

NESTING AND POSTFLEDGING ECOLOGY OF NEOTROPICAL MIGRANT
SONGBIRDS IN MISSOURI FOREST FRAGMENTS

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by
JULIANNA MARIE ARNTZEN JENKINS

Dr. John Faaborg, Dissertation Supervisor

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The undersigned, appointed by the dean of the Graduate School, have examined the dissertation entitled

NESTING AND POSTFLEDGING ECOLOGY OF
NEOTROPICAL MIGRANT SONGBIRDS
IN MISSOURI FOREST FRAGMENTS

presented by JULIANNA M. A. JENKINS,

a candidate for the degree of DOCTOR OF PHILOSOPHY

and hereby certify that in their opinion it is worthy of acceptance.

Professor John Faaborg

Dr. Frank Thompson

Professor Lori Eggert

Professor Raymond Semlitsch

.....Thanks, Mom.

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NESTING AND POSTFLEDGING ECOLOGY OF NEOTROPICAL MIGRANT SONGBIRDS IN MISSOURI FOREST FRAGMENTS

Julianna M. A. Jenkins

ABSTRACT

The postfledging period, after fledging and before migration, is a critical stage for Neotropical migrant songbirds. The postfledging period encompasses an interval of high mortality that can greatly affect population growth models. Several species of mature forest nesting birds have been documented using very different habitat late in the summer, suggesting shifting habitat requirements during the postfledging period. I monitored nests and used radio-telemetry to observe postfledging juveniles of two species, the Ovenbird (*Seiurus aurocapilla*) and Acadian Flycatcher (*Empidonax virescens*), which overlap in nesting territories but differ in natural history. Monitoring was done in Missouri mature-forest fragments from 2012 to 2015. I document juvenile ecology and investigate how risks and habitat selection vary from the nesting period to the postfledging period and observe if trends are preserved across guilds.

In chapter 1, I describe postfledging juvenile behavior, parental care, and space use. I used generalized linear mixed models within an information theoretic framework to evaluate the relationship of postfledging movement rates to intrinsic, temporal, and local-habitat variables. Fledgling Acadian Flycatchers (n = 45) utilized more vertical space and had 59% smaller natal home-ranges than fledgling Ovenbirds (n = 62). I found strong positive effects of age on movement distances for both study species and found a negative effect of foliage density on Ovenbird movements. My work provides a new source of support for the theory that habitat quality for postfledging Ovenbirds and other

ground foraging forest songbirds increases with forest understory or groundcover foliage density.

The few postfledging survival rates published to date are as variable as nest survival across regions and fragmentation gradients. However, factors that negatively impact nest survival may benefit postfledging individuals or not be as important postfledging. In chapter 2, I used an information-theoretic approach to determine support for effects of intrinsic, temporal, edge and local vegetation factors on survival in each stage and examined the potential effect of the resulting survival estimates on population growth. I did not find support for survival tradeoffs in habitat between stages. Nest period survival was comparable between species (~0.30) while postfledging period survival was 43% lower for Ovenbirds (~0.50) than for Acadian Flycatchers (~0.89). Projected population growth was sensitive to estimates of postfledging survival in our populations.

In chapter 3, I compared resource selection for nest-sites and by postfledging juveniles using Bayesian discrete choice resource selection models evaluated with an information theoretic approach. Resource selection models indicated that Acadian Flycatcher habitat selection requirements relaxed from nesting to postfledging, with only canopy cover positively contributing to selection postfledging. Resource selection for Ovenbirds shifted from a preference for open understory mature forest nest sites, to increased selection for high understory foliage density and sapling density. Habitat management based upon nesting requirements would likely be sufficient for postfledging Acadian Flycatchers, but insufficient for postfledging Ovenbirds.

The following chapters are formatted for individual publication in separate journals so

formatting may be inconsistent.

CHAPTER 1

POSTFLEDGING OVENBIRD AND ACADIAN FLYCATCHER BEHAVIOR AND MOVEMENT PATTERNS IN CENTRAL MISSOURI FOREST FRAGMENTS

ABSTRACT

The postfledging period, occurring between fledging and first migration, is a critical time for Neotropical migrant songbirds. However, our knowledge of many aspects of songbird postfledging ecology remains vague or absent. Understanding variation in postfledging behavioral development and movement rates will help inform resource requirements. We conducted a radio-telemetry study of postfledging Ovenbirds (Parulidae: *Seiurus aurocapilla*) and Acadian Flycatchers (Tyranidae: *Empidonax virescens*) in mature-forest fragments from 2012 to 2015 in Missouri, USA. We documented variability in behavior, parental care, and space use and tested if movement rates could be explained by temporal factors, local-habitat variation, or the individual bird's condition at fledging. Postfledging Acadian Flycatchers (n = 45) were mainly observed in mid- and over-story canopy and had smaller natal home-ranges than Ovenbirds (n = 62) which were usually observed on the ground or in the understory. We found strong positive effects of age on movement distances for both study species. We did not find strong effects of vegetation structure on daily movement patterns for postfledging Acadian Flycatchers, however we observed a change in foraging space use that may have confounded the limitations of our lateral distance analysis. Ovenbird daily movements were significantly affected by the

understory foliage density and saw timber density of the prior location. Our work provides a new source of support for the theory that habitat quality for postfledging Ovenbirds and other ground foraging forest songbirds increases with forest understory or groundcover foliage density. We suggest that researchers use models of daily movement to further test and strengthen resource quality hypotheses generated by habitat selection and survival studies.

INTRODUCTION

The postfledging period occurring between fledging and first migration is a critical time for Neotropical migrant songbirds, likely accounting for the highest rate of mortality in the first annual cycle (Anders and Marshall 2005, Cox et al. 2012). While we have made progress understanding postfledging survivorship and basic habitat-use for a small but growing number of songbirds (e.g. Anders et al. 1997, King et al. 2006, Streby and Andersen 2013), our knowledge of many aspects of songbird postfledging ecology remains vague or absent (Anders and Marshall 2005). The majority of published postfledging studies focus on investigating factors affecting survival, i.e. evading predation or starvation (Anders et al. 1998, Naef-Daenzer et al. 2001). Few studies have investigated related mechanisms behind mortality risk, such as movement rates, which are likely linked to finding appropriate foraging habitat while eluding predation (Vitz and Rodewald 2010, Ausprey and Rodewald 2013b).

The postfledging stage consists of two phases differentiated by parental involvement and juvenile development. For a week or more after fledging, juveniles are dependent upon adults for supplementary food and guidance. Over time, parental care is reduced. The majority of mortalities take place during this initial postfledging interval as

individuals gain mobility, complete the first basic molt, and learn to forage (reviewed in Cox et al. 2014). Dependent juvenile movements are likely limited by parental behavior, especially if adults maintain territories to attempt second broods. Parental movement constraints likely relax as the postfledging period progresses, as adults are no longer required to bring food to a central nest location and can instead move juveniles to rich foraging areas. Dependent family group movement patterns can vary within and between species (Russell 2000). Anders et al. (1998) described two different movement patterns for postfledging Wood Thrush *Hylocichla mustelina* in Missouri. ‘Stationary’ individuals remained near the nest site and repeatedly visited areas within the nesting territory, while ‘drifting’ family groups moved progressively farther from the nest and did not utilize any area heavily during dependence.

The second phase of the postfledging period, the independent postfledging period, begins when adults no longer provide supplementary food to juveniles. The timing of postfledging songbird independence is variable and is usually earlier for species that attempt second broods and for species that breed in the northern hemisphere (Russell 2000, Gruebler and Naef-Daenzer 2008). After independence, juvenile movements are no longer limited by parental behavior; as such, independence is often associated with large movements away from the dependent natal area. Dispersal movements may be driven by parents evicting older offspring to attempt a second brood or by a need to find safe staging areas to prepare for migration. However, independence does not always mean dispersal away from parents or natal territories. In some species, parents and juveniles wander as a group until migration or juveniles remain in natal territories until migration or they finish molting (reviewed in Russell 2000).

Understanding variation in postfledging movements will help strengthen our knowledge of habitat selection and basic requirements of the postfledging period. The collection of locations used by dependent postfledging juveniles defines a natal home-range (Anders et al. 1998). Breeding territory (nesting home-range) size has been inversely associated with productivity (Rolstad and Rolstad 1995, McLoughlin and Ferguson 2000) and large postfledging natal home-ranges have been hypothesized to help explain area-sensitivity for some interior forest songbirds (Anders et al. 1998, Vitz and Rodewald 2010). However, examining daily postfledging movements is likely more informative for understanding habitat quality than comparing overall natal home-range sizes for periods where individual behavior and ability change with time. Natal home-range is likely determined more by parental behavior and summarizes use over the entire dependent postfledging period, likely containing both heavily used and ignored areas (Manly 2011). Individual fledglings likely have more control over their daily movements and resource selection in both the dependent and independent periods. Daily juvenile movements may vary with the condition of the individual, the foraging and cover value of habitat, and other factors such as season or weather that change over time (Grüebler and Naef-Daenzer 2008, Vitz and Rodewald 2010, Van Overveld et al. 2011) which also likely influence an individual's survival (King et al. 2006).

Dependent period postfledging movements must balance the needs of the juvenile with the needs of the parent. We hypothesize that daily movement rates would be more influenced by an individual's ability to move (age and condition) and the immediate survival value of the habitat already occupied and providing cover from predators and food resources. While we hypothesized that overall distance moved away from the nest,

with the exception of initial fledging (escaping researcher), would be more affected by larger scale factors such as the adults' seasonal requirements. For example, birds that fledge early in the season may be pressured to move away from the nest more quickly if adults attempt second broods, and birds that fledge late in the season may be pressured to move to highly structured nonbreeding areas sooner if adults are preparing to molt. We observed behavior and movement patterns of postfledging Ovenbirds and Acadian Flycatchers in forest fragments imbedded in an agricultural landscape matrix. Ovenbirds and Acadian Flycatchers are both Neotropical migrant songbirds that breed in the mature forests of Eastern North America. Both species are insectivorous and have different nesting and foraging strategies. Ovenbirds are mainly ground foraging birds, often seen gleaning insects from leaf-litter, while Acadian Flycatchers are salliers, catching insects on the wing and searching for and consuming prey while perched. Ovenbirds build roofed nests on the ground and have a very short nestling period, fledging young 7 to 9 days post-hatch (Porneluzi et al. 2011). Acadian Flycatchers are low-canopy open-cup nesters and have a long nestling period, fledging young 13 to 14 days post-hatch (Mumford 1964, Whitehead and Taylor 2002). Acadian Flycatchers are able to fly at least short distances when fledged, while Ovenbird juveniles are nonvolant for at least a few days post-fledging. Our objectives were to document variability in behavior, parental care, and space use of postfledging Acadian Flycatchers and Ovenbirds and determine if postfledging daily movements could be explained by temporal factors (e.g. season, age), local-habitat variation, or by the individual bird's condition at fledging. We expected to see large variation in behaviors and movement patterns between species due to their very different nesting and foraging strategies.

METHODS

Study Area

We studied nesting and post-fledging ecology on three forested sites in Boone, Randolph, and Howard counties in Central Missouri, U.S.A. from 2012 to 2015. We studied the Thomas S. Baskett Wildlife Research and Education Center (Baskett; 38° 44'N, 92°12'W; 890 ha) in 2012 to 2015, the Rudolf Bennitt State Conservation Area (Bennitt; 39° 8' N, 92° 15' W; 1146 ha) in 2013 to 2015, and Three Creeks Conservation Area (Three Creeks; 38° 49'N, 92°17'W; 575 ha) in 2014 to 2015. Study sites consisted of mixed-hardwood forest, interspersed with successional red cedar *Juniperus virginiana* stands. Sites were situated within a matrix of forest patches, old-fields, and active agriculture. Acadian Flycatchers were present at all three sites and nesting Ovenbirds were only present at Bennitt and Baskett. In our pilot study during 2012, we only monitored Ovenbirds at Baskett.

Radio Telemetry

We found nests from mid-May to mid-August and monitored nests every 3–5 days following standard methods until nest failure or fledging (Martin and Geupel 1993). We captured all available nestlings on the day of projected fledging (day 8 for Ovenbirds and day 13 for Acadian Flycatchers) and recorded nestling mass (± 0.1 g). We supplemented Ovenbird nest captures with opportunistically hand-caught nonvolant fledged juveniles 1–2 days out of the nest; we rarely captured postfledging Acadian Flycatchers. We attached colored-leg bands and a standard U.S. Geological Survey leg band to all captured Ovenbirds and attached radio transmitters to one or two (rarely three) individuals per brood. All captured Acadian Flycatcher nestlings received a standard U.S.

Geological Survey leg 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% to 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, MN USA). In 2013–2015, transmitters weighed 0.3g, were 1.8% to 2.8% of Ovenbird mass and 2.3% to 3.3% of Acadian Flycatcher mass at time of attachment, and had an expected battery life of 44, 29, and 44 days respectively (2013 and 2015: model A2414 ATS, 2014: model PicoPip Ag337 Biotrack, Wareham, Dorset, UK).

We relocated radio-marked birds by homing daily, or as close to every day as possible, 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 relocated individuals until the signal was no longer detectable (transmitter battery failure or dispersal out of study area) or until we determined mortality. Since behavior and locations of siblings are not likely independent, observations from one individual per brood were used in behavior and distance models. 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 make the assumption that our presence did not alter their behavior or habitat-use significantly. We recorded locations in Universal Transverse Mercator (UTM) coordinates with handheld GPS units (GPS error < 10m). We measured local vegetation features after individuals left the area. We sampled vegetation of at least every other observed location. We were unable to sample every location due to time and labor constraints. We selected habitat variables

that we hypothesized could most simply model forest structure. We measured the diameter at breast height (DBH) of all stems greater than 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 stem densities per hectare (ha) of saplings (3.0–12.5 cm DBH), pole timber (12.5–27.5 cm DBH), saw timber (> 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 (2 m tall × 0.3 m wide) measurements taken from 11.3 m in each cardinal direction from the central point.

Behavioral Observations

We attempted to minimize disturbance to individuals and waited 5–30 minutes for resumption of normal activity to begin observations. We attempted to vary the time of day observations took place, however the majority took place between 6 AM and 2 PM. We recorded the bird's location in vertical space (ground, understory, low canopy, high canopy), their social association (distance to adult/parent/sibling or alone), and observed active behaviors (begging, fed by parent, foraging, perch/rest, flight, walk/hop). Since multiple locations and behaviors could be observed in one observation, we used binary coding (1 = observed, 0 = not observed) for each categorical variable of interest. We recorded 'parental care' as observed if 'begging', 'fed by parent', or 'attended by adult (adult < 1 m)' was observed. We defined independence as the mean age when we no longer observed parental care. We calculated time to independence using only data from individuals that survived the observation period with radios intact and report the mean age of independence ± standard error. Due to the variable and short-term nature of our observations, we present only proportions of observations where a behavior was

observed. Since juveniles gain mobility and behavioral skills as they age, we report the proportion of observations that a behavior was observed for each age. Post-independence age classes were combined into one proportion since sample size per age dropped significantly after independence.

Movements

We calculated daily movement rates based on the linear distance between successive points divided by the elapsed time in days. We considered a bird to have dispersed if it made a sudden long-distance movement (≥ 300 m) or made several consistent movements away from the nest without returning (Anders et al. 1998). We used the 95% minimum convex-hull polygon (MCP) method to calculate natal (dependent stage) home-range sizes for all dependent individuals that had ≥ 10 relocations using the `adehabitatHR` package in R (Calenge 2006). We used MCP rather than kernel home-range areas because we did not meet minimum sample recommendations for kernels (Seaman et al. 2011). We measured linear dispersal distances from natal home-range centroids using the `near` tool in ArcMap (ESRI 2012). We report the mean MCP natal home-range size, dispersal distances, and age at dispersal \pm standard error (SE) for each species.

Movement Models

We used generalized linear mixed models within an information-theoretic framework to evaluate the relationship of postfledging daily movements to intrinsic, temporal, and local-habitat variables (Burnham and Anderson 2002, Bolker et al. 2009). We developed candidate models a priori based upon plausible hypothesis and evaluated

models using Aikaike's information criterion adjusted for small sample sizes (AICc; Table 1). We based inference on the best supported model as no model that overcame the 2 AICc unit penalty added informative parameters (Burnham and Anderson 2002, Arnold 2010). We fit models with gamma distribution and a log link and assessed overdispersion by calculating the ratio of the sum of squared Pearson residuals to the residual degrees of freedom (GLIMMIX procedure, SAS 9.3, SAS Institute, Cary, NC). We confirmed noncollinearity of covariates by determining the variance inflation factor was < 2.0 for all covariates. We included individual ID as a random effect to account for the non-independence of repeated observations of individuals in all models and calculated the variance attributable to individual for each top model. We used data from both the dependent and independent stages and included age (days since fledging) in all models to account for developmental effects. We included lag-distance (previous distance from nest) as a fixed covariate in all models of distance from the nest to account for spatial autocorrelation between successive individual daily distances. We used ordinal date of fledging to represent season because ordinal date outperformed other seasonal variables (2-category season, 3-category season, ordinal date, ordinal date², ordinal date³) in initial model comparisons for both species. We did not include site in any models because initial comparisons of models with a fixed effect of site were not supported. We included mass at fledging as a measure of individual condition. Birds in better condition are likely able to more rapidly achieve and maintain sustained flight, improving their chance of escaping predation and making long distance movements (Naef-Daenzer et al. 2001b). Vegetation sampled from prior locations were used to predict movements (i.e. for each distance from point a to b, we used the vegetation sampled from a to model movement

distance to b). We suggest that willingness to move decreases after locating habitat that provides cover from predator and foraging resources. We did not include data from day one movements from the nest to avoid confounding factors surrounding initial fledging distances (i.e. escaping researchers after radio attachment). We normalized all continuous variables before conducting analysis.

RESULTS

We attached radio transmitters to 62 Ovenbird fledglings from 48 broods and 45 Acadian Flycatcher fledglings from 45 broods. We recorded 29 Ovenbird mortalities and 10 Acadian Flycatcher mortalities; all but one recorded mortality occurred during the dependent period. Ovenbirds that survived the study period with radios intact were monitored for 27.47 ± 2.81 days (max = 49, min = 23). Acadian Flycatchers that survived the study period with radios intact were monitored for 27.11 ± 1.57 (min = 15, max = 46) days. Ovenbirds weighed 14.52 ± 0.06 g and Acadian Flycatchers weighed 11.36 ± 0.04 g at time of capture. Ovenbirds fledged 2.86 ± 0.05 young and Acadian Flycatchers fledged 2.39 ± 0.03 young per successful nest. Fledging date ranged from 26 May to 15 July for Ovenbirds and 12 June to 5 August for Acadian Flycatchers. Ovenbirds juveniles were independent from adults 23.14 ± 1.04 days after fledging. Acadian Flycatchers were independent 19.52 ± 1.21 days after fledging.

We used 541 observations from 38 Acadian Flycatchers and 626 observations from 43 Ovenbirds in behavioral summaries. Ovenbird broods were split-up initially between parents after fledging, while Acadian Flycatcher broods were not. Fledglings were seen with siblings 40% and 14% of the time for Acadian Flycatchers and Ovenbirds, respectively. Both species gradually increased time foraging in their first

week out of the nest; however, rates of begging or being fed by adults did not decline until independence (Fig. 1). Dependent postfledging Acadian Flycatchers were mainly observed in midstory and overstory canopy levels, while Ovenbirds were usually observed on the ground or understory (Fig. 2). Both species increased rates of movement during observations over time, Acadian Flycatchers increased observed flight, while Ovenbirds increased both walking and flight over time (Fig. 3).

