Behavioral Development and Habitat Structure Affect Postfledging Movements of Songbirds

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ABSTRACT Postfledging survival of neotropical migrant songbirds has been linked to seasonal and annual changes in the environment and to individual condition. Understanding what influences variation in postfledging movements may provide insight into the differential value of habitat across life-history stages. We conducted a radio-telemetry study of postfledging ovenbirds (*Seiurus aurocapilla*; $n = 45$) and Acadian flycatchers (*Empidonax virescens*; $n = 62$) in mature-forest fragments from 2012 to 2015 in Missouri, USA. We documented variability in behavior and space use and used generalized linear mixed models to evaluate the relationship of postfledging movement rates to individuals' condition, temporal variables, and local habitat variables. We found effects of age and season on movement distances for both study species. Additionally, daily movements of fledgling ovenbirds were negatively related to understory foliage density, a characteristic previously linked to increased survival. Habitat features are useful in predicting the postfledging movements of ovenbirds. By including behavioral development (age) and season in movement models, we were able to isolate and detect habitat effects on movement of ovenbirds and Acadian flycatchers. We suggest researchers use models of daily movement to further strengthen resource quality hypotheses generated by habitat selection and survival studies. © 2016 The Wildlife Society.

KEY WORDS Acadian flycatcher, *Empidonax virescens*, habitat, movements, natal home range, ovenbird, postfledging, *Seiurus aurocapilla*.

The juvenile postfledging life-stage in neotropical migratory songbirds encompasses potentially high mortality and rapid developmental change, making it a period of interest for conservation biologists (Anders and Marshall 2005, Cox et al. 2014). Postfledging survival of neotropical migrants has been linked to various factors (e.g., annual and seasonal variation in the environment, physical condition of or age of fledglings); however, responses are not always obvious, especially regarding habitat (Vitz and Rodewald 2011, Streby and Andersen 2013, Cox et al. 2014, Jenkins et al. 2016, Naef-Daenzer and Grüebler 2016). Few studies have investigated the mechanisms behind postfledging mortality risk, such as behavioral development and movement rates, which are likely linked to finding appropriate foraging sites while eluding predation (Vitz and Rodewald 2010, Ausprey and Rodewald 2013, Haché et al. 2014). Understanding what influences variation in movements may provide insight into what defines resource quality and how selection for vegetation structure changes across life-history stages.

Postfledging movements are influenced by intrinsic and extrinsic factors. Intrinsic factors (e.g., age, condition, physical development) may influence an individual's ability to move. Fledglings in better condition and older more developed individuals are able to more rapidly achieve and maintain sustained flight and make long-distance movements (Naef-Daenzer et al. 2001, Cox et al. 2014). External factors (e.g., presence of predators, competitors, caregivers, habitat, weather) could also directly or indirectly influence movements (Grüebler and Naef-Daenzer 2008, Vitz and Rodewald 2010, Van Overveld et al. 2011). Parental care declines over the postfledging period, eventually leading to fledgling independence and often to dispersal from the natal area (Anders et al. 1998, Streby and Andersen 2012, Ausprey and Rodewald 2013). Early postfledging movements are likely responsive to parental behavior, especially if adults constrain movements and maintain territories to attempt second broods (Russell 2000).

Risk of predation, available food resources, and vegetation structure likely influence the perceived quality of habitat and affect movement decisions. Movements toward structurally complex areas, such as young forest and shrubland, forest edges, and treefall gaps have been documented for many postfledging songbirds (Anders et al. 1998, Vitz and

Rodewald 2010, Streby and Andersen 2013). Upon reaching dense cover, mortality and movements by fledglings decrease (Anders et al. 1998), potentially because dense cover provides food and security from predators. Dense vegetation provides visual and structural protection from predators limiting the necessity for long-distance escape movements (Anders et al. 1998). Foraging success may also improve in dense vegetation because insect community diversity and abundance increase with structural diversity (Blake and Hoppes 1986, Crist et al. 2006, Moorman et al. 2012). Naef-Daenzer and Grüebler (2016) reported that postfledging survival and fledging date varied with species nesting strategy. Preferred foraging sites and cover while foraging may also change with foraging guild; a canopy gleaner may prefer areas of dense canopy, regardless of understory, whereas ground foragers may prefer dense understory or groundcover.

We conducted a radio-telemetry study of postfledging juveniles of 2 forest breeding neotropical migrant songbirds: a canopy species, the Acadian flycatcher (*Empidonax virescens*), and a ground species, the ovenbird (*Seiurus aurocapilla*). We compared a canopy and ground nesting species to examine if postfledging behavior and movements differ with nest placement and foraging guild. Ovenbirds have a short nestling period, fledging young 7–9 days post-hatch (Porneluzi et al. 2011). Acadian flycatchers have a long nestling period, fledging young 13–14 days post-hatch (Mumford 1964, Whitehead and Taylor 2002). Acadian flycatchers are able to fly at least short distances immediately postfledging, whereas ovenbird juveniles are nonvolant for at least a few days postfledging. Postfledging survival on our study areas was 0.50 (23-day period) for ovenbirds and 0.88 (19-day period) for Acadian flycatchers (Jenkins et al. 2016). Our objectives were to document behavioral development and space use and determine if postfledging daily movements could be explained by temporal factors (e.g., year, season, age), habitat factors (e.g., foliage density, tree density), or by the individual bird's condition at fledging (mass). We predicted that daily movement rates would increase as birds aged and would decline with increased vegetation density, which may provide denser cover and food resources. We predicted that distance moved away from the nest would increase with age, decrease with vegetation density, and would change as the season progressed. We expected to see variation in behaviors and movement patterns between species because of their different life-history strategies. We focused on fledgling movements because they are closely tied to the needs and risks faced by individuals through time and decisions to stay or move from a site should be related to availability of cover and food.

