* 64:209–216.
- Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson III (1997). Variation in local-scale edge effects: Mechanisms and landscape context. *Ecology* 78:2064–2075.
- Donovan, T. M., F. R. Thompson III, J. Faaborg, and J. R. Probst (1995). Reproductive success of migratory birds in habitat sources and sinks. *Conservation Biology* 9:1380–1395.
- Dybala, K. E., T. Gardali, and J. M. Eadie (2013). Dependent vs. independent juvenile survival: Contrasting drivers of variation and the buffering effect of parental care. *Ecology* 94:1584–1593.
- Environmental Systems Resource Institute (ESRI) (2012). *ArcGIS Desktop: Release 10.1*. Redlands, CA, USA.
- Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, S. C. Latta, et al. (2010). Recent advances in understanding migration systems of New World land birds. *Ecological Monographs* 80:3–48.
- Fink, M. L. (2003). Post-fledging ecology of juvenile Wood Thrush in fragmented and contiguous landscapes. Ph.D. dissertation, University of Missouri, Columbia, MO, USA.
- Flaspohler, D. J., S. A. Temple, and R. N. Rosenfield (2001). Species-specific edge effects on nest success and breeding bird density in a forested landscape. *Ecological Applications* 11:32–46.
- Greenburg, R. (1980). Demographic aspects of long-distance migration. In *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, Editors). Smithsonian Institution Press, Washington, D.C., USA. pp. 493–504.
- Grüebler, M. U., F. Korner-Nievergelt, and B. Naef-Daenzer (2014). Equal nonbreeding period survival in adults and juveniles of a long-distant migrant bird. *Ecology and Evolution* 4:756–765.
- Grzybowski, J. A. (2005). An estimate of juvenile survival in Black-capped Vireos and its implications to source–sink analyses of songbirds. In *Bird Conservation Implementation and Integration in the Americas: Proceedings of the Third International Partners in Flight Conference* (C. J. Ralph and Terrell D. Rich, Editors). USDA Forest Service General Technical Report PSW-GTR-191, U.S. Dept. of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA. pp. 810–812.
- Haché, S., E. M. Bayne, and M.-A. Villard (2014). Postharvest regeneration, sciurid abundance, and postfledging survival and movements in an Ovenbird population. *The Condor: Ornithological Applications* 116:102–112.
- Hahn, D. C., and J. S. Hatfield (1995). Parasitism at the landscape scale: Cowbirds prefer forests. *Conservation Biology* 9:1415–1424.
- Hersek, M. J., M. A. Frankel, J. A. Cigliano, and F. E. Wasserman (2002). Brown-headed Cowbird parasitism of Ovenbirds in suburban forest fragments. *The Auk* 119:240–243.
- Hirsch-Jacobson, R. (2011). Population dynamics of a migrant songbird: Do we need to monitor the entire breeding season? Ph.D. dissertation, University of Missouri, Columbia, MO, USA.
- Jenkins, J. M. (2016). Nesting and postfledging ecology of Neotropical migrant songbirds in Missouri forest fragments. Ph.D. dissertation, University of Missouri, Columbia, MO, USA.
- King, D. I., R. M. Degraaf, M.-L. Smith, and J. P. Buonaccorsi (2006). Habitat selection and habitat-specific survival of fledgling Ovenbirds (*Seiurus aurocapilla*). *Journal of Zoology* 269:414–421.
- Lowther, P. E. (1993). Brown-headed Cowbird (*Molothrus ater*). In *The Birds of North America*, no. 47 (A. Poole, Editor). Birds of North America, Philadelphia, PA, USA. doi:10.2173/bna.47
- Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra (2015). A call for full annual cycle research in animal ecology. *Biology Letters* 11:20150552. doi:10.1098/rsbl.2015.0552
- Marra, P. P., and R. Holmes (2001). Consequences of dominance-mediated habitat segregation in American Redstarts during the nonbreeding season. *The Auk* 118:92–104.
- Martin, T. (1993). Nest predation and nest sites. *BioScience* 43: 523–532.
- Martin, T. E., and G. R. Geupel (1993). Nest-monitoring plots: Methods for locating nests and monitoring success. *Journal of Field Ornithology* 64:507–519.
- Mumford, R. E. (1964). *The Breeding Biology of the Acadian Flycatcher*. Museum of Zoology, University of Michigan, Ann Arbor, MI, USA.
- Naef-Daenzer, B., F. Widmer, and M. Nuber (2001). Differential post-fledging survival of Great and Coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* 70:730–738.
- Oppel, S., V. Dobrev, V. Arkumarev, V. Saravia, A. Bounas, E. Kret, M. Velevski, S. Stoychev, and S. C. Nikolov (2015). High juvenile mortality during migration in a declining population of a long-distance migratory raptor. *Ibis* 157:545–557.
- Porneluzi, P., M. A. Van Horn, and T. M. Donovan (2011). Ovenbird (*Seiurus aurocapilla*). In *The Birds of North America*,