Even though Ovenbirds were not capable fliers at fledging, their initial daily distances and distances from the nest did not appear to be limited (Figs. 4 and 5); newly fledged Ovenbirds could be found a mean 57.73 ± 9.30 m (range 9–150 m) from the nest site the day after fledging, compared to Acadian Flycatchers, who moved on average 26.57 ± 3.90 m (range 9–102 m) one day after fledging. Acadian Flycatchers utilized more vertical area than Ovenbirds (Fig. 2), which may account for the shorter lateral distances moved. We calculated home-range areas for 28 Acadian Flycatchers and 29 Ovenbirds (Fig. 6 and Fig. 7). Acadian Flycatcher natal home-ranges covered 0.85 ± 0.16 ha (range 0.23–1.77 ha) and Ovenbird natal ranges covered 2.06 ± 0.25 ha (range 0.79–6.22 ha). We recorded distinct long-distance dispersal events for 10 Acadian Flycatchers and 8 Ovenbirds, and short wandering dispersals for 8 individuals from both species. Acadian Flycatcher initial long-distance dispersals were 840 ± 155 m from natal range centroids and took place 28.50 ± 2.52 days postfledging. Ovenbird initial long-distance dispersals were 618 ± 79 m from their natal range centroid and took place 29.75 ± 3.34 days postfledging. Short wandering dispersal movements were 169 ± 68 m and 199 ± 71 m away from natal range centroids for Acadian Flycatchers and Ovenbirds respectively.

Models of daily movement incorporated 395 Ovenbird observations and 316 Acadian Flycatcher observations and models of daily distance from the nest incorporated 266 Ovenbird locations and 317 Acadian Flycatcher locations. The best supported model of daily movement for Ovenbirds was age + foliage density (0–2 m) + sapling density + saw timber density and had a model weight of 0.42 (Table 2). Ovenbird daily movements were positively related to age and saw timber density, negatively related to understory foliage density, and were not related to sapling density (Fig. 8). The best supported model of Acadian Flycatcher daily successive distances was age + season + year + (season x year) and had a model weight of 0.4. The two models that overcame the 2 point penalty for additional variables were not well supported (Table 2). Acadian Flycatcher movements were positively related to age and varied by season (Fig. 9).

The best supported model of Ovenbird daily distance from the nest was lag-distance + age + season + (age x season) and had a model weight of 0.4 (Table 3). The best supported model of Acadian Flycatcher dispersal from the nest was lag-distance + age and had a model weight of 0.18; the five models that overcame the 2-point penalty for additional variables added season x age, condition, and year but were not well supported (Table 3). Distance from the nest was positively related to age in each species, however Ovenbirds that fledged later in the season moved farther from the nest more quickly than Ovenbirds that fledged earlier in the season (Fig. 10). Individual accounted for a greater percentage of the random effect variance in the response of distance from nest than in daily successive distances, and contributed more variance in Ovenbird distance models (20% and 12% respectively) than in Acadian Flycatcher distance models (15% and 3% respectively).

DISCUSSION

Postfledging Ovenbirds and Acadian Flycatchers differ in parental care strategies and natural history; however, both reached independence at similar ages post-hatching and long distance dispersal movements occurred ~ 30 days postfledge. Ovenbird broods were initially split postfledging but often rejoined the other half of the family group or other postfledging dependent family groups once juveniles were able to fly. Adult Ovenbirds were commonly observed accompanying (alarm chipping or guarding) juveniles past independence. Acadian Flycatchers remained in close association with siblings and adults up until independence. Mean Acadian Flycatcher postfledging natal-ranges were smaller than Ovenbird's, however they utilized more vertical territory, foraging in low, mid, and high canopy open-space. Our Acadian Flycatcher mean natal-range was within the mid-range of reported values for Acadian Flycatchers in Ohio riparian forests (Ausprey and Rodewald 2013a). Mean Ovenbird natal home-range size was twice as large in Ohio contiguous forest (5.0 ha; Vitz and Rodewald 2010).

To our knowledge we are the first to publish initial long-distance dispersal distances for Acadian Flycatchers. Ovenbird dispersals in our forest fragments may have been restricted by proximity of edges with open areas. Ovenbird mean dispersal distances in Ohio contiguous forest was twice as large as in our fragmented forests (1314 m; Vitz and Rodewald 2010). Mean dispersal movements of Ovenbirds from two large tracts of mature forest in Minnesota were also longer than observed in our mature forest fragments (849–1113 m; Streby and Andersen 2012). Our maximum recorded distance for Ovenbirds and Acadian Flycatchers were 901 m and 1857 m, respectively; however,

longer movements may have gone undetected if final destinations were outside the study area, especially if birds moved onto private land inaccessible by road.

Individuals of both species seemed to select similar post-dispersal habitats, with Ovenbirds utilizing dense habitat near the ground and Acadian Flycatchers near the canopy. One edge area bordering a road and old field was used by two dispersed independent Acadian Flycatchers and one independent Ovenbird. Independent juveniles of both species were commonly observed near other heterospecifics, without much direct interspecies interaction, suggesting that proximity was due to similar habitat preferences rather than social association. We also observed independent postfledging Ovenbirds with conspecifics on several occasions, while independent Acadian Flycatcher juveniles were rarely seen with other flycatchers. While Ovenbird and Acadian Flycatcher postfledging movements did not react to habitat features in the same way, neither species was commonly observed utilizing open areas. Ovenbirds appeared to be less restricted in habitat selection postfledging than Acadian Flycatchers; postfledging Acadian Flycatchers were observed in forest near edges, but never observed in areas without canopy coverage while a few Ovenbirds were located foraging under shrubs or cedar stands in old pasture areas within 50 m of a forest edge (e.g., Fig. 7B).

Individual age and initial body condition are commonly hypothesized to affect survival probability due to correlations with movement ability (Naef-Daenzer et al. 2001b, Cox et al. 2014). We confirmed strong positive effects of age on movement distances for both study species; in general, birds moved farther from their nest and farther from their last location as they aged. This pattern is consistent with studies of other postfledging passerines (Yackel Adams et al. 2001, White and Faaborg 2008, Vitz

and Rodewald 2010). Our observations of ‘flight’ and other movement types also increased in frequency as birds aged, further supporting age as a major predictor in ability to move (and thus escape predation). We hypothesized that heavier (larger) birds would be able to make longer movements more quickly than lighter (weak) individuals. The effects of mass or other indices of condition at fledging on postfledging survival are mixed in the literature, with studies reporting positive effects or no effect (Dhondt 1979, Anders et al. 1997, Naef-Daenzer et al. 2001a, Streby and Andersen 2013, Vitz and Rodewald 2013, Haché et al. 2014). We did not find support for an effect of mass at fledging on movement distances; however, by including only initial mass at fledging in our analysis that included all postfledging ages, as in most other postfledge survival studies, we are only really testing a carry-over effect of the juvenile’s initial condition. Vitz and Rodewald (2010) limited their analysis to distance moved 2-days after leaving the nest by fledging Ovenbirds and worm-eating warblers *Helmitheros vermivorum* and found that condition at fledging was the best supported model, compared to brood size, nest-site understory density, and nest survival rate for that brief time period. It would be valuable to resample individual juvenile condition periodically throughout the postfledging period to satisfactorily test the effect of individual body condition on all postfledging movements, but in practice, repeated sampling would be difficult and likely affect postfledging behavior. The inconsistent effect of mass on daily movements and survival may also indicate that poor initial condition is only noteworthy when either resources are scarce or long-distance movements to appropriate postfledging habitat are required.

We predicted that distance from the nest would be most affected by general factors that affect parental behaviors, such as season. We had expected to find strong support for a seasonal effect in Acadian Flycatchers, which can be double brooded in our study region (Hirsch-Jacobson 2011). There was some support for the effects of juvenile age and season on distance from nest for both species, but season was only included in the top model of Ovenbird distance from the nest. We did not confirm many cases of Acadian Flycatchers double brooding on our study sites, however our nest searching effort declined in July. Our results may also be confounded if the availability of high-canopy foraging space increased as the season progressed and conspecifics reduced territoriality. Ovenbirds that fledged later in the season moved greater distances at each age than those that fledged earlier in the season. This increase in average movement over the season may reflect increased movement pressure from adult Ovenbirds as migration approaches to move to nonbreeding habitat areas that provide high densities of food resources while providing structural protection from predators while they undergo pre-migratory molt. Mist-net and telemetry studies have reported mature-forest breeding adults and juveniles, often mid-molt, using dense nonbreeding habitat such as clear-cuts, forest edges, and forest openings postfledging (Anders et al. 1998, Vega Rivera et al. 1998, Pagen et al. 2000, Marshall et al. 2003). Several of our Ovenbirds utilized dense forest edge or cedar patches postfledging.

We hypothesized that birds would move shorter distances once they reached ‘suitable’ habitat that offered foraging opportunities while providing cover from predators. Ovenbird daily movements were significantly affected by the understory foliage density and saw timber density of the prior location. Our work strengthens the

theory that habitat quality for postfledging Ovenbirds, and other ground foraging forest songbirds, increases with forest understory or groundcover foliage density (Anders et al. 1997, Vitz and Rodewald 2011, Streby and Andersen 2013, Streby et al. 2014). It fits the theory that understory density, rather than any specific nonbreeding habitat, like early successional forest, is required (Vitz 2008). Rather, nonbreeding habitat is likely used when adequate dense understory is not present on breeding areas (Vitz 2008, Streby and Anderson 2013). While dense vegetative structure would disrupt flycatcher sally foraging, it may improve Ovenbird ground foraging since insect diversity is often positively correlated to habitat structure (Didham 1997). Higher insect and fruit densities have been found in nonbreeding and other densely structured areas utilized by postfledging forest songbirds compared to mature forest areas (Blake and Hoppes 1986, Didham 1997, Keller et al. 2003, Streby et al. 2011). Dense understory/groundcover also likely provides visual and structural protection from predators limiting the necessity for long distance escape movements.

We did not find strong effects of vegetation structure on daily movement patterns for postfledging Acadian Flycatchers. However, Ausprey and Rodewald (2013) found that Acadian Flycatchers (n=11) in riparian forests expanded natal home-ranges as honeysuckle *Lonicera maackii* cover increased and suggested that this meant that unrestricted foraging space was more valuable postfledging than cover from predation. We observed a change in foraging space use that may have confounded the limitations of our lateral distance analysis. Acadian Flycatchers prefer to forage in open areas under dense canopy (Whitehead and Taylor 2002). While nesting Acadian Flycatchers were observed foraging primarily in the midstory canopy, where nests are typically located, we

found postfledging individuals and family groups almost as often in high oak-hickory overstory canopy. If high canopy foraging areas become socially available to midstory canopy nesting species postfledging, as observed in our study, then future movement models and habitat selection studies need to include three-dimensions to adequately test for habitat effects on sallyers in mature forest areas. In addition, cover from predation may look differently for species that forage in open space than for those foraging on the ground; areas of high structural density where individuals can view large areas for prey and potential predators, may be of greater importance for Acadian Flycatchers. Habitat providing cover from predation is likely more important for Ovenbirds and other ground nesters, who are nearly flightless at fledging with limited hopping ability (Porneluzi et al. 2011) than for Acadian Flycatchers who are volant at fledging.

We showed that habitat features are useful in predicting the postfledging movements of mature forest nesting insectivorous songbirds. We also showed that the foraging guild of insectivorous forest breeding species should be considered when investigating postfledging movement ecology; three dimensions are likely needed to model postfledging sallyer movements. We are the first to show that movements throughout the postfledging period can be predicted by habitat features of prior locations. Furthermore, our observations strengthen the idea that habitat connectivity, specifically canopy cover, is important to dispersing independent postfledging birds (Desrochers and Hannon 1997, Vitz and Rodewald 2010). Since birds likely make larger movements away from low quality habitat, we suggest that researchers use models of daily movement rate to further test and strengthen resource quality hypotheses generated by habitat selection and survival studies.

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Table 1. A priori candidate model set for generalized linear mixed models of movement rate. An additional term ‘lag-distance’ was added to all nest distance models to account for spatial autocorrelation.

id	Model
0	intercept (null)
1	age
2	age + season
3	age + condition
4	age + vegetation
5	age + year
6	age + season + condition
7	age + season + year
8	age + season + vegetation
9	age + condition + vegetation
10	age + condition + year
11	age + vegetation + year
12	age + season + condition + year
13	age + season + condition + vegetation
14	age + condition + vegetation + year
15	age + season + condition + vegetation + year
16	age + season + (age × season)
17	age + season + condition + (age × season)
18	age + season + year + (age × season) + (season × year)
19	age + season + year + (season × year)
20	age + season + year + (age × season)
21	age + season + vegetation + (age × season)
22	age + season + condition + year + (age × season)
23	age + season + condition + year + (year × season)
24	age + season + condition + year + (age × season) + (age × year)
25	age + season + condition + vegetation + (age × season)

- 26 age + season + condition + vegetation + year + (season × age)
- 27 age + season + condition + vegetation + year + (season × year)
- 28 age + season + condition + vegetation + year + (season × age) + (season × year)
-

Table 2. Summary of model selection results from the best-ranked a priori candidate models of the effects of age, vegetation, season, year, and condition on daily successive distances moved by postfledging Ovenbirds and Acadian Flycatchers in central Missouri, 2012–2015. Null models are included for comparison.

Model	Deviance	K	ΔAIC_C	w_i
Ovenbirds				
age + foliage density + sapling + saw timber	3935.03	7	0	0.42
null	3962.97	3	19.7	<0.01
Acadian Flycatchers				
age + season + year + (season \times year)	2969.99	9	0	0.37
age + season + condition + year + (year \times season)	2968.91	10	1	0.22
age + season + year + (age \times season) + (season \times year)	2969.50	10	1.6	0.16
null	3002.38	3	19.9	<0.1

Table 3. Summary of model-selection results from the best-ranked a priori candidate models of the effects of age, vegetation, season, year, and condition on distance from the nest by postfledging Ovenbirds and Acadian Flycatchers in central Missouri, 2012–2015. Null models are included for comparison. All nest distance models had lag-distance to account for spatial autocorrelation.

Model	Deviance	K	ΔAICc	w_i
Ovenbirds				
age + season + (age \times season)	2933.02	7	0	0.429
null	3018.22	4	78.9	<0.01
Acadian Flycatchers				
age	3329.87	5	0	0.178
age + season + (age \times season)	3325.88	7	0.2	0.163
age + condition	3329.31	6	1.5	0.083
age + season + condition + (age \times season)	3325.23	8	1.6	0.079
age + season + condition + year + (age \times season)	3325.23	8	1.6	0.079
age + season + year + (age \times season)	3323.43	9	2	0.067
null	3445.95	4	114	<0.01

Figure 1. Proportions of observations where juveniles were seen foraging increased over time while begging/fed by adult remained relatively stable for Acadian Flycatchers and Ovenbirds during the dependent postfledging period in Missouri forest fragments, 2012–2015.

Figure 2. Acadian Flycatchers spent most of their time in the low (e.g. Maples) and high Canopy (e.g. Oak/Hickory), and were rarely seen on the ground or in shrubs, while Ovenbirds, were mainly seen on the ground, and after week one, were also sometimes observed in the understory (shrubs) and low canopy. Observations from Missouri forest fragments, 2012–2015.

Figure 3. Acadian Flycatchers and Ovenbirds increased their movements and decreased their ‘rest’ after week one in Missouri forest fragments in 2012–2015.

Figure 4. Daily distances traveled over time for 32 postfledging Acadian Flycatchers (a) and 36 postfledging Ovenbirds (b) in Missouri forest fragments in 2012–2015.

Figure 5. Distance moved from nest over time for 32 postfledging Acadian Flycatchers (a) and 26 postfledging Ovenbirds (b) in Missouri forest fragments in 2012–2015.

Figure 6. Examples of Acadian Flycatcher postfledging land use of a long distance dispersal to old field/forest edge (a) to a hillside with dense understory (b) and to mixed cedar deciduous patch near an old pasture (c). Green polygons represent 95% MCP natal home-ranges.

Figure 7. Examples of Ovenbird postfledging land use of (a) a wandering independent juvenile, (b) a long distance movement to the edge of an old field and to road and (c) to a cedar wetland Yellow polygons represent 95% MCP natal home-ranges.

Figure 8. Predictions of the best supported model showing the effects of age (a), foliage density (b), saw timber density (c), and sapling density (d) on the probability of postfledging Ovenbird daily successive movements. Estimates are reported for the dependent period (a), and for the range of each vegetation variable recorded (b, c, d) while other covariates are held at their means. Shaded areas represent 95% confidence intervals.

Figure 9. Predictions of the best supported model showing the effects of age (a) and the interaction of season and year (b) on the probability of Acadian Flycatcher daily successive movements. Estimates are reported for the range of dates recorded. For a, ordinal date is held at the mean, and year was held at observed frequencies. 95% confidence intervals for beta estimates of 2014 and 2015 were not significantly different so estimates were created holding 2014 and 2015 at 0.5. Shaded area (a) and grey lines (b) represent 95% confidence intervals.

Figure 10. Prediction of the best supported model showing the effects of age on the probability of (a) Acadian Flycatcher distance from the nest and (b) Ovenbird distance from the nest for early (10th percentile) and late (90th percentile) fledging birds. Estimates are reported for dependent stage ages, holding lag-distance at the mean. Shaded areas represent 95% confidence intervals. Late fledging Ovenbirds move away from the nest more quickly than early fledging juveniles.

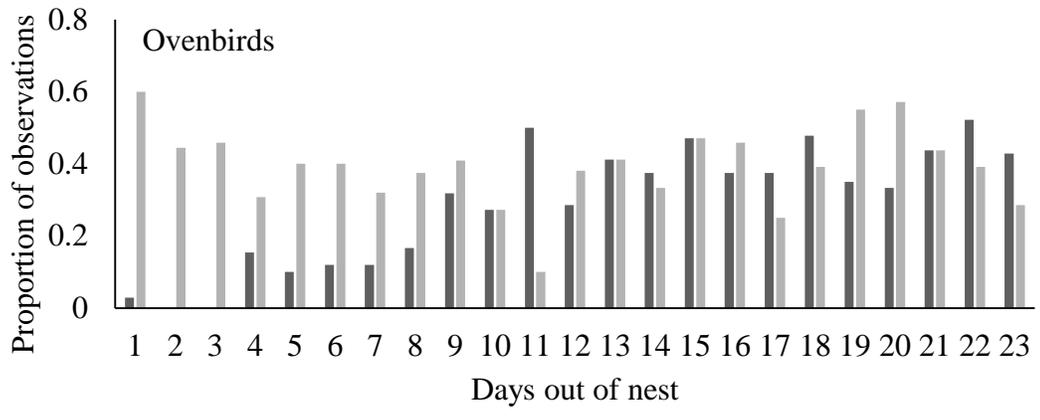
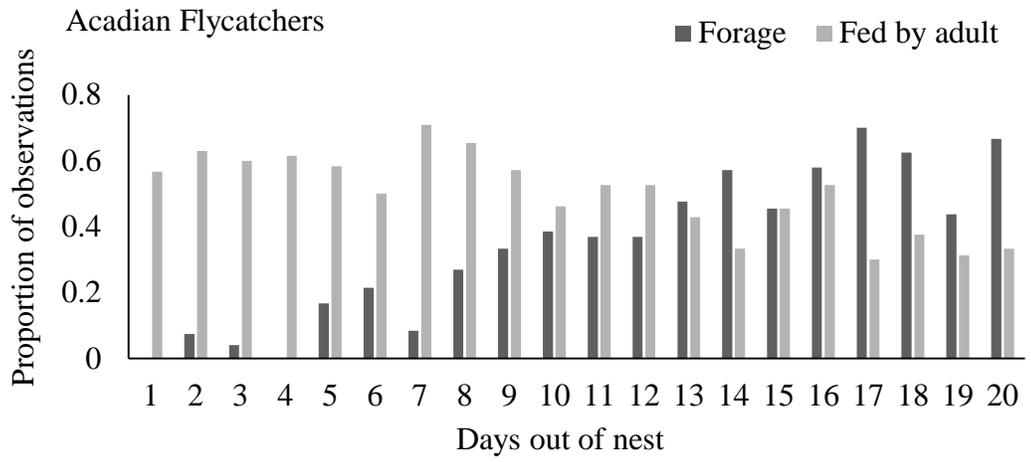


Figure 1.

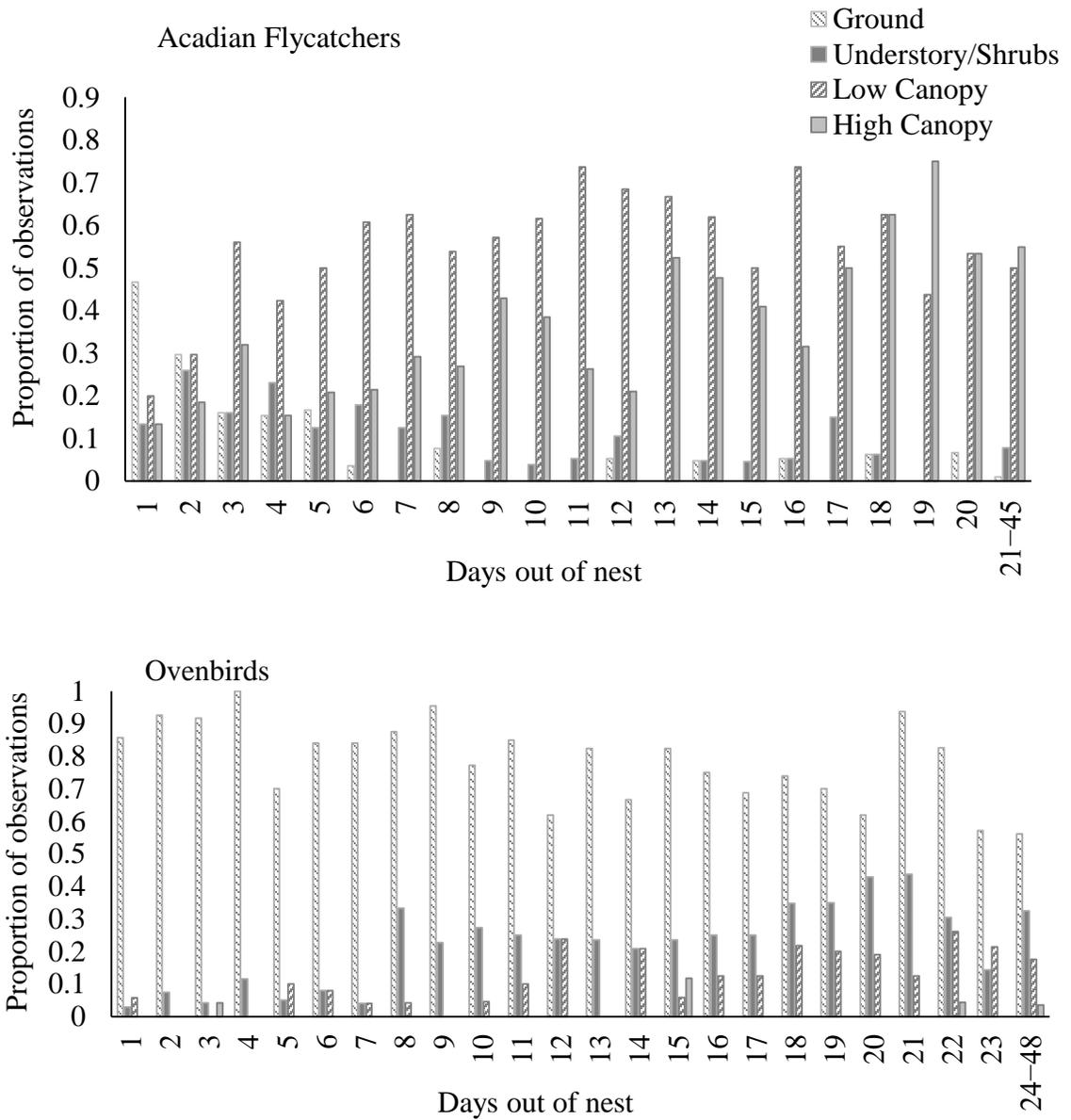


Figure 2.

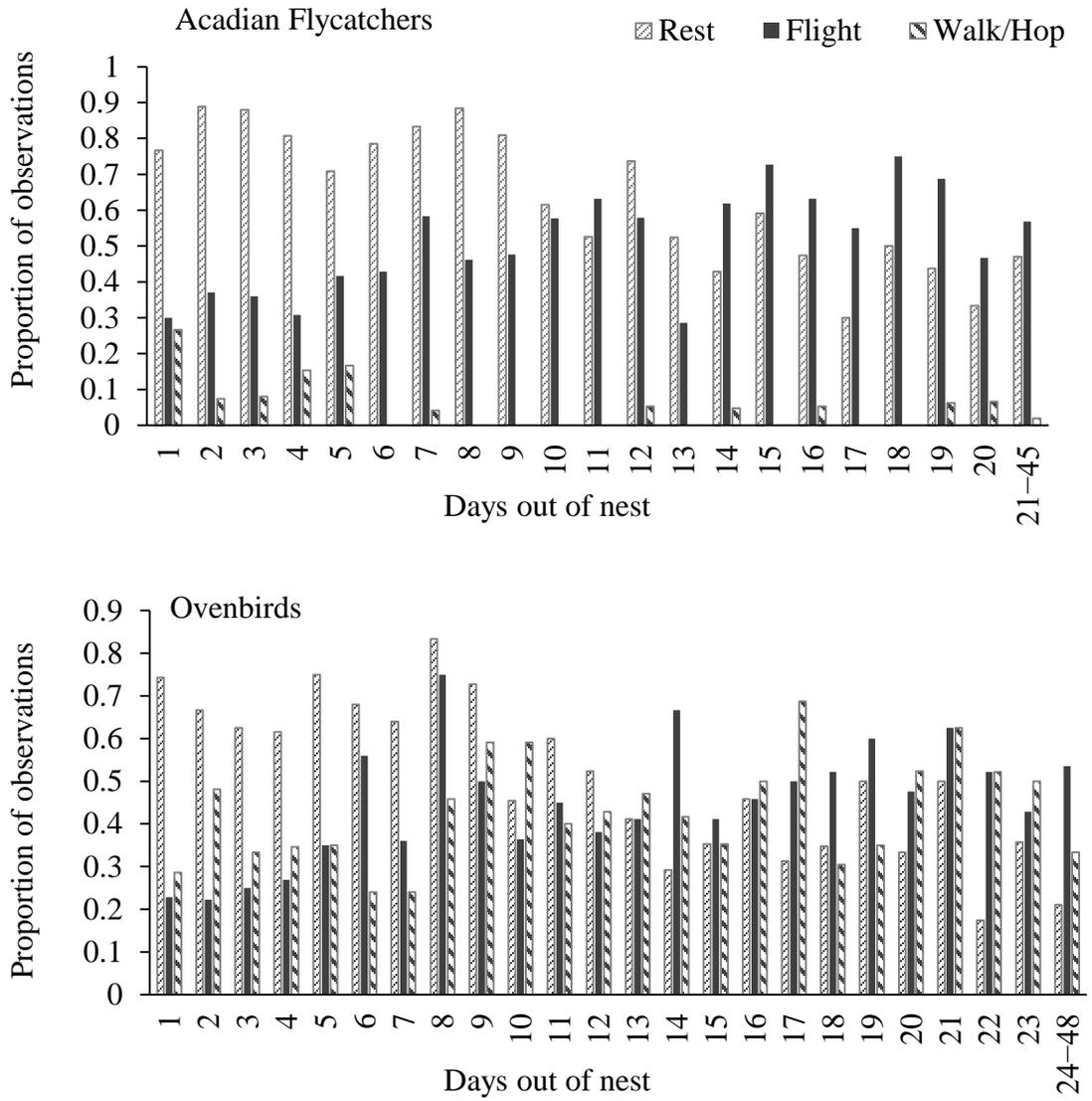


Figure 3.

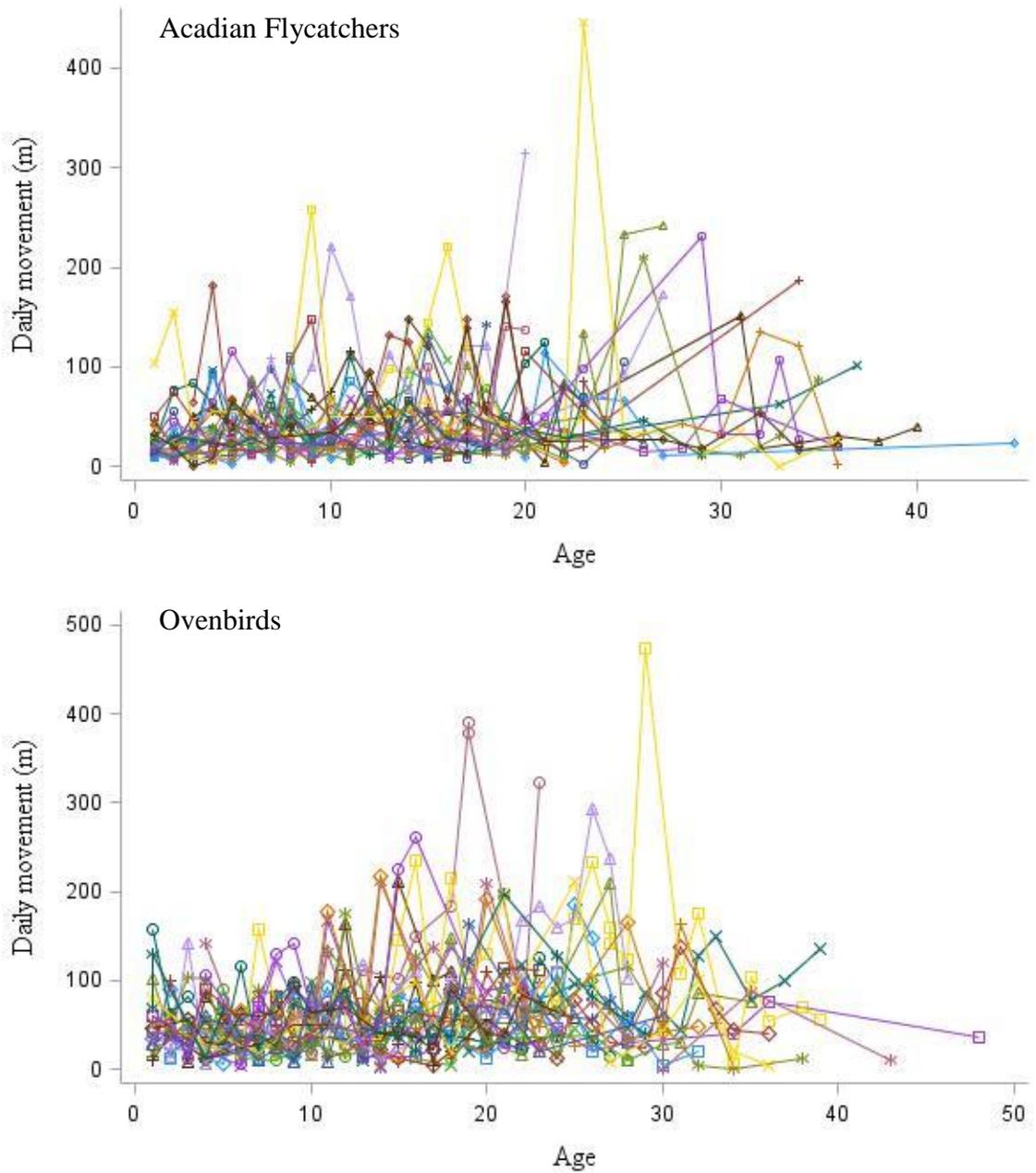


Figure 4.

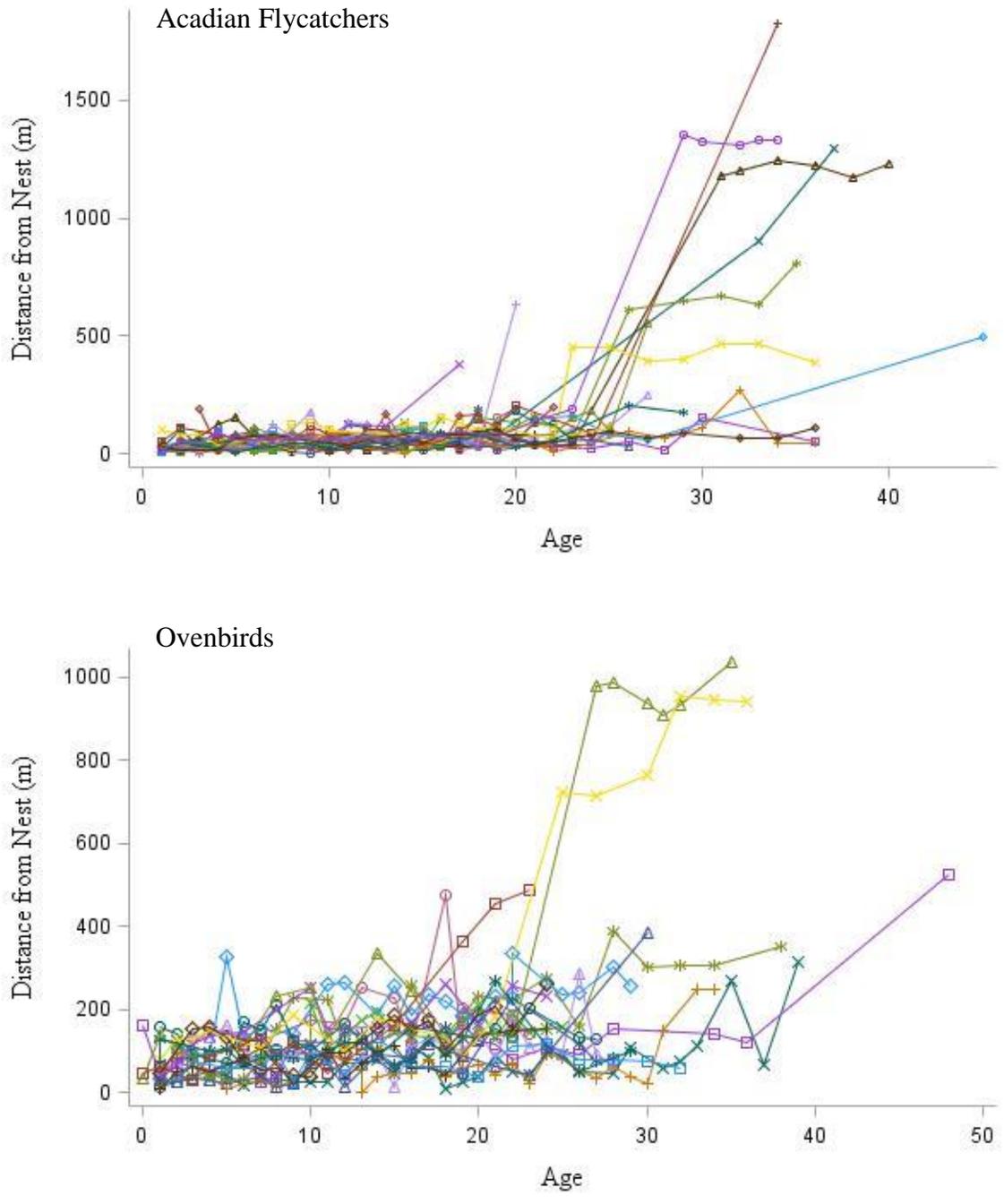


Figure 5.

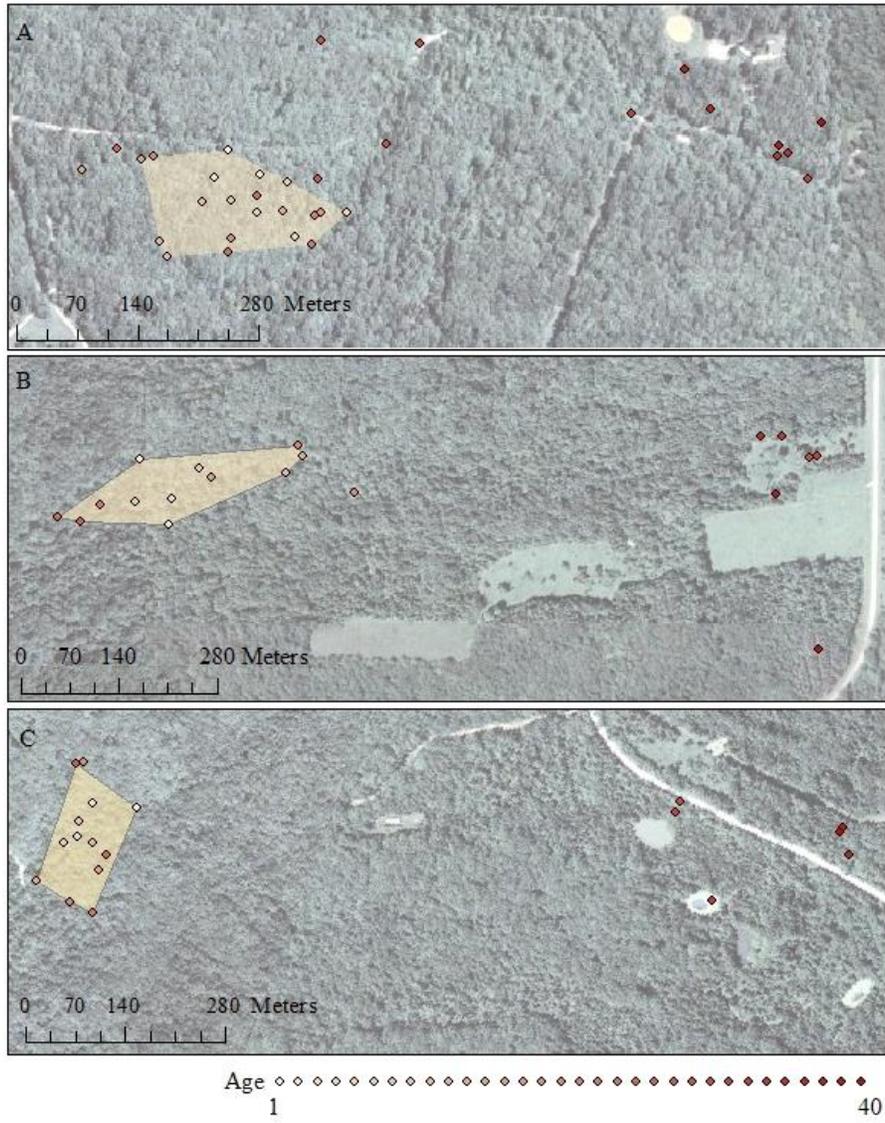


Figure 6.