- no. 88 (A. Poole, Editor). Birds of North America, Philadelphia, PA, USA. doi:[10.2173/bna.88](https://doi.org/10.2173/bna.88)
- Pulliam, H. R. (1988). Sources sinks and population regulation. *American Naturalist* 132:652–661.
- Rappole, J., and A. Tipton (1991). New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62:335–337.
- Ricklefs, R. E. (1973). Fecundity, mortality, and avian demography. In *Breeding Biology of Birds* (D. S. Farner, Editor). National Academy of Sciences, Washington, D.C., USA. pp. 336–435.
- Runge, C. A., J. E. M. Watson, S. H. M. Butchart, J. O. Hanson, H. P. Possingham, and R. A. Fuller (2015). Protected areas and global conservation of migratory birds. *Science* 350:1255–1258.
- Rush, S. A., and B. J. M. Stutchbury (2008). Survival of fledgling Hooded Warblers (*Wilsonia citrina*) in small and large forest fragments. *The Auk* 125:183–191.
- Rushing, C. S., T. B. Ryder, and P. P. Marra (2016). Quantifying drivers of population dynamics for a migratory bird throughout the annual cycle. *Proceedings of the Royal Society of London, Series B* 283:20152846. doi:[10.1098/rspb.2015.2846](https://doi.org/10.1098/rspb.2015.2846)
- SAS Institute (2008). SAS-STAT User's Guide. Version 6, 4th edition. SAS Institute, Cary, NC, USA.
- Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski Jr., and W. A. Link (2014). The North American Breeding Bird Survey, results and analysis 1966–2013. Version 01.30.2015. USGS Patuxent Wildlife Research Center, Laurel, MD, USA.
- Schmidt, K. A., S. A. Rush, and R. S. Ostfeld (2008). Wood Thrush nest success and post-fledging survival across a temporal pulse of small mammal abundance in an oak forest. *Journal of Animal Ecology* 77:830–837.
- Schreiber, L. A., C. P. Hansen, M. A. Rumble, J. J. Millsbaugh, F. R. Thompson III, R. S. Gamo, J. W. Kehmeier, and N. Wojcik (2016). Greater Sage-Grouse apparent nest productivity and chick survival in Carbon County, Wyoming. *Wildlife Biology* 22:37–44.
- Shaffer, T. L. (2004). A unified approach to analyzing nest success. *The Auk* 121:526–540.
- Shaffer, T. L., and F. R. Thompson III (2007). Making meaningful estimates of nest survival with model-based methods. In *Beyond Mayfield: Measurement of Nest-Survival Data* (S. L. Jones and G. R. Geupel, Editors). *Studies in Avian Biology* 34: 84–95.
- Sherry, T. W., and R. T. Holmes (1996). Winter habitat quality, population limitation, and conservation of Neotropical–Nearctic migrant birds. *Ecology* 77:36–48.
- Shipley, A. A., M. T. Murphy, and A. H. Elzinga (2013). Residential edges as ecological traps. *The Auk* 130:501–511.
- Sillett, T. S., and R. T. Holmes (2002). Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296–308.
- Streby, H. M., and D. E. Andersen (2011). Seasonal productivity in a population of migratory songbirds: Why nest data are not enough. *Ecosphere* 2:1–15.
- Streby, H. M., and D. E. Andersen (2012). Movement and cover-type selection by fledgling Ovenbirds (*Seiurus aurocapilla*) after independence from adult care. *The Wilson Journal of Ornithology* 124:620–625.
- Streby, H. M., and D. E. Andersen (2013). Survival of fledgling Ovenbirds. *The Condor* 115:403–410.
- Streby, H. M., J. M. Refsnider, S. M. Peterson, and D. E. Andersen (2014). Retirement investment theory explains patterns in songbird nest-site choice. *Proceedings of the Royal Society of London, Series B* 281:20131834. doi:[10.1098/rspb.2013.1834](https://doi.org/10.1098/rspb.2013.1834)
- Temple, S., and J. Cary (1988). Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conservation Biology* 2:340–347.
- Thompson, F. R., III (2007). Factors affecting nest predation on forest songbirds in North America. *Ibis* 149:98–109.
- Thompson, F. R., III, T. M. Donovan, and R. M. Degraaf (2002). A multi-scale perspective of the effects of forest fragmentation on birds in eastern forests. In *Effects of Habitat Fragmentation on Birds in Western Landscapes: Contrasts with Paradigms from the Eastern U.S.* (T. L. George and D. S. Dobkin, Editors). *Studies in Avian Biology* 25:8–19.
- Vitz, A. C., and A. D. Rodewald (2011). Influence of condition and habitat use on survival of post-fledging songbirds. *The Condor* 113:400–411.
- Vormwald, L. M., M. L. Morrison, H. A. Mathewson, M. C. Cocimano, and B. A. Collier (2011). Survival and movements of fledgling Willow and Dusky flycatchers. *The Condor* 113: 834–842.
- West, P. (2009). *Tree and Forest Measurement*, second edition. Springer-Verlag, Berlin, Germany.
- Whitehead, D. R., and T. Taylor (2002). Acadian Flycatcher (*Empidonax vireescens*). In *The Birds of North America*, no. 614 (A. Poole, Editor). Birds of North America, Philadelphia, PA, USA. doi:[10.2173/bna.614](https://doi.org/10.2173/bna.614)