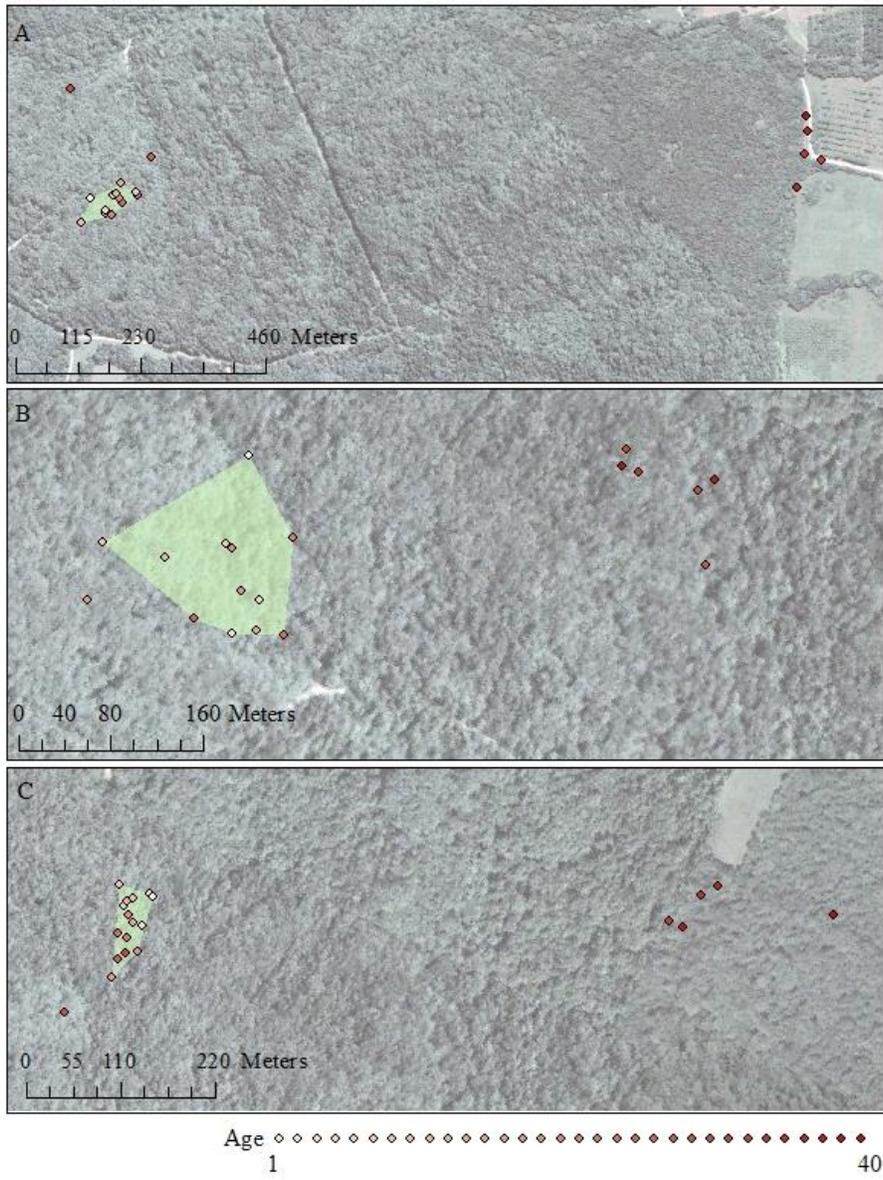


Figure 7.

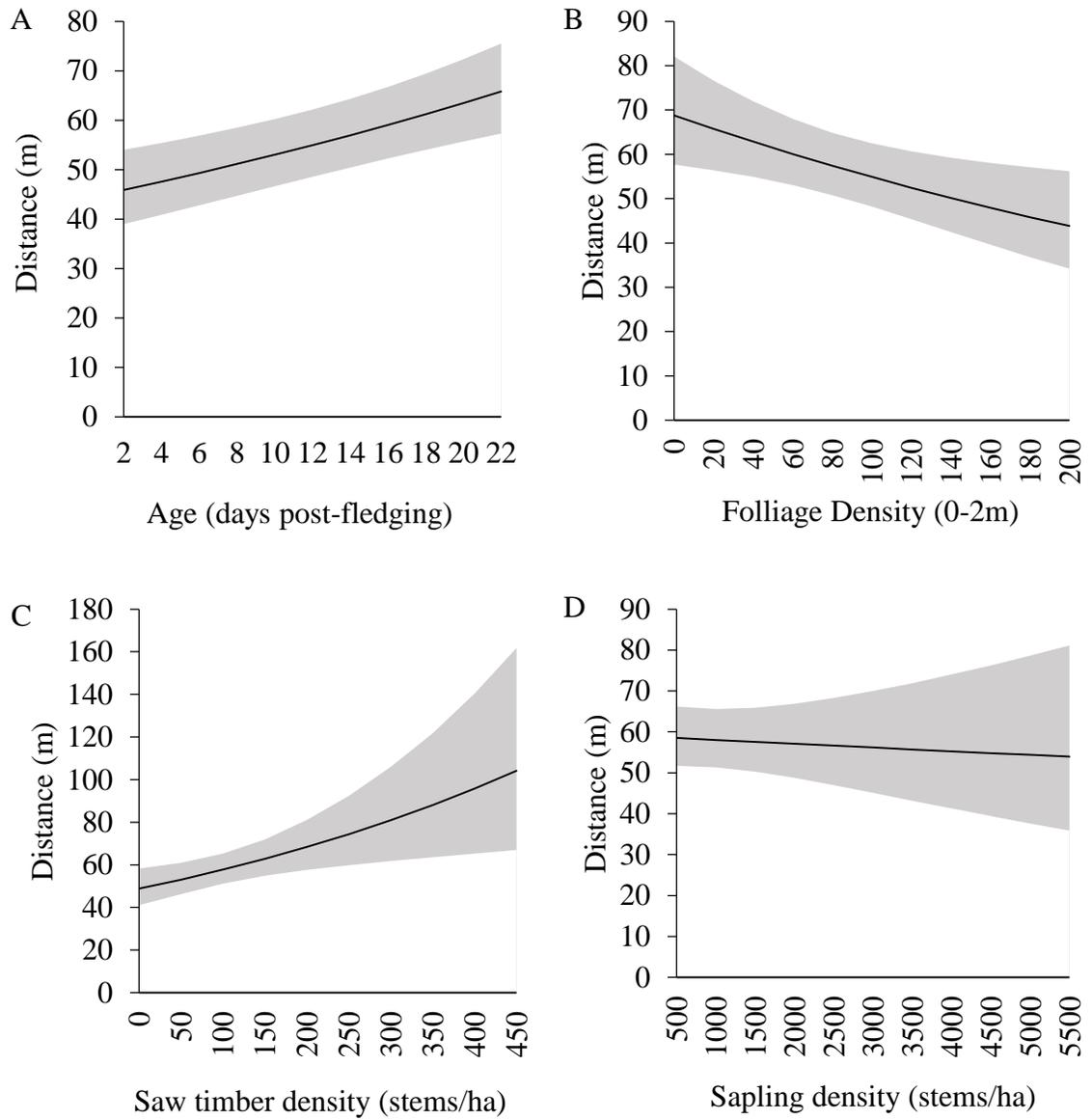


Figure 8.

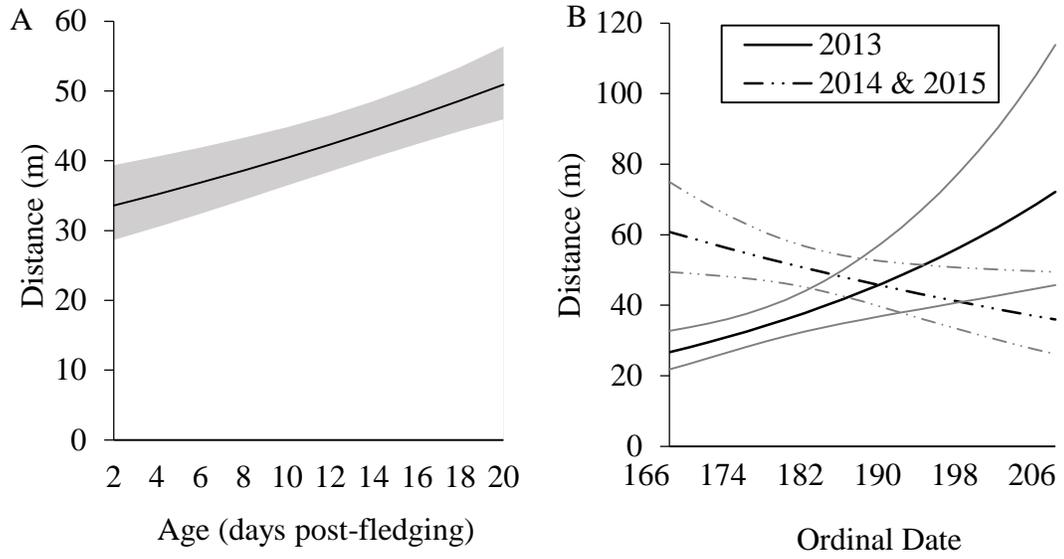


Figure 9.

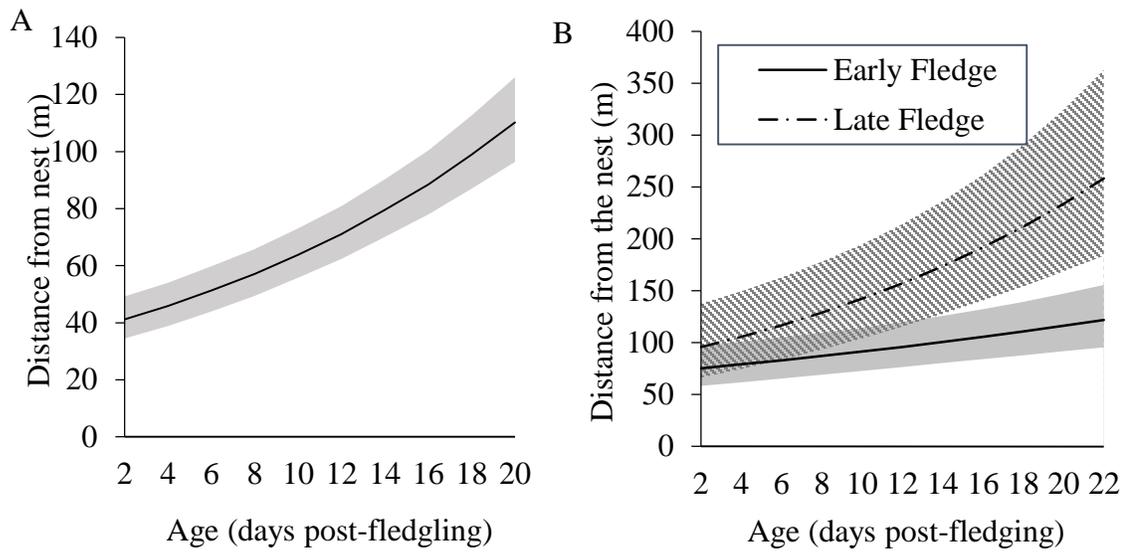


Figure 10.

CHAPTER 2.

COMPARING NEST AND POSTFLEDGING SURVIVAL IN OVENBIRDS AND ACADIAN FLYCATCHERS IN MISSOURI FOREST FRAGMENTS

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, however 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. Nest and postfledging period survival for Ovenbirds was 0.27 ± 0.06 and 0.50 ± 0.09 respectively. Acadian Flycatcher nest and postfledging period survival was 0.30 ± 0.03 and 0.89 ± 0.11 , respectively. 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

characteristic associated with core mature forest, however postfledging survival may have improved near nonforest edges. When we replaced an arbitrary estimate of juvenile survival (half of adult survival) with an estimate incorporating empirical postfledging survival Acadian Flycatcher population growth was more affected (13-26% increase in λ) than Ovenbird population growth (3-6% change). Our results illustrate that we should not assume that species occupying similar nesting habitat will have similar changes in risk post-fledging.

INTRODUCTION

Identifying the mechanisms regulating population dynamics is a cornerstone of population ecology; however, factors limiting population growth remain largely ambiguous (Krebs 2002). This is especially true for populations with complex annual cycles, like migratory birds (Faaborg et al. 2010, Marra et al. 2015, Runge et al. 2015, Rushing et al. 2016). While fluctuations in juvenile survival are as influential as changes in fecundity or adult survival on population growth models (Gaillard et al. 1998, Donovan and Thompson 2001, Cox et al. 2014), information on juvenile survival through the first year is still rare (Anders and Marshall 2005). There is a rich literature describing factors affecting Neotropical migrant songbird fecundity at the nest stage, but juvenile survival has been estimated using assumptions that do not allow yearly variation or stochasticity. Typically, first year survival has been arbitrarily designated as half of adult survival (Ricklefs 1973, Greenburg 1980, Temple and Cary 1988). Recent advances in miniaturization and battery life of radio transmitters have enabled the expansion of breeding season research into the postfledging period for a growing number of migrant species, after juveniles leave the nest and before the initiation of migration. Reported

postfledging mortality rates are as variable as nest survival across landscapes but steadily improve until juveniles gain independence from adults, at which time survival rates are comparable to annual adult survival rates (reviewed in Cox et al. 2014). We can significantly improve population growth models and species conservation by incorporating empirical estimates of postfledging survival that vary in response to factors that influence survival in both the nesting and postfledging stages.

Predation is the primary cause for nest failure and postfledging juvenile mortality in Neotropical migrant passerine birds (Martin 1993a, Robinson et al. 1995, Donovan et al. 1997, Anders et al. 1997). Nest predation and parasitism of forest nesting species are often greatest in fragmented or heavily disturbed landscapes (Donovan et al. 1995, Robinson et al. 1995, Cox et al. 2012). Nest factors influencing predation risk of songbird nests include temporal factors, factors intrinsic to the species or individual (e.g., nest placement or individual condition), local habitat features, and landscape features (Thompson 2007). 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 (Naef-Daenzer et al. 2001). Intrinsic factors hypothesized to affect nest success include variance in nest placement (e.g., nest concealment, and nest height), variance in brood size, adult behavior (e.g., nest visitation rates), and nest parasitism (reviewed in Thompson 2007). Intrinsic factors hypothesized to influence postfledging survival include nestling condition at fledging, the size of the fledged brood, presence of parasite young (Naef-Daenzer et al. 2001, Jenkins and Faaborg 2016) and experience of parents (Rush and Stutchbury 2008). Landscape-level habitat features, such as percent forest cover or extent of fragmentation, may affect nest and juvenile 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).

The effect of local habitat features on survival is especially interesting to conservation biologists, as direct action affecting survival can be taken through land management. Effects of habitat features on nest success are regularly investigated at a variety of scales (reviewed in Martin 1993b, Burhans and Thompson 1998, Thompson 2007) and an increasing number of studies are exploring habitat feature effects on juvenile survival, although the majority have been univariate tests (reviewed in Cox et al. 2011). Habitat requirements may relax during the postfledging period because adults can lead mobile juveniles to areas that maximize their survival by minimizing predation risk while maximizing food acquisition. Many mature forest breeding species use non-nesting habitat such as forest edges and early successional forest during the postfledging period (Anders et al. 1998, Vega Rivera et al. 1998, Pagen et al. 2000, Burke 2013). This shift may be in response to shifting risks or due to shifting food sources. Dense vegetative structure around a nest or juvenile location may make it difficult for a predator to see or maneuver to its target (Martin 1993a, Anders et al. 1998, King et al. 2006); however dense structure may impede foraging efforts of some guilds. Variation in insect and fruit abundance over time and between habitats may also explain some observed postfledging habitat shifts (Anders et al. 1998, Vega Rivera et al. 1999, White et al. 2005).

Factors that negatively impact nest survival may benefit postfledging individuals or may not be as important in the postfledging period. We examined nest and

postfledging survival of two mature forest breeding passerines with different nesting and foraging strategies: the Ovenbird (*Seiurus aurocapilla*) and the Acadian Flycatcher (*Empidonax vireescens*). 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 each stage. We were especially interested if the effects of habitat features on survival shifted between stages. We predicted similar species-level responses to temporal factors, likely due to representative changes in predator community activity, and similar responses to intrinsic factors, like mass at fledging. 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 and predicted lower nest survival and higher juvenile survival probabilities for Ovenbirds in closer proximity to areas with greater understory structure and predicted higher Acadian Flycatcher survival probabilities near areas with more canopy structure and less understory structure. We used a simple projection model to determine sensitivity of population growth to postfledging survival estimates.

METHODS

Study Sites

We conducted our study from 2012–2015 on three 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. All sites are situated within a matrix of forest patches, old-fields, pasture, and cropland. Acadian Flycatchers nested at all three sites and Ovenbirds nested at Bennitt and Baskett; in 2012, however, we only monitored Ovenbirds at Baskett.

Study Species

Both the Ovenbird and Acadian Flycatcher are Neotropical migrant songbirds that nest within large tracts of mature deciduous forests across the Eastern United States. 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); however, both species are area-dependent and sensitive to fragmentation (Whitehead and Taylor 2002, Porneluzi et al. 2011). In our study region, Ovenbirds arrive the final week of April and initiate breeding in early May; in general, nesting attempts stop in late July. Ovenbirds are ground nesting birds with clutches ranging from 2 to 5 eggs, and have a 12–13 day incubation period, with juveniles fledging ~8 days after hatching (Porneluzi et al. 2011). Adults will renest after nest failure but do not attempt a second clutch after successfully fledging young. 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 and in low canopies, staying in semi-dependent family groups for up to 20–30 days (J. M. A. Jenkins personal observation). Studies from both contiguous forest and forest fragments report postfledging juvenile Ovenbirds (during dependent and independent stages) using areas of dense ground cover, such as

clear-cuts or secondary growth forest (Lowther 1993, King et al. 2006, Porneluzi et al. 2011, Vitz and Rodewald 2011, Streby and Andersen 2012, Burke 2013).

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 build low canopy open cup nests, typically 4–7 meters above ground. Clutches typically contain 2–3 eggs, hatch after 13–15 days, and fledge 13–14 days post-hatch (Whitehead and Taylor 2002). Adults will renest after nest failure; 28% of females in our study region fledged a second brood when monitored into September in 2007-2009 (Hirsch-Jacobson 2011). Acadian Flycatcher fledglings, unless prematurely fledged, are able to make short flights and typically remain in the canopy. 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 post-fledging (J.M.A. Jenkins personal observation). There is less information available for postfledging Acadian Flycatchers; Ausprey and Rodewald (2011) found that postfledging survival was not strongly related to urbanism or forest edge.

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 morphologic measurements, including mass (± 0.1 g). We supplemented Ovenbird nest captures with opportunistically hand-caught nonvolant 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 legband 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 0.3g, 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 respectively (2013 & 2015: model A2414 ATS, 2014: model PicoPip Ag337 Biotrack, Wareham, Dorset, UK).

We located birds daily by homing, or as close to every day as possible, 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 from 5–20 min. We recorded locations of nests and juveniles in Universal Transverse Mercator (UTM) coordinates with handheld GPS units (GPS error < 10m). 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 amongst juvenile feathers or body parts; (3) the transmitter signal was lost and bird was <14 days postfledge 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 post-fledge; 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, and when possible by helicopter. If the signal was still lost at the end of the potential battery-life, we censored it after the last actual observation since the bird could have made a long distance movement or been taken by a predator.

Vegetation Sampling

We sampled habitat structure at each nest and each fledgling location, or as close to every relocation as work load allowed. 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 because we reasoned the predator moved the transmitter. 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 ha⁻¹. 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), saw timber (>27.5 cm DBH), and snags greater than 12.5 cm DBH (West 2009). We estimated understory foliage density using the average of four density board (0.3 m wide x 2.0 m tall) measurements taken from 11.3 m in each cardinal direction from the central point. Density board measurements were divided into three regions, low (0–0.3 m), mid (0.3–1.0 m) and high (1–2 m). We 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 nonforest 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). Nonforest edge included all forest boundaries adjacent to ponds, roads, powerline 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). Since we monitored multiple Ovenbird juveniles from the same brood, we adjusted standard errors for repeated measures using general estimating equations identifying brood as the subject with proc genmod (SAS Institute 2008). 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 nonforest edge on survival. We first tested a priori nest and juvenile survival models within four 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 date², ordinal date³, 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 the categorical variable of 2-seasons using the 50th percentile of fledging dates and the 3-season category using the 33rd and 66th percentile of all fledging dates 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, saw timber density, total basal area ha^{-1} , and canopy cover. If distance to nonforest 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 tested against a null model and evaluated using Akaike's information criterion adjusted for small sample sizes (AICc). The nest survival null model included: the intercept and a fixed effect of site. The postfledging survival null model included: the 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 and/or landscape effects between our study locations. We include a fixed effect of age (days out of the nest) in all postfledging models since juveniles are most vulnerable immediately after leaving the nest and, to our knowledge, all published postfledging survival models have found a strong effect of time out 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 AICc was lower than the null model and was within 2 AICc units of the best model without adding uninformative parameters to the final additive model set (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 period 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) and used a 30 day Acadian Flycatcher 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, the mean number of days juveniles were dependent upon parents (J. M. A. Jenkins personal observation).

Population Growth Modelling

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 λ is the population growth rate, P_A is the annual survival of adult females, P_J is the annual survival of juveniles, and β is the number of fledged juvenile females produced annually (Pulliam 1988). A λ equal to one, greater than one, and less than one represents a stable, growing, and declining population respectively. We calculated β 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 as half of adult survival or something similar (Ricklefs 1973, Greenburg 1980, Temple and Cary 1988). When post-fledging

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. Non-breeding season studies of other migratory birds, including Black-throated Blue Warblers (*Dendroica caerulescens*), American Redstarts, (*Setophaga ruticilla*), and Barn Swallows (*Hirundo rustica L.*), have found equal survival rates for non-breeding adult and juvenile migratory birds (Marra and Holmes 2001, Sillett and Holmes 2002, Gruebler et al. 2014). However, some penalty for inexperience may be present during migration (e.g., Opper et al. 2015) and juvenile birds may be excluded from high quality wintering habitat (Sherry and Holmes 1996) which may increase mortality (Marra and Holmes 2001). We assumed that $P_{PF} < P_W$ and modeled two 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. Our growth estimates are for illustrative purposes only. We present all summary variables as means \pm standard errors (SE).

RESULTS

Ovenbird Survival

We monitored 94 Ovenbird nests every 2.8 ± 0.06 days for a total of 308 observations. Thirty-nine Ovenbird nests successfully fledged 2.86 ± 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 and 19 parasitized Ovenbird nests 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 ± 2.08 % visually concealed. Two Ovenbird nest failures showed evidence of adult mortality (adult feathers and legs at nest entry).

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 nonvolant 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 ten days of the postfledging period and 13 individuals died before the first relocation. Three individuals from one nest were killed in a weather event day one and were censored from the analysis. All other Ovenbird mortalities were categorized as predation. We were only able to conclusively identify the predators for 4 individuals; 3 individuals at Baskett were tracked to the bellies of ratsnakes (*Pantherophis obsoletus*) at 1, 3, and 10 days postfledging and 1 individual at Rudolf was tracked to a racer snake (*Coluber constrictor*) 4 days postfledge. We found an additional radio that appeared to have been passed by a snake and we tracked another Ovenbird to a tree cavity for 3 consecutive days (5 days postfledge), a likely snake predation. We found the legs and radio of 1

Ovenbird in a dry creek bed (3 days postfledge). We found 2 slightly chewed Ovenbird juveniles (small punctures) at 2 and 11 days postfledging. We found one Ovenbird decapitated with the body largely intact (5 days postfledging). We found the radio and crushed bands of one Ovenbird one day out of the nest. We found 4 Ovenbird transmitters with many Ovenbird feathers, avian feces, or damage from teeth (2 and 3 days postfledge). Eleven Ovenbird signals were lost while birds were too young to be independent and were not with resighted family groups (max 7 days postfledge). Of these 11 signals, we found 1 signal 1.4 km from its nest, the last known location, with a helicopter. We believe that these individuals were picked up by larger avian or mammalian predators and either taken into burrows or carried out of our search zone. Multiple siblings in a brood were predated 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 ± 1.26 days (min = 23). Ovenbird nests and juvenile locations differed in mean understory foliage density, litter depth, shrub density, groundcover, overall tree density, and distance from nonforest 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 which included the covariates: site, 3-season, saw timber density and snag density (Table 2 and Figure 1). Of the model averaged covariates, saw timber 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 which included the covariates: site, mass, age, sapling density, basal area ha^{-1} , 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 saw timber density increased (Figure 1C). Overall nest period (25 days) and postfledging period (0-23 days) survival for Ovenbirds was 0.27 ± 0.06 and 0.50 ± 0.09 respectively.

Acadian Flycatcher Survival

We monitored 264 Acadian Flycatcher nests every 3.56 ± 0.04 days for a total of 1258 observations. Eighty Acadian Flycatcher nests successfully fledged 2.39 ± 0.03 young weighing 11.36 ± 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 ± 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 ± 1.57 (min = 15) days. The majority of juvenile observations came from Basket (77%) with 7% from Rudolf, and 16% from Three Creeks. Five transmitters fell off before radio failure (harness strap failure) and were censured 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 predations. We were only able to conclusively identify one predator: one Acadian Flycatcher signal was tracked to the belly of a copperhead snake (*Agkistrodon contortrix*) 2 days postfledging (the nest of that individual was low ~1.5 m). One other individual was likely also depredated by a snake 26 days postfledging; the radio signal was tracked to a high tree cavity for >3 days (this individual was independent but still on its natal territory). We found 2 radios with feathers and avian feces (2 and 3 days postfledging). Five Acadian Flycatcher radio signals were lost while birds were too young to be independent (max 7 days postfledge) and were not observed with family groups; We believe that these individuals were picked up by larger avian or mammalian predators and either taken into burrows or carried out of our search zone. 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 Flycatcher nesting and postfledging survival model selection was 4002 days and 695 days respectively. 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 since saw timber 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 saw timber 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) survival of Acadian Flycatchers was 0.30 ± 0.03 and 0.89 ± 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 8). 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 8). 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 projected a 5% lower growth rate compared to the arbitrary estimate (Table 8).

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 postfledge 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 ($\beta = - 0.72$), and positively associated with small trees ($\beta = 1.36$; Vitz and Rodewald 2011). This difference 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, however 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 saw timber 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. 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 (Chapter 1) and we found that postfledging Ovenbird resource selection was positively affected by understory foliage density (Chapter 3). 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, powerline 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 postfledging 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 (*Wilsonia citrina*) postfledging survival did not differ between large and small forest fragments in Pennsylvania where 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; however, we began nest searching after Ovenbird spring arrival, so we may have missed some early nest attempts and Ovenbirds finished attempting nests earlier than Acadian Flycatchers: mid-July vs. 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 or no mortality around 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, postfledging foraging behavior exhibited by our two species. The longer nestlings remain in the nest, the larger (higher mass) and more resilient they are once fledged (Cox et al. 2011). 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 force-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 we are aware of for postfledging survival of Acadian Flycatchers is a period survival (22 day) of 0.72 ± 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 and 0.88 for Willow Flycatchers (*E. traillii*) and Dusky Flycatchers (*E. oberholseri*), respectively (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. 2011). Ovenbird postfledging survival is lower in highly managed (harvested) forest in New Brunswick, Canada: 0.45 for 14 days (Hache 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, Hache et al 2014) are rare in our Missouri forest fragments where snakes are the most common nest predator (Cox et al. 2012) and were the only predator 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.

The 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 changes in risk post-fledging. We did not detect survival tradeoffs for habitat utilized in the nesting and postfledging periods, however, 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 is variable. The addition of a postfledging component to nesting studies, even if only for two weeks postfledging (Cox et al. 2013; however, see Dybala et al. 2013), would greatly improve our understanding of both potential tradeoffs of habitat features, or fragmentation effects, and improve our understanding of the variation in postfledging juvenile survival.

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Figure 1. Predictions of the best supported models showing the effects of season (**A**), site (**B**), saw timber 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.

Figure 2. Predictions of the best supported models showing the effects of age (**A**), sapling density (**B**), mass (**C**), basal area (**D**), distance to nonforest 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.

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.

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.

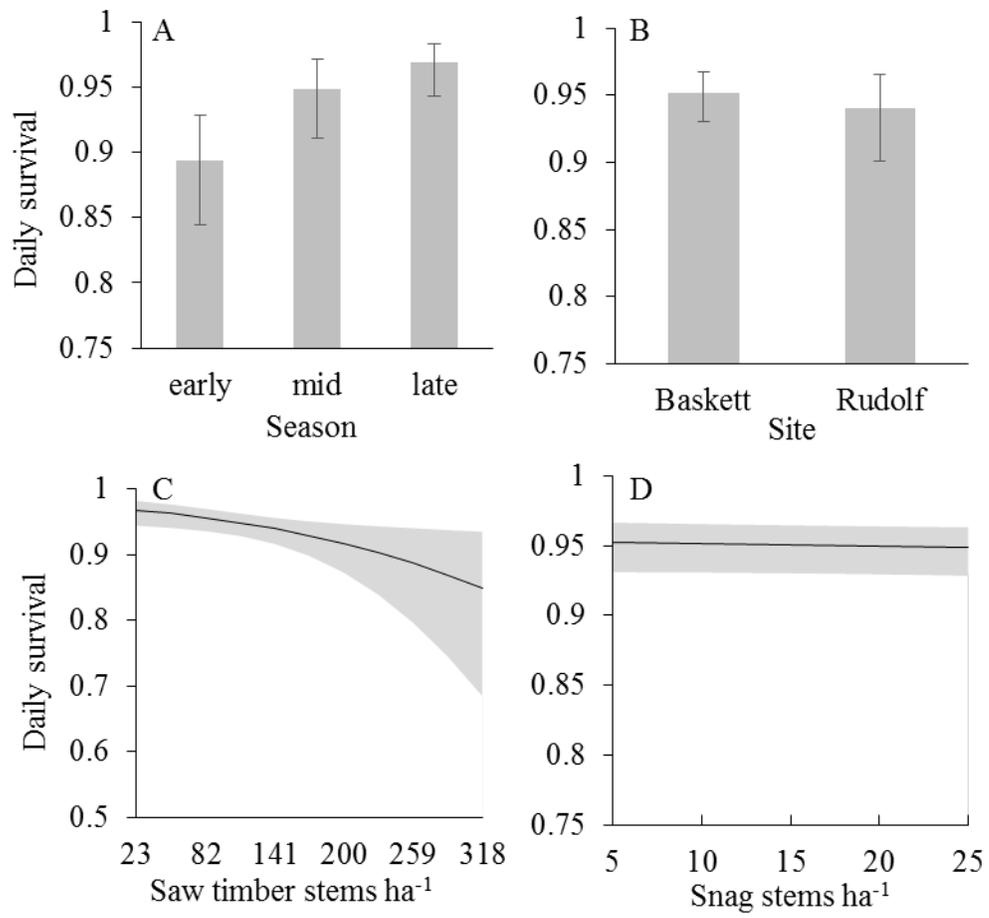


Figure 1.

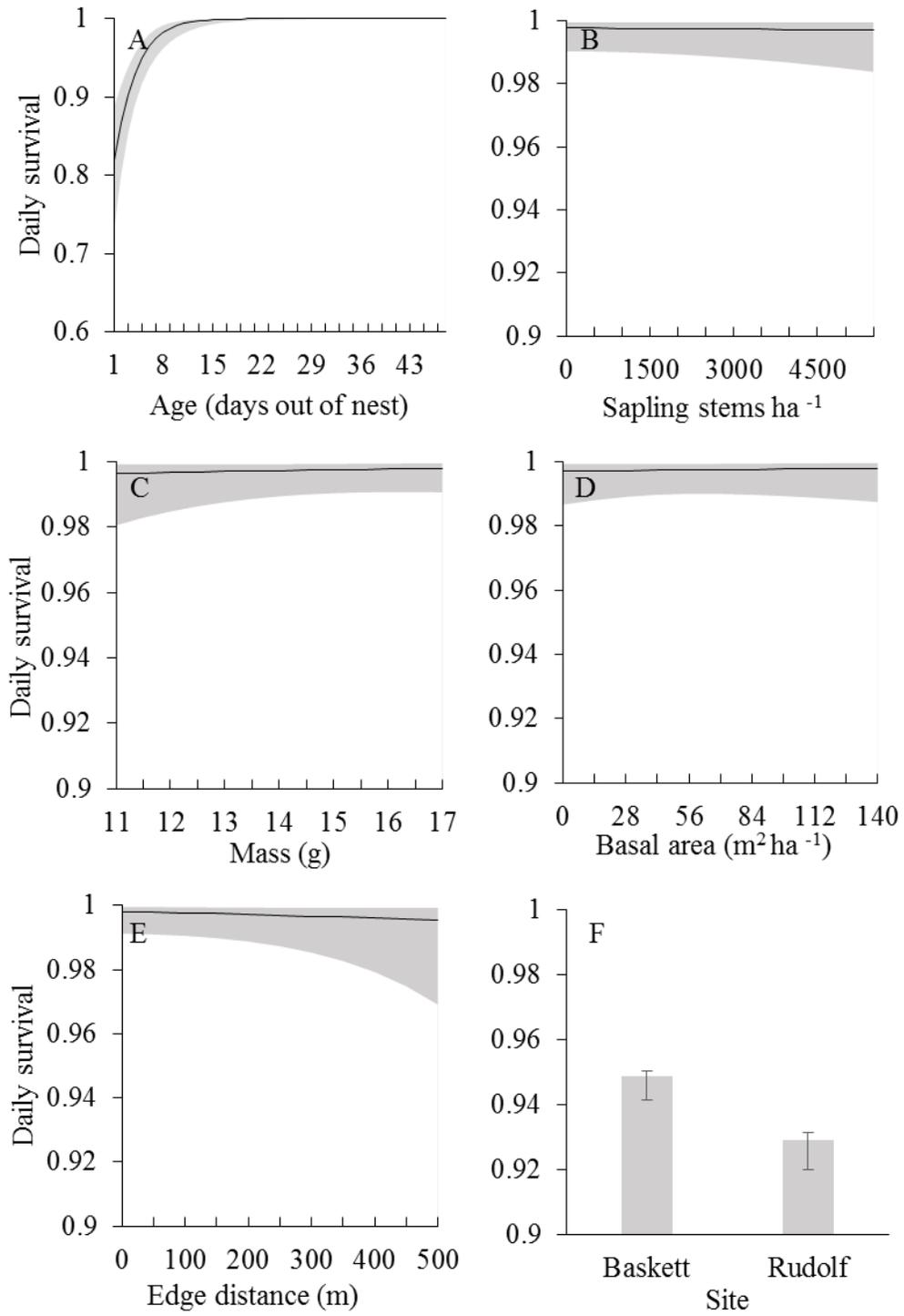


Figure 2.

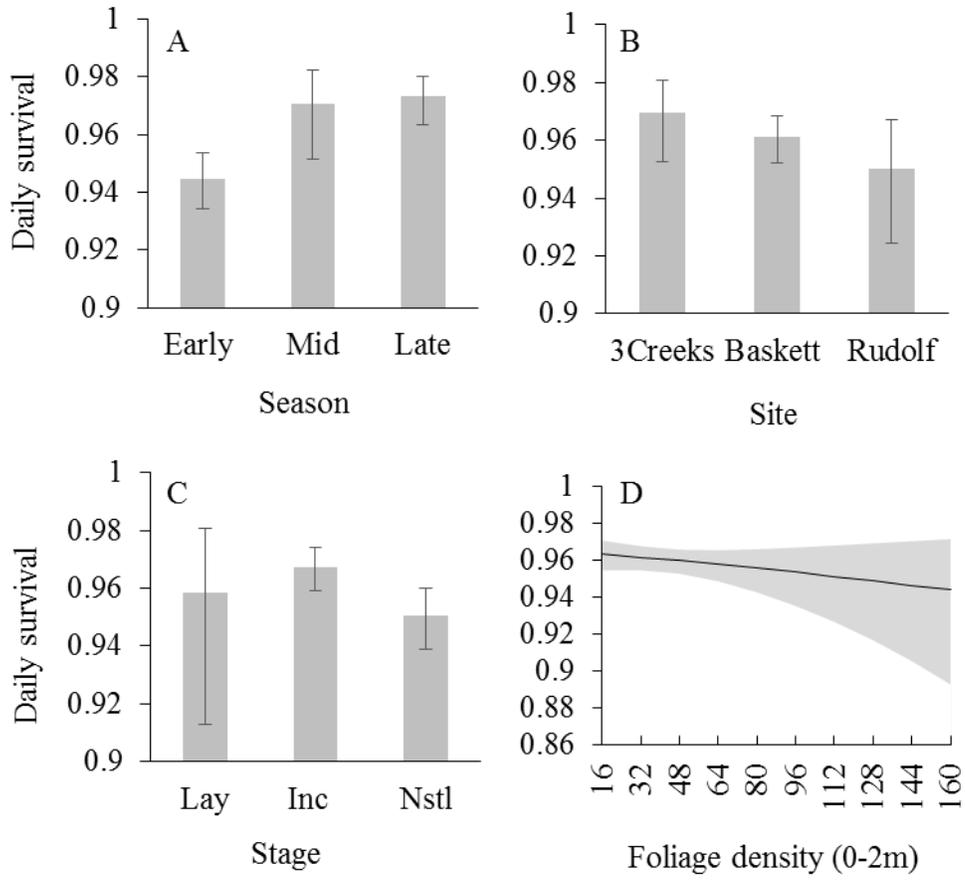


Figure 3.