## APPENDIX

**APPENDIX TABLE 5.** Model-averaged coefficients ( $\beta$ ), unconditional standard error (SE), and confidence intervals (CI) from the 2 best-supported models of the probability of Ovenbird nest survival in Missouri, 2012–2015.

Parameter	$\beta$	SE	95% CI
Intercept	3.29	0.38	2.53, 4.06
TriSeason-1	-1.33	0.38	-2.09, -0.56
TriSeason-2	-0.52	0.44	-1.40, 0.36
Site-Baskett	0.22	0.33	-0.43, 0.88
Site-Rudolf	0.00	0.00	0.00, 0.00
Sawtimber density	-0.34	0.14	-0.62, -0.07
Snag density	-0.16	0.17	-0.50, 0.19

**APPENDIX TABLE 6.** Model-averaged coefficients ( $\beta$ ), unconditional standard error (SE), and confidence intervals (CI) from the 5 best-supported models of postfledging Ovenbird survival in Missouri, 2012–2015, with repeated measures accounting for multiple individuals per brood.

Parameter	$\beta$	SE	95% CI
Intercept	5.74	0.68	4.38, 7.10
Site-Baskett	0.34	0.38	-0.43, 1.10
Mass	0.16	0.21	-0.27, 0.58
Age	3.39	0.59	2.23, 4.56
Sapling	-0.04	0.07	-0.18, 0.11
Basal area ha <sup>-1</sup>	0.05	0.10	-0.16, 0.26
Edge distance	-0.21	0.22	-0.65, 0.23

**APPENDIX TABLE 7.** Model-averaged estimated coefficients ( $\beta$ ), unconditional standard error (SE), and confidence intervals (CI) for the 2 best-supported models of Acadian Flycatcher nest survival in Missouri, 2013–2015.

Parameter	$\beta$	SE	95% CI
Intercept	3.62	0.27	3.08, 4.16
Stage-INC	0.44	0.16	0.12, 0.75
Stage-LAY	0.18	0.41	-0.63, 1.00
TriSeason-1	-0.75	0.18	-1.12, -0.38
TriSeason-2	-0.09	0.30	-0.70, 0.51
Site-Baskett	-0.25	0.26	-0.77, 0.27
Site-Rudolf	-0.52	0.29	-1.10, 0.06
Site-3Creeks	0.00	0.00	0.00, 0.00
Foliage density	-0.12	0.12	-0.35, 0.11

**APPENDIX TABLE 8.** Estimated coefficients ( $\beta$ ), standard error (SE), and confidence intervals (CI) from the best-supported candidate model of postfledging Acadian Flycatcher survival in Missouri, 2013–2015.

Parameter	$\beta$	SE	95% CI
Intercept	7.38	1.52	4.39, 10.36
Age	2.58	0.84	0.94, 4.23
Site-Baskett	-0.02	1.41	-2.77, 2.74
Site-Rudolf	-1.94	1.44	-4.76, 0.89
Litter	1.10	0.61	-0.09, 2.30
Ordinal date	-0.77	1.05	-2.82, 1.28
Ordinal date <sup>2</sup>	-1.13	0.54	-2.19, -0.08
Ordinal date <sup>3</sup>	0.72	0.49	-0.24, 1.68
Mass	-0.74	0.40	-1.52, 0.04
Tree density	-0.75	0.32	-1.37, -0.14