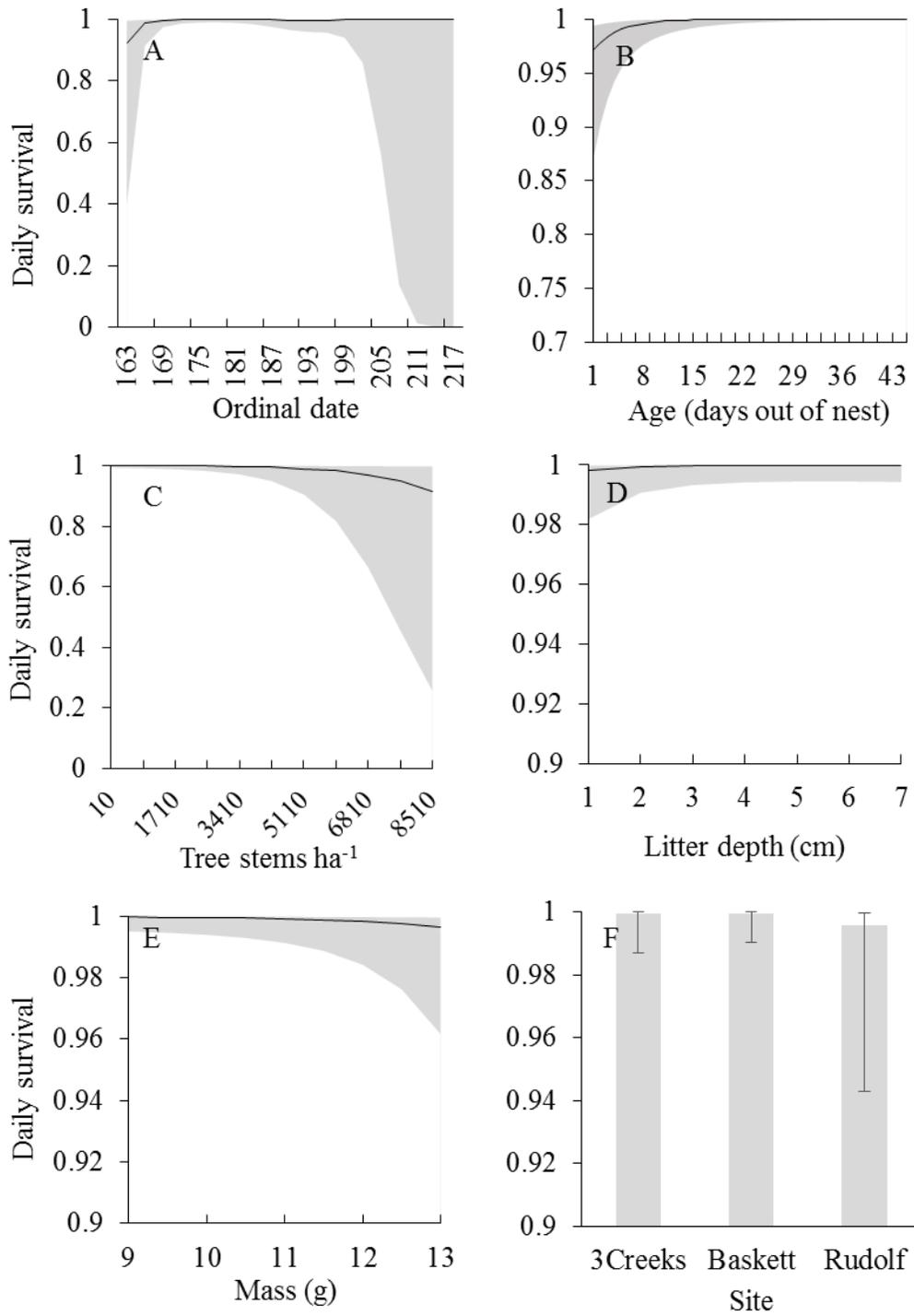


Figure 4.

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 2012–2015. F and P values are given for generalized linear model with fixed effect of site and stage (nest vs. postfledge).

	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 (0–2m)	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 ⁻¹	975 \pm 51	1278 \pm 56	10.77	0.001	959 \pm 104	1263 \pm 49	4.79	0.03
Pole timber stems ha ⁻¹	155 \pm 9	189 \pm 9	3.48	0.06	194 \pm 23	206 \pm 10	0.03	0.87
Sapling stems ha ⁻¹	714 \pm 51	778 \pm 43	0.45	0.50	653 \pm 105	731 \pm 38	0.31	0.58
Saw timber stems ha ⁻¹	106 \pm 4	115 \pm 3	3.77	0.05	112 \pm 6	106 \pm 3	0.57	0.45
Snag stems ha ⁻¹	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 ⁻¹	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

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 (ΔAIC_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	ΔAIC_c^*	w_i
Ovenbird nests				
Site + 3-Seasons + Saw Timber + Snag	240.70	6	0.00	0.13
Site + 3-Seasons + Saw Timber	243.45	5	0.72	0.09
Site + 3-Seasons + Saw Timber + Snag + Canopy	240.43	7	1.77	0.05
Null (Site)	264.89	2	11.75	<0.01
Ovenbird postfledging juveniles				
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.

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 (ΔAIC_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	ΔAIC_c^*	w_i
Acadian Flycatcher nests				
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
Acadian Flycatcher postfledging juveniles				
Age + Site + Litter + Ordinal Date ³ # + Mass + Tree Density	56.63	10	0.00	0.15
Age + Site + Litter + Ordinal Date ³ # + Mass + Tree Density + Total Basal Area	54.90	11	0.34	0.13
Age + Site + Litter + Ordinal Date ³ # + Mass + Saw Timber	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.

Table 4. Population growth estimates (λ) and model parameter values for Missouri forest fragment populations from 2012-2015 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 greater than one, less than one, and equal to one represents a growing, declining, or stable population respectively.

	λ	P_A	P_J	β	P_{PF}	P_W^*	P_N	n	Y_N
Ovenbirds									
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
Acadian Flycatchers									
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 ~2 months in the nest and postfledging.

APPENDIX

Table 5. Model averaged coefficients (β), unconditional standard error (SE) and confidence intervals (CI) from the two best supported models of the probability of Ovenbird nest survival in Missouri, 2012–2015.

Parameter	β	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
Saw timber density	-0.34	0.14	-0.62,	-0.07
Snag density	-0.16	0.17	-0.50,	0.19

Table 6. Model averaged coefficients (β), unconditional standard error (SE) and confidence intervals (CI) from the five best supported models of postfledging Ovenbird survival in Missouri, 2012–2015, with repeated measures accounting for multiple individuals per brood.

Parameter	β	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 ⁻¹	0.05	0.10	-0.16,	0.26
Edge distance	-0.21	0.22	-0.65,	0.23

Table 7. Model averaged estimated coefficients (β), unconditional standard error (SE) and confidence intervals (CI) for the two best supported models of Acadian Flycatcher nest survival in Missouri, 2013–2015

Parameter	β	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

Table 8. Estimated coefficients (β), standard error (SE) and confidence intervals (CI) from the best supported candidate model of postfledging Acadian Flycatcher survival in Missouri, 2013–2015.

Parameter	β	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 ²	-1.13	0.54	-2.19,	-0.08
Ordinal date ³	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

CHAPTER 3

HABITAT SELECTION CHANGES BETWEEN NESTING AND POSTFLEDGING FOR MISSOURI OVENBIRDS AND ACADIAN FLYCATCHERS

ABSTRACT

Recent work has suggested that resource selection on the breeding grounds may change during the postfledging period. However, the degree to which selection preferences change from nesting to postfledging and whether all or only a few species alter their resource use is unclear. We compare resource selection for nest sites and resource selection by postfledging juvenile Ovenbirds (*Seiurus aurocapilla*) and Acadian Flycatchers (*Empidonax vireescens*) followed with radio telemetry in Missouri mature-forest fragments in 2012–2015. We used an information theoretic approach with Bayesian discrete choice modeling to evaluate support for local vegetation factors on the probability of selection for nest-sites and locations utilized by postfledging juveniles. Resource selection models indicated that Acadian Flycatcher habitat selection relaxed from nesting to postfledging, with only canopy cover positively contributing to selection postfledging. Resource selection for Ovenbirds shifted from a preference for open understory mature forest nest sites, to increased selection for high understory foliage density and sapling density. Habitat management based upon nesting requirements would likely be sufficient for postfledging Acadian Flycatchers, but insufficient for postfledging Ovenbirds.

INTRODUCTION

The risks and requirements of Neotropical migrant birds change over the course of their complex annual cycle (Faaborg et al. 2010, Rushing et al. 2016). Habitat selection theory predicts that higher quality habitat will be selected and occupied more frequently than lower quality habitat (Hutto 1985, Jones 2001). Resource selection models often inform conservation efforts; however, songbird habitat selection studies have mainly focused on factors affecting nest-site selection or breeding territory density (Marra et al. 2015). Adequate conservation will not be achieved until we understand in what parts of the annual cycle and to what magnitude resource selection preferences change. For example, resource selection during the postfledging period, lasting from fledging until migration, may differ from the nesting season (Anders et al. 1998).

The postfledging period can span an equal or greater amount of time than the nesting period. The postfledging period can also encompass a period of high juvenile mortality that significantly affects population models (Donovan and Thompson III 2001, Cox et al. 2014, Streby et al. 2014). Mature forest-nesting birds have been captured postfledging in nonbreeding habitat, including early-successional forest, wildlife openings, riparian forest, and regenerating harvested forest, suggesting significant shifts in resource requirements from nesting to postfledging (Akresh et al. 2009, Chandler et al. 2012, Burke 2013). Relatively few species have been monitored throughout the postfledging period (Cox et al. 2014); the majority of radio-telemetry studies have focused on a few species. The degree to which resource preferences shift and whether all or a few species change their postfledging habitat use is still unclear (Burke 2013, Cox et al. 2014)

The drivers of habitat selection during the postfledging period are likely different from drivers of breeding territory selection. Selection during the nesting period is likely dominated by the need to locate appropriate nest-sites. Hypothesis for the drivers of nest-site selection include: the location's vulnerability to predation (Martin 1993), vulnerability to brood parasitism (Burhans 1997), microclimate (Rauter et al. 2002) and the availability of food and other resources (Martin 1995, Burke and Nol 1998). Postfledging period resource selection is likely driven by similar considerations; however, since movements and site occupation length are no longer constrained as juveniles become mobile, the underlying risks and rewards of different habitat features likely shift. The two leading hypotheses explaining habitat selection during the postfledging period are the optimal foraging and the predator avoidance hypothesis (Anders et al. 1998, Vega Rivera et al. 1998, White et al. 2005). The optimal foraging hypothesis predicts that birds should shift habitat use to areas where they can expend the least amount of energy to attain food. The predator avoidance hypothesis predicts that individuals will move to areas that provide the most protection from predation. Other postfledging resource selection hypotheses that have received limited support include: prospecting (searching for future breeding territory), intraspecific competition (adults pushing juveniles out of breeding areas), and migration initiation (summarized in Russell 2000).

Ovenbirds (*Seiurus aurocapilla*) and Acadian Flycatchers (*Empidonax virescens*) are insectivorous Neotropical migrant songbirds that nest within mature deciduous forests across eastern North America. Both species are considered area-dependent breeders, sensitive to fragmentation (Whitehead and Taylor 2002, Porneluzi et al. 2011). Ovenbirds

spend the majority of their time foraging on the ground in leaf litter, while Acadian Flycatchers forage by sallying in open areas under closed canopy. Acadian Flycatchers are low-canopy open-cup nesters; juveniles, unless prematurely fledged, are able to make short flights at fledging and typically remain in canopy layers throughout the postfledging period. Flycatcher young remain dependent upon parents for ~19 days post-fledging (Chapter 1) and have relatively high postfledging survival rates (0.72-0.89; Ausprey and Rodewald 2011, Chapter 2). Ovenbirds build camouflaged domed nests on the ground; young cannot fly for several days postfledging and spend the majority of their time on the ground or in understory vegetation. Ovenbird juveniles remain in dependent family groups for ~23 days (Chapter 1) and have a wide range of reported postfledging survival rates (0.70–0.42; Vitz and Rodewald 2011, Streby and Andersen 2011). Both dependent and independent postfledging Ovenbirds have been reported using areas of dense cover including nonbreeding habitats such as clear-cuts or secondary growth forest in contiguous forests (Lowther 1993, Hersek et al. 2002, King et al. 2006, Porneluzi et al. 2011, Vitz and Rodewald 2011, Streby and Andersen 2012, Burke 2013).

We compared resource selection by nesting adults (nest-site selection) and postfledging juvenile Ovenbirds and Acadian Flycatchers in Missouri forest fragments. We monitored all available nests and conducted a radio telemetry study of postfledging juveniles. We predicted that Ovenbird postfledging habitat selection preferences would be more disparate from nest-site selection than habitat selected by Acadian Flycatchers based upon their foraging styles, nest locations, and mobility at fledging. We predicted that dense understory/ground vegetation structure would provide optimal cover for postfledging juvenile Ovenbirds while they foraged. However, such habitat would be

selected against during nesting when dense understory or groundcover could block sightlines from the nest and reduce camouflaging leaf litter. We predicted little change in resource selection between nesting and postfledging for Acadian Flycatchers who require open areas under closed canopy for both nesting and foraging, and predicted selection away from dense continuous vertical habitat, such as forest edges with high sapling and understory densities. We used an information theoretic approach with Bayesian discrete choice modeling to evaluate support for local vegetation factors on the probability of selection for nest-sites and locations utilized by postfledging juveniles. We modeled the probability that an individual bird will select one resource relative to all other available resources as a discrete choice from a choice-set (Cooper and Millsbaugh 1999).

Understanding how habitat features affect different songbird guilds during the nesting and postfledging periods of the breeding season will inform conservation efforts.

STUDY SITE

We studied nesting and post-fledging ecology on three forested sites in Central Missouri (Boone, Randolph, and Howard counties) from 2011–2015. We surveyed the Thomas S. Baskett Wildlife Research and Education Center (38° 44'N, 92°12'W; 890 ha) from 2012–2015. In 2013–2015, we surveyed Rudolf Bennitt State Conservation Area (39° 8' N, 92° 15' W; 1146 ha). We surveyed Three Creeks Conservation Area (38° 49'N, 92°17'W; 575 ha) in 2014–2015. All study sites were mixed-hardwood forest, interspersed with successional red cedar (*Juniperus virginiana*) stands and were situated within a matrix of forest patches, old-fields, and agriculture. Acadian Flycatchers were present at all three sites, while nesting Ovenbirds were only present at Rudolf and Baskett forests. In 2012 we only monitored Baskett Ovenbirds.

METHODS

Field Methods

We found nests from mid-May to mid-August and monitored nests every three to five days following standard methods until nest failure or fledging (Martin and Geupel 1993). On the day of projected fledging, day 8 for Ovenbirds and day 13 for Acadian Flycatchers, we captured all available nestlings and recorded nestling mass (± 0.1 g). We supplemented Ovenbird nest captures with opportunistically hand-caught nonvolant fledged juveniles (1–2 days out of the nest; we rarely captured postfledging Acadian Flycatchers). We attached colored-leg bands and a standard U.S. Geological Survey leg band to all captured Ovenbirds and attached radio transmitters to one or two (rarely three) individuals per brood. All captured Acadian Flycatcher nestlings received a standard U.S. Geological Survey leg 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, MN, USA). In 2013–2015, transmitters weighed 0.3g, 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 respectively (2013 & 2015: model A2414 ATS, 2014: model PicoPip Ag337 Biotrack, Wareham, Dorset UK,).

We located juvenile birds daily, or as close to every day as possible, by homing using handheld receivers (model R410-ATS and Model R1000-Communication Specialists Inc. Orange, CA USA) and handheld directional antennas (Yagi 3-element

and H-Type ATS). We located individuals until the transmitter signal was no longer detectable (transmitter battery failure or dispersal out of study area) or until we determined mortality. We recorded locations in Universal Transverse Mercator (UTM) coordinates with handheld GPS units (GPS error < 10m). We selected two random points to complete the choice-set for each nest and live juvenile location. Random samples of available habitat were approximately 50 m away at a random azimuth from the used location. We constrained random samples to ‘reasonable’ habitats based upon prior knowledge of species natural history. For example, we did not allow a random sample for either species to occur in open water and we allowed random samples for Acadian Flycatcher juveniles but not Ovenbird juveniles to occur over a canopy covered road. If a random location was inappropriate, we chose a new random azimuth until a suitable available habitat was encountered. We considered random sites as available due to their close proximity to use sites; 50m is within the range of juvenile daily movements for both species throughout the postfledging period (Chapter 1).

We sampled environmental resources at each used and random available location. We calculated canopy cover at each point using the average of four spherical densiometer readings (one in each cardinal direction). We averaged litter depth measurements taken at the central point and 2m from the central point in each cardinal direction. We measured the diameter at breast height (DBH), of all stems greater than 3cm DBH in a 10-factor basal area wedge plot and recorded trees as deciduous, coniferous (primarily cedars), or dead trees (snags). We calculated stem densities per hectare of saplings (3.0–12.5 cm DBH), pole timber (12.5–27.5 cm DBH), saw timber (>27.5 cm DBH), and snags greater than 12.5 cm DBH (West 2009). We estimated understory foliage density using the

average of four density board (0.3 m x 2 m) measurements taken from 11.3m in each cardinal direction from the central point. We calculated distance to nearest nonforest edge for point remotely in ArcGIS (ESRI 2012) using the 30m 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). Nonforest edge included all forest boundaries adjacent to ponds, roads, and powerline cuts, and other landcover classes that were visible from aerial photos; trails and roads with full canopy coverage were not considered edge.

Modeling Resource Selection

We used multinomial logit discrete choice models in a Bayesian framework to model the probability an individual would select the used or available location if given a choice between the 3 locations (Cooper and Millspaugh 1999). Choice sets were defined as 3 locations available to the individual at the time the choice was made: the used location and two paired randomly available locations. We used random-effect (hierarchical) multinomial logit discrete choice models within a Bayesian framework for juvenile resource selection models to account for repeated observations of individuals. We modeled the ‘utility’ of the used locations (U_{ij}^{used}) in choice set i of juvenile j as a linear function of vegetation coefficients (Veg_1, \dots, Veg_w) and individual-level regression coefficients ($\beta_{1j}, \dots, \beta_{wj}$):

$$U_{ij}^{used} = \beta_{1j}Veg_{1ij}^{used} + \dots + \beta_{wj}Veg_{wij}^{used}$$

The utility of available locations (U_{ij}^{avail}) was calculated in the same manner using the vegetation sampled at random available sites. Using these utility functions we modeled the probability of selecting used locations as:

$$\psi_{ij}^{used} = \frac{\exp(U_{ij}^{used})}{\exp(U_{ij}^{used}) + \exp(U_{ij}^{avail1}) + \exp(U_{ij}^{avail2})}$$

We modeled population-level resource selection of juveniles by assuming that individual-level coefficients for juvenile j arise from normal population level distributions (Thomas et al. 2006). For example, we assume $(\beta_{1,1}, \dots, \beta_{1,J}) \sim N(\mu_1, \sigma_1^2)$, where J is the total number of individuals sampled. Hereafter, we refer to the set of parameters governing each juvenile population-level distribution ($[\mu_1, \sigma_1^2], \dots, [\mu_w, \sigma_w^2]$) as population-level regression coefficients. We calculated the probability of selection for nest-site choice sets at the population-level directly with the formulas above excluding the random effect of individual j . For ease of reading, we hereafter refer to each regression coefficient distribution by the name of the associated vegetation covariate.

For all models, posterior distributions for each parameter were estimated using Markov chain Monte Carlo (MCMC) methods implemented in JAGS (Plummer 2015) using the jagsUI package (Kellner 2015) in program R (R Core Team 2015). We selected vague prior distributions for all model parameters. We assumed normal $N(0, 0.01)$ prior distributions, on all nest regression coefficients and all juvenile population-level mean hyperparameters (μ_1, \dots, μ_w) . We assumed diffuse inverse-gamma distributions $\mathcal{Y}(1, 0.0001)$ for each juvenile standard deviation hyperparameter $(\sigma_1, \dots, \sigma_w)$. The Brooks-Gelman-Rubin convergence diagnostic (Rhat = 1) was used to determine adequate convergence for all hyperparameters (Brooks and Gelman 1998). Estimates for nest site models were based on 3 MCMC chains of 75000 iterations, with a burn-in of 25000 iterations and a thin rate of 50, yielding 3000 total samples from the joint posterior. Estimates for juvenile Ovenbird habitat use were based on 3 MCMC chains of 300000 iterations, with a burn-in of 150000 iterations and a thin rate of 50, yielding 9000 total

samples from the joint posterior. Estimates for juvenile Acadian Flycatcher habitat use were based on 3 MCMC chains of 400000 iterations, with a burn-in of 150000 iterations and a thin rate of 50, yielding 15000 total samples from the joint posterior.

We used an information theoretic approach to evaluate relative support for each resource selection model using the Watanabe-Akaike information criterion (WAIC) estimating expected predictive error; WAIC is a fully Bayesian alternative to Akaike's Information Criterion (AIC; Burnham and Anderson 2002, Hooten and Hobbs 2015). Bayesian model selection can be sample size specific and is not as constrained by large sample size theory (Thomas et al. 2004). We compared a global model, an understory-level model, stand-level model, and a null model for each group of resource selection observations. We did not consider landscape-scale effects since juveniles were restricted by the landscape chosen by adults. Models were composed of uncorrelated variables describing understory and stand structure. We confirmed noncollinearity of covariates by determining the variance inflation factor was < 2.0 for all covariates. The global model included: leaf litter depth (litter), understory foliage density (0–2 m), sapling stems ha^{-1} , pole stems ha^{-1} , saw timber stems ha^{-1} , average canopy cover, and distance to nonforest edge. We were interested in potential interactions between distance to nonforest edge and the other vegetation variables. Rates of nest parasitism and nest predation for forest songbirds are often higher near forest edges (Donovan et al. 1997, Flaspohler et al. 2001) and mortality rates of postfledging juvenile Spotted Towhees (*Pipilo maculatus*) were higher near forest edges (Shipley et al. 2013). Before model selection, we evaluated support for edge interactions with all covariates in each habitat selection category (nest and juveniles, both species), and for interactions between the nesting substrate (litter

depth for Ovenbirds and sapling density for Acadian Flycatchers) and all other variables in nest-site selection categories. We considered an interaction to be supported if the mean interaction effect retained its sign in 90% of posterior trials ($f \geq 0.90$). Supported interactions were included in all other models of its parts. We examined the contribution of the covariates in the top performing model (lowest WAIC); covariates with bounds not including zero were interpreted as supported and contributing to selection (Thomas et al. 2004).

RESULTS

We collected 170 complete choice sets for Acadian Flycatcher nests and 53 complete choice sets for Ovenbird nests from 2013-2015. We collected 422 choice sets for 39 Acadian Flycatcher juveniles with 10.8 ± 0.97 (range 1–20) sets per individual and 508 choice sets for 42 Ovenbird juveniles with 12.1 ± 1.16 (range 1–27) sets per individual. We did not sample random locations for nests in 2012 and were not able to sample choice sets for all juvenile locations due to the time intensive nature of sampling. Instead, we sampled choice sets for every other juvenile relocation and increased our sampling to every observation (once per day) when workload allowed.

Interactions between distance to edge and litter depth ($f = 1.0$) and between sapling density and saw timber density ($f = 0.98$) were included in all models of Acadian Flycatcher nest-site selection. The interaction of distance to edge and sapling density ($f = 0.96$) was included in all models of juvenile Acadian Flycatcher resource selection. The global model and understory models were the two best-fitting models for both Acadian Flycatcher nest-site selection and juvenile resource selection (Table 1). Both models

outperformed the null model of random selection. Covariates with bounds not including zero included pole timber density, saw timber density, and canopy cover for nest-site selection and only canopy cover for juvenile resource selection (Table 2). There was little variation between individual and population-level covariates of Acadian Flycatcher juveniles (Figure 1); there was high variability in utility of foliage density among individuals (Figure 1c). Increasing pole and saw timber densities reduced the relative probability of use for Acadian Flycatcher nesting, while increasing canopy cover increased the relative probability of use for both nesting and postfledging juvenile resource selection (Table 2; Figure 2).

Interactions between litter depth and saw timber density ($f = 0.98$), litter depth and canopy cover ($f = 0.91$) and between distance to edge and litter depth ($f = 0.96$) were included in all Ovenbird nest-site selection models. No interactions were included in Ovenbird juvenile models. The stand level model was the top performing Ovenbird nest site model, while the global model was the best-fitting juvenile Ovenbird model (Table 3). All models outperformed the null model of random selection. Covariates with bounds not including zero included canopy cover and litter depth in nest-site selection models and canopy cover, understory foliage density, and sapling density for juvenile resource selection (Table 4). There was little variation between individual and population-level covariates of Ovenbird juveniles (Figure 3), however the litter depth and foliage density coefficients had very diffuse distributions among individuals (Figure 3b and 3c). The relative probability of use for an Ovenbird selecting a nest-site increased with saw timber density and litter depths. The relative probability of use for postfledging juvenile

Ovenbirds increased with canopy cover, understory foliage densities, and sapling densities (Table 4; Figure 4).

DISCUSSION

As predicted, resource selection by Ovenbirds was more dissimilar between nesting and postfledging than by Acadian Flycatchers. We predicted that dense understory and ground vegetation structure would be selected against during Ovenbird nesting as the foliage could block sightlines from the nest and reduce camouflaging leaf litter. We did not detect any significant contribution of understory density to nest site selection; however, nesting Ovenbirds were more likely to select sites with higher canopy coverage and deep litter. This is consistent with previous findings that Ovenbirds select nest-sites with high canopy cover, mature forest, low ground cover, and high litter depths (Smith and Shugart 1987, Wenny et al. 1993, Porneluzi et al. 2011). We did not detect significant avoidance of edge, as observed in some studies (Hann 1937, Porneluzi and Faaborg 1999) although this may be due to the relatively fine scale at which we sampled random locations (~50 m).

Understory foliage density, sapling density and canopy cover contributed significantly to postfledging juvenile Ovenbird resource selection. Structurally complex areas with high stem and foliage densities likely mitigate risk of predation by obscuring young birds from view and by providing a barrier to predators (Anders et al. 1998). We often found young non-volant Ovenbirds crouched under foliage or perched within downed branches waiting for food to be delivered by adults. Later in the postfledging period as birds became more mobile, it was common for family groups to be found foraging within dense shrubby edge areas or in thick cedar stands. Insect abundance is

also likely correlated with vegetation density and insect communities are likely more diverse in areas with high structural diversity (Blake and Hoppes 1986, Crist et al. 2006, Moorman et al. 2012). Therefore, our work supports both the predator avoidance and optimal foraging theories of resource selection for postfledging juvenile Ovenbirds. Our work reinforces the theory that habitat quality increases with forest understory structure for postfledging Ovenbirds and for other postfledging ground foraging forest songbirds (Anders et al. 1997, Vitz and Rodewald 2011, Streby and Andersen 2013, Streby et al. 2014). Our work in a mature-forest landscape demonstrated that areas of dense understory structure such as treefall gaps, edges, and cedar patches in mature forest can be used as an alternative to areas of younger successional forest, such as regenerating clear cuts (Vitz 2008, Streby and Anderson 2013).

We predicted little change in resource selection between nesting and postfledging for Acadian Flycatchers because they require open areas under closed canopy for both nesting and foraging. Pole timber and saw timber were negatively related, and canopy cover positively related, to flycatcher nest-site selection. This is consistent with prior studies that found that Acadian Flycatchers place nests more often in areas with open understory (Schmidt and Whelan 1999, Bakermans and Rodewald 2006). We did not find great shifts in resource selection for postfledging juvenile Acadian Flycatchers with our discrete choice models; only canopy cover was related to selection postfledging. That is not to say that selection was the same postfledging as nesting. Postfledging birds were observed in a greater range of habitat types. Postfledging birds appeared less restricted in their vertical space use within mature forest areas, utilizing all canopy layers, whereas nesting flycatchers were mainly observed foraging and defending nests in the low or mid-

canopy (Chapter 1). We also found older postfledging juvenile Acadian Flycatchers in ‘non-nesting’ habitats including forest edges and cedar patches (Chapter 1). Postfledging Acadian Flycatchers in Ohio riparian forests were found in areas with significantly greater shrub cover than seen at nest sites (Ausprey and Rodewald 2011). Nesting Acadian Flycatchers are likely more restricted in their selection compared to postfledging juveniles due to their need to defend and maintain low canopy nests (Mumford 1964, Whitehead and Taylor 2002). Nesting birds may also be restricted in foraging space-use via interspecific interactions with high canopy nesting flycatchers, which may change after nesting is completed. Postfledging flycatchers in our study area seemed to only require a thick canopy layer of some sort (sapling, edge, or high canopy) to safely perch and look for prey.

Habitat selection during both the nesting and postfledging periods was non-random. However, for any given choice, the relative probability of use of the chosen site averaged only slightly better than random. Discrete choice models are only as good as the variables included; it is plausible that we are missing some vital components of selection, especially for fledgling Acadian Flycatchers where only canopy cover was significant to selection. Secondly, there was not a great deal of heterogeneity in choice sets from mature-forest core areas, which weakens the ability to detect preference for variables of interest. Our models may have performed better if we had included larger choice sets or more disparate choice sets (McFadden 1978). Finally, in random discrete choice models, while the model does not require large sample approximations, the quality of population-level parameters and the size of standard errors depends upon the number of animals and the number of samples per individual (Cooper and Millspaugh 1999, Thomas et al. 2006).

In general, our standard errors were large. We met the recommended number of animals (>20), however, we were not able to meet the suggested >50 samples for any one individual due to the short term nature of the postfledging period and transmitter battery life (Alldredge and Ratti 1986).

Even with these shortcomings, discrete choice models are more powerful than simple comparisons of used vs. available vegetation. The composition of choice sets is allowed to change over time and between individuals. Since a unique choice set is selected for each choice, there is no variation in factors that often add to selection variability within choice sets, such as an individual's age or sex (McDonald et al. 2006). Discrete choice model outcomes are also more intuitive than past models of selection, such as logistic regression. Discrete choice models estimate the probability that a specific unit is selected in a single choice set, rather than the likelihood that a unit is selected at least once after many choices (Cooper and Millspaugh 1999, McDonald et al. 2006). Additionally, Bayesian hierarchical discrete choice models allow researchers to examine variation in selection preferences among individuals and across the population without making sweeping assumptions or deleting observations; all parameters in Bayesian analysis are treated as random variables with probability distributions, thus both the population average and average variance can be examined fairly simply and individuals with fewer observations will tend to conform more strongly to the population distribution (Thomas et al. 2006, Carter et al. 2010). While discrete choice models are becoming more common in studies of wildlife resource selection, few have been utilized for songbird resource selection. We show that Bayesian discrete choice models are useful for investigating resource selection by individuals and by populations, even when choice sets

and sample sizes are limited. Utilizing the same methods in both time periods allowed us to reduce potentially confounding factors such as climate and landscape effects.

Understanding resource selection in each stage of the annual cycle is critical to informing successful conservation of migrant songbirds; however, songbird habitat selection studies have mainly focused on factors affecting nest-site selection or breeding territory density (Marra et al. 2015). Our results illustrate that mature-forest birds alter habitat use to varying degrees during the postfledging period. We found relaxed habitat requirements for postfledging juvenile Acadian Flycatchers and relatively large shifts in habitat requirements by postfledging juvenile Ovenbirds towards dense understory. Habitat management based upon nesting habitat requirements would likely be sufficient for postfledging juvenile Acadian Flycatchers but would not necessarily provide quality postfledging habitat for Ovenbirds. We recommend that postfledging habitat selection be considered in future conservation programs dealing with Neotropical migrants and other forest breeding songbirds.

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Table 1. Model selection results for Acadian Flycatchers in central Missouri, 2013–2015.

Models with lower Watanabe-Akaike information criterion (WAIC) values are more supported. The null model signifies equal probability for selecting any of the choices in the choice set. Deviance (Dev) is a measure of model fit and $p_{D,2}$ is a measure of model complexity.

Model		$p_{D,2}$	Dev	WAIC	Δ WAIC	Rank
Nests						
global	litter + foliage + sapling + pole + saw + canopy + edge + edge×litter + sapling×saw	8.9	351.27	361.18	0.00	1
understory	litter + foliage + canopy + edge + edge×litter	5.0	353.20	362.76	1.58	2
null		0.0	373.53	373.53	12.36	3
stand	sapling + pole + saw + sapling×saw	4.1	369.09	373.54	12.37	4
Fledglings						
understory	litter + foliage + canopy	4.6	913.47	918.36	0.00	1
global	litter + foliage + sapling + pole + saw + canopy + edge + edge×sapling	10.2	909.71	920.46	2.10	2
null		0.0	927.23	927.23	8.87	3
stand	sapling + pole + saw + edge + edge×sapling	5.3	923.12	928.72	10.35	4

Table 2. Mean, lower (2.5%), and upper (97.5%) credibility intervals of population-level selection parameters from the best fit nest-site and fledgling Acadian Flycatcher habitat selection models based on data from 2013–2015 in central Missouri.

Covariates	Nests				Fledglings			
	Mean	2.5%	97.5%	f	Mean	2.5%	97.5%	f
litter	-0.05	-0.34	0.23	0.63	0.16	-0.01	0.32	0.97
foliage	-0.21	-0.53	0.10	0.90	0.01	-0.18	0.20	0.52
sapling	0.04	-0.17	0.24	0.64	–	–	–	–
pole timber	-0.31	-0.57	-0.07	1.00	–	–	–	–
saw timber	-0.27	-0.53	-0.02	0.98	–	–	–	–
canopy	0.63	0.26	1.05	1.00	0.35	0.15	0.15	0.15
edge	0.04	-0.59	0.69	0.54	–	–	–	–
edge × litter	0.47	0.13	0.81	1.00	–	–	–	–
sapling × saw	0.18	-0.01	0.37	0.97	–	–	–	–

f is the proportion of the posterior with the same sign as the mean; i.e., our confidence that the parameter is positive or negative.

Table 3. Model selection results for Ovenbirds in central Missouri, 2012–2015. Models with lower Watanabe-Akaike information criterion (WAIC) values are more supported. The null model signifies equal probability for selecting any of the choices in the choice set. Deviance (Dev) is a measure of model fit and $p_{D,2}$ is a measure of model complexity.

Model		$p_{D,2}$	Dev	WAIC	Δ WAIC	Rank
Nests						
stand	sapling + pole + saw + litter + litter×saw + litter×can + canopy + edge + litter×edge	6.4	102.54	110.07	0.00	1
understory	litter + foliage + canopy + edge + saw + edge×litter + litter×canopy + litter×saw	6.9	103.00	111.94	1.87	2
global	litter + foliage + sapling + pole + saw +canopy + edge + litter×saw + litter×canopy + litter×edge	7.3	102.97	115.04	4.97	3
null	even likelihood (1/3)	0.0	116.45	116.45	6.38	4
Fledglings						
global	litter + foliage + sapling + pole + saw +canopy + edge	14.3	1042.00	1056.61	0.00	1
understory	litter + foliage + canopy	8.9	1049.00	1058.45	1.84	2
stand	sapling + pole + saw	3.6	1105.00	1108.74	52.13	3
null	even likelihood (1/3)	0.0	1116.00	1116.19	59.58	4

Table 4. Mean, lower (2.5%), and upper (97.5%) credibility intervals of population-level selection parameters from the best fit nest-site and fledgling Ovenbird habitat selection models based on data from 2012–2015 in central Missouri.

Covariates	Nests				Fledglings			
	Mean	2.5%	97.5%	f	Mean	2.5%	97.5%	f
litter	1.07	0.467	1.741	0.631	-0.1	-0.31	0.059	0.9
foliage	–	–	–	–	0.68	0.447	1.054	1
sapling	0.14	-0.36	0.618	0.899	0.16	0.053	0.281	1
pole timber	0.31	-0.13	0.746	0.638	0	-0.15	0.142	0.5
saw timber	-0.23	-0.71	0.237	0.995	-0.1	-0.21	0.071	0.8
canopy	1.698	0.587	2.955	0.984	0.43	0.24	0.652	1
edge	0.441	-0.71	1.639	1	0.03	-0.45	0.472	0.6
edge × litter	-0.311	-0.87	0.197	0.544	–	–	–	–
litter × saw	0.5	0.003	1.052	0.998	–	–	–	–
litter × canopy	0.559	-0.24	1.328	0.968	–	–	–	–

f is the proportion of the posterior with the same sign as the mean; i.e., our confidence that the parameter is positive or negative.

Figure 1. Population parameter estimates (**a**) and individual level parameter estimates (**b-d**) for the most supported model of resource selection by postfledging juvenile Acadian Flycatchers in Missouri from 2013–2015.

Figure 2. Estimated relative probability (\pm 95% credible intervals) of Acadian Flycatcher resource selection for nests (solid lines) and fledglings (dotted line) as a function of a site's pole timber density (**a**), saw timber density (**b**), and canopy coverage (**c-d**). Probability curves for each graph were created by holding covariates of the best performing models at their means for Acadian Flycatcher nests and fledglings in Missouri, 2013–2015.

Figure 3. Population-level parameter estimates (**a**) and individual-level parameter estimates (**b-h**) for the most supported model of resource selection by postfledging juvenile Ovenbirds in Missouri from 2012–2015.

Figure 4. Estimated relative probability (\pm 95% credible intervals) of Ovenbird resource selection for nests (solid lines) and fledglings (dotted line) as a function of a site's canopy coverage (**a & c**), litter depth (**b**), understory foliage density (**d**), and sapling density (**e**). Probability curves for each graph are created by holding covariates of the best performing models at their means over the range of values observed for Ovenbird nests and fledglings in Missouri, 2012–2015.

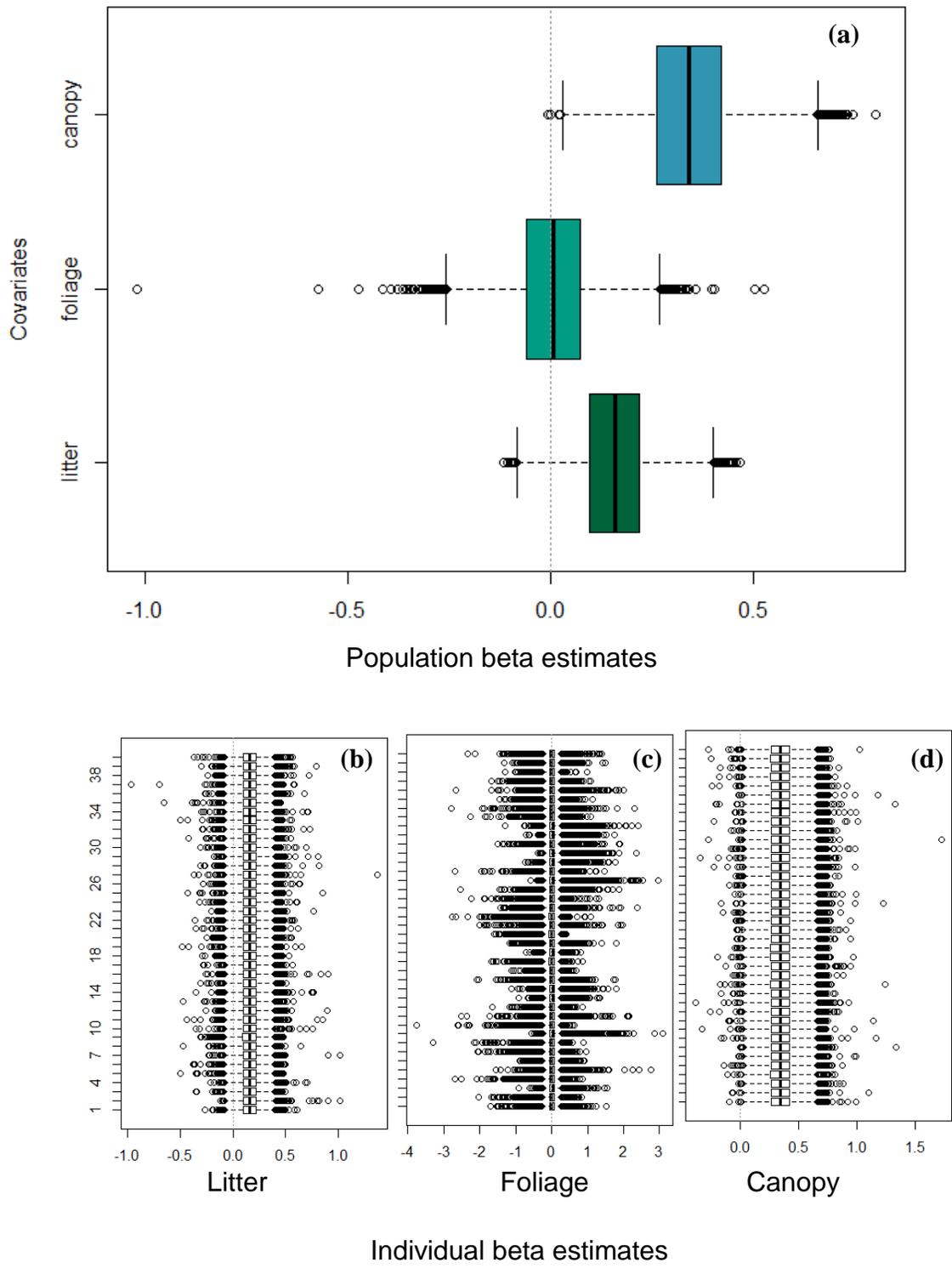


Figure 1.

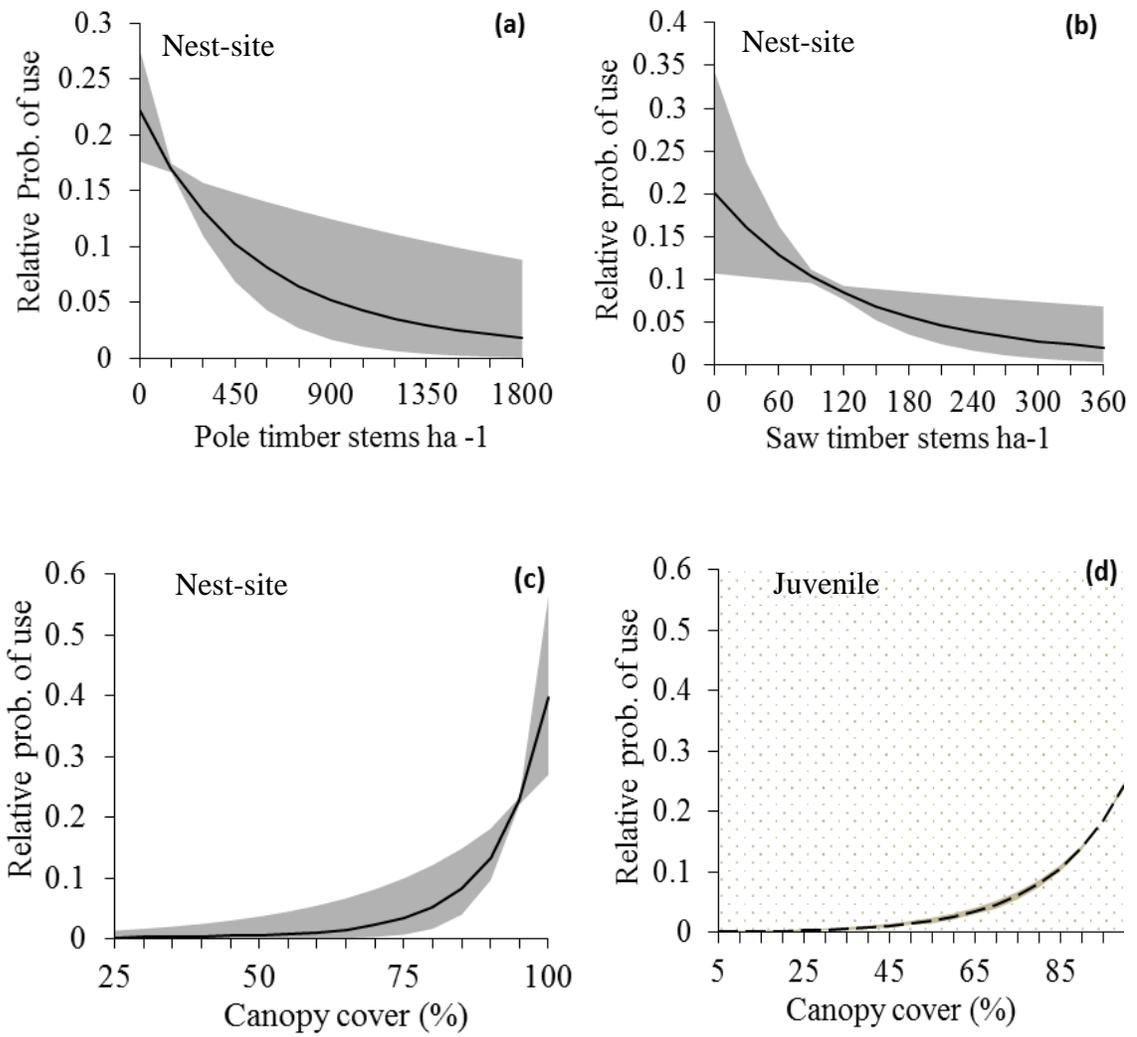


Figure 2.

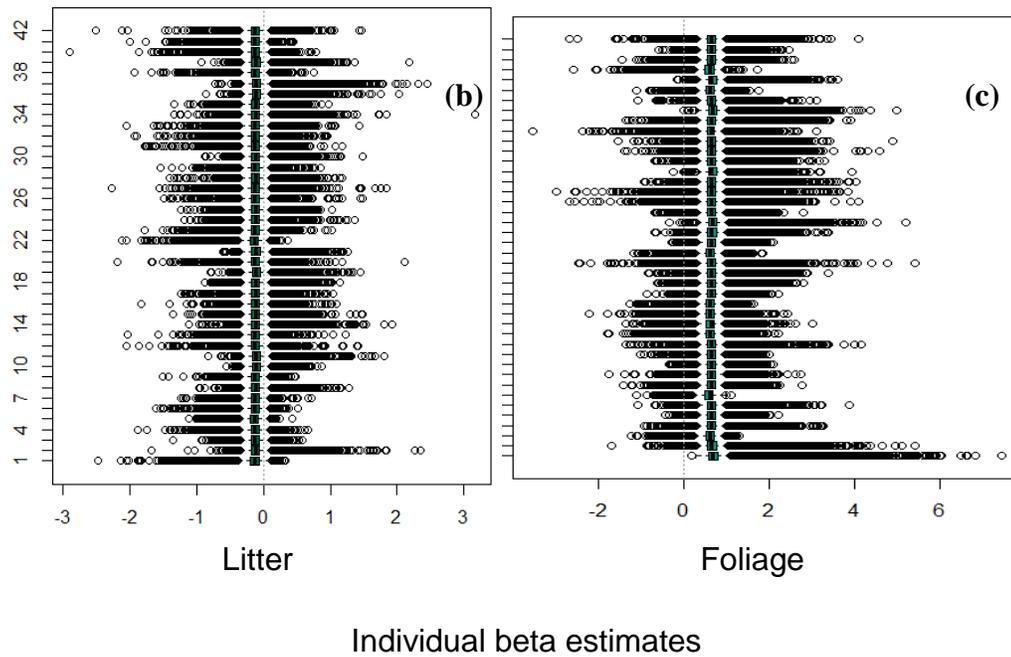
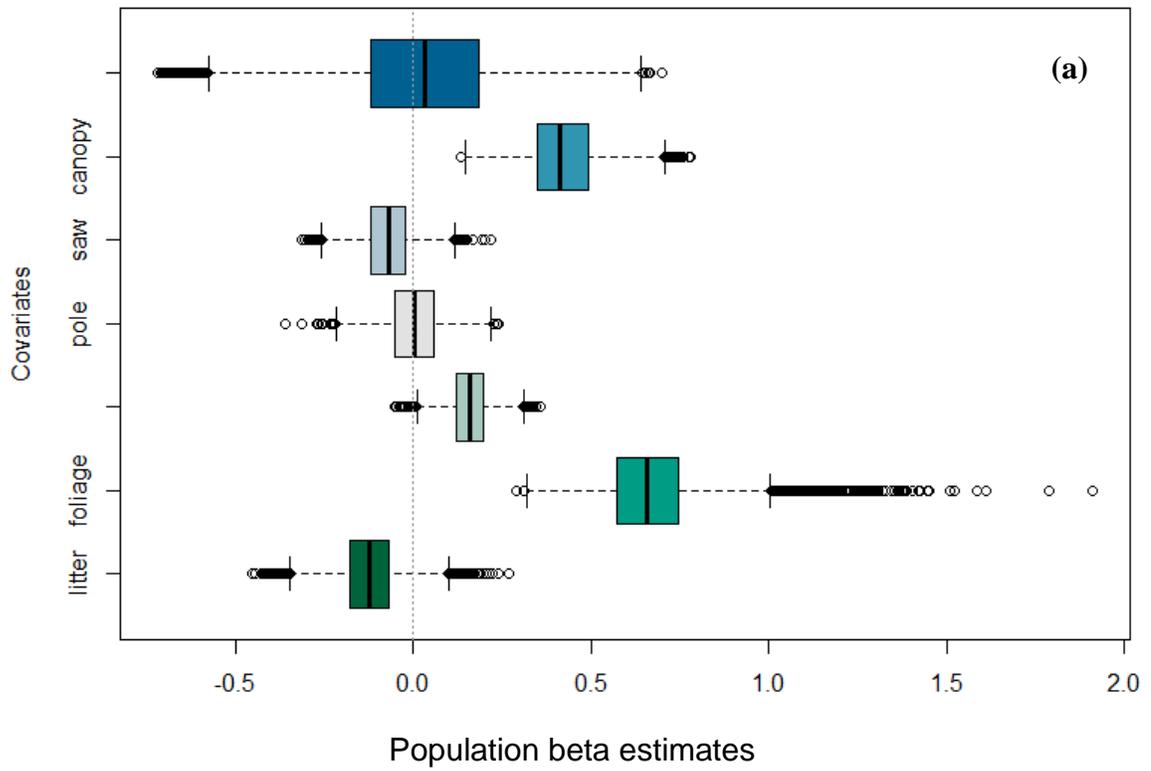


Figure 3. (part 1)

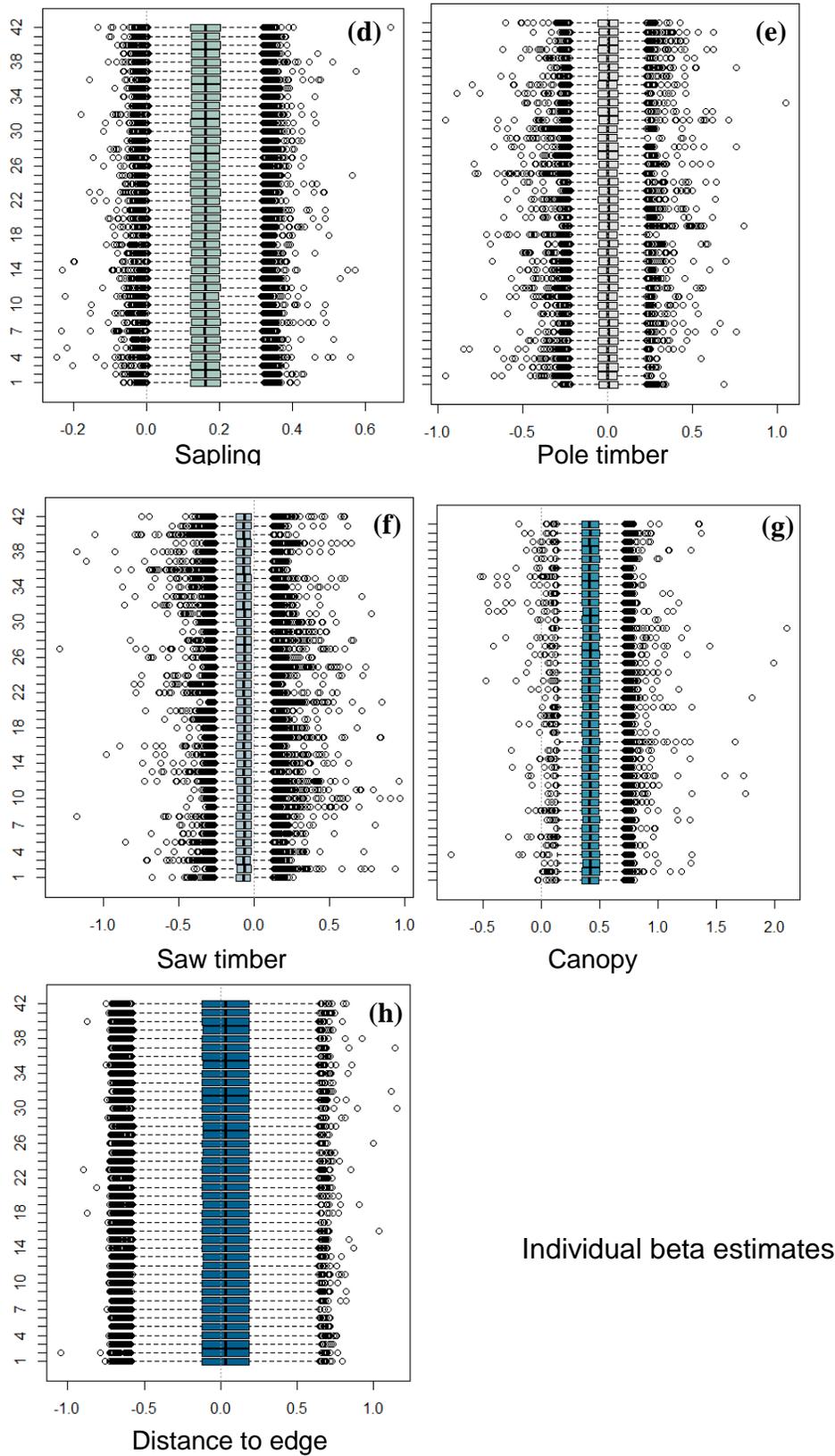


Figure 3.

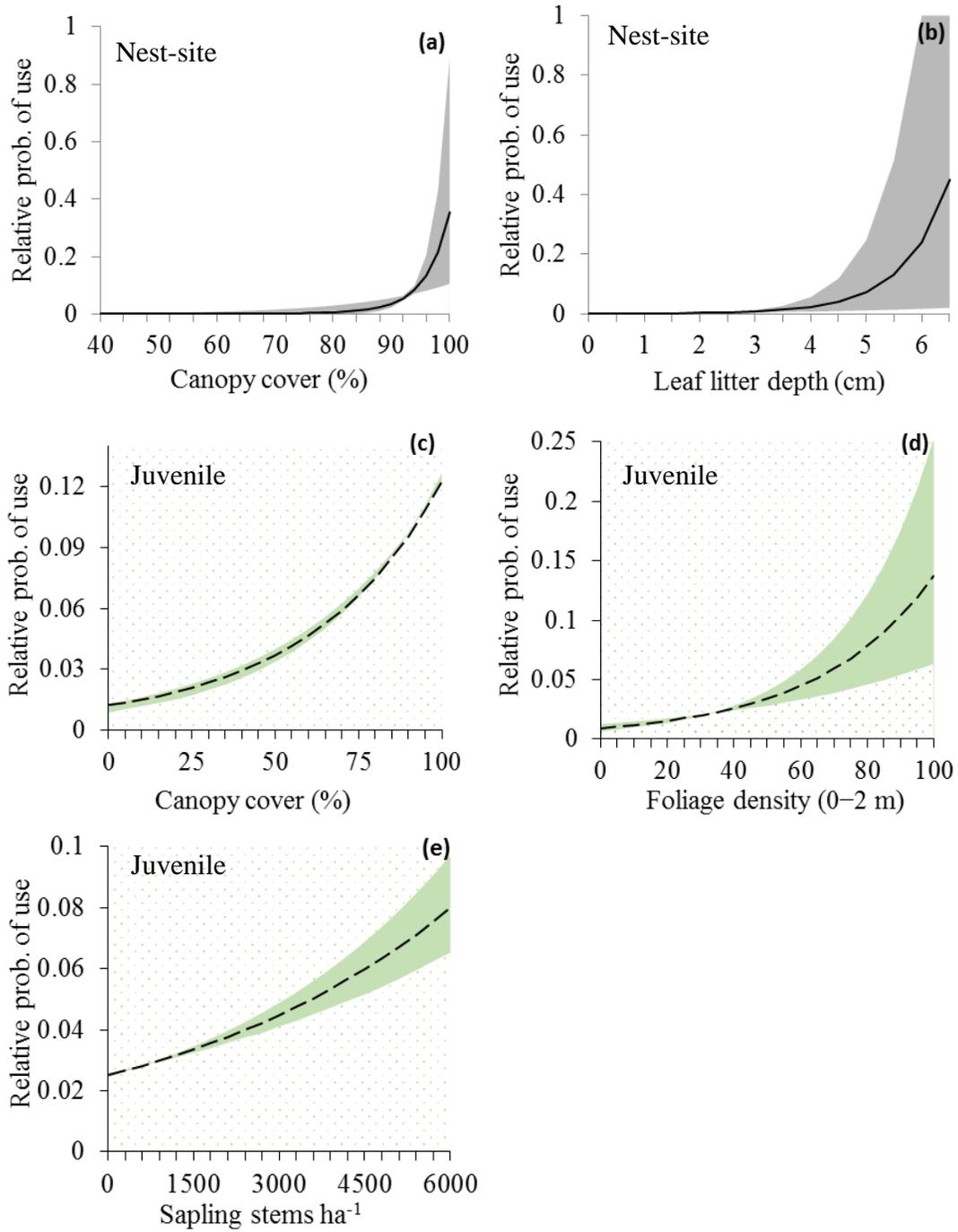


Figure 4.

VITA

Julianna Marie Arntzen Jenkins was born and raised in Wisconsin, USA. She received her B.S. in Biology and a Certificate in Environmental Studies in 2008 at the University of Wisconsin, Madison. She explored the fields of ecology and ornithology for several years after gaining her undergraduate degree, pursuing internships at the Maria Mitchell Association in Nantucket, MA, the Keahou Bird Breeding Center in Volcano, HA, and the International Crane Foundation in Baraboo, WI. She worked for the Science Division of the Wisconsin Department of Resources, as a Research Technician and as Assistant Uplands Biologist from 2010-2011. She joined the University of Missouri in 2011.