STUDY AREA

We studied 3 forested sites in Boone, Randolph, and Howard counties in central Missouri, USA from 2012 to 2015. Our sites were among the largest tracts of forest in a landscape that was approximately 35% forest and 65% pasture, cropland, and old fields. We collected data at the Thomas S. Baskett Wildlife Research and Education Center (Baskett; 890 ha; 38° 44′N, 92°12′W) in 2012 to 2015, the

Rudolf Bennitt State Conservation Area (Bennitt; 1146 ha; 39° 8′ N, 92° 15′ W) in 2013 to 2015, and Three Creeks Conservation Area (Three Creeks; 575 ha; 38° 49′N, 92°17′W) in 2014 to 2015. Acadian flycatchers were present at all 3 sites and nesting ovenbirds were present only at Bennitt and Baskett. We monitored only ovenbirds at Baskett in 2012. Other common breeding birds were Louisiana waterthrush (*Parkesia motacilla*), worm-eating warbler (*Helmitheros vermivorum*), eastern wood-peewee (*Contopus virens*), wood thrush (*Hylocichla mustelina*), red-eyed vireo (*Vireo olivaceus*), summer tanager (*Piranga rubra*), great crested flycatcher (*Myiarchus crinitus*), tufted titmouse (*Baeolophus bicolor*), northern cardinal (*Cardinalis cardinalis*), and indigo bunting (*Passerina cyanea*). This region has been the focus of several long-term bird nest predation studies; the western ratsnake (*Pantherophis obsoletus*), raccoon (*Procyon lotor*), rodents, and various avian predators are most commonly identified as nest predators, all of which are also potential postfledging predators (e.g., Thompson and Burhans 2003, Cox et al. 2012).

The climate of the region is warm, humid, and continental with mean January and July temperatures of −2°C and 23°C, respectively, and mean annual precipitation of 1,083 mm (1981–2010 Boone County Regional Airport; National Climatic Data Center, http://ggweather.com/normals/MO.html#C, accessed 30 Aug 2016). Topography consists of ridge tops separated by ravines that feed ephemeral and perennial streams, with narrow floodplains. Study sites were predominately mature, upland forest with an overstory dominated by oak (*Querus* spp.) and hickory (*Carya* spp.), interspersed with stands of red cedar (*Juniperus virginiana*) resulting from old-field succession. The understory plant community included flowering dogwood (*Cornus florida*), viburnum (*Viburnum* sp.), hophornbeam (*Ostrya virginiana*), serviceberry (*Amelanchier arborea*), and sugar maple (*Acer saccharinum*). Ground cover included aromatic sumac (*Rhus aromatica*), Virginia creeper (*Parthenicissus* sp.), buck brush (*Symphoricarpos orbiculatus*), and poison ivy (*Toxicodendron radicans*).

METHODS

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 (i.e., day 8 for ovenbirds and day 13 for Acadian flycatchers) and recorded mass (±0.1 g). We supplemented ovenbird nestling captures with opportunistically hand-caught nonvolant fledglings, 1−2 days out of the nest; we rarely captured postfledging Acadian flycatchers. We attached colored leg bands and a standard United States Geological Survey (USGS) leg band to all captured ovenbirds and attached radio-transmitters to 1−3 ovenbirds per brood. All captured Acadian flycatcher nestlings received a standard USGS leg band and 1 flycatcher per nest received a single colored leg band and a radio-transmitter. We attached transmitters using a leg-loop harness made with flexible cording (Rappole and Tipton 1991). In 2012,

transmitters weighed 3.5–5.0% of ovenbird juvenile mass at time of attachment and had an expected battery life of 22 days (0.55 g model A1015; Advanced Telemetry Systems [ATS], Itasca, MN, USA). In 2013–2015, transmitters weighed 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 days in 2013, 29 days in 2014, and 44 days in 2015 (0.3 g, 2013 and 2015: model A2414, ATS; 2014: model PicoPip Ag337, Biotrack, Wareham, Dorset, UK). The University of Missouri's Animal Care and Use Committee approved our protocols (protocol # 7463 and 8418).

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, CA, USA) and handheld directional antennas (Yagi 3-element and H-Type; ATS). We relocated individuals until the signal was no longer detectable (i.e., transmitter battery failure or dispersal out of study area) or until we determined mortality. We determined Universal Transverse Mercator (UTM) coordinates with handheld global positioning system (GPS) units (GPS error <10 m). We recorded the coordinates of the location where we first sighted or flushed the individual. We attempted to minimize our disturbance, but our presence may have altered postfledging individuals' behavior or habitat use.

We made behavioral observations for every relocation, but observations varied in length and time of day. The majority of observations took place between 0600–1400 hours and lasted 5–20 minutes depending upon level of perceived disturbance to family groups. For each relocation we recorded the bird's location in vertical space (i.e., ground, low understory [0−2 m], understory and sub-canopy [∼2−15 m], overstory canopy [∼10−25 m]) and their mobility (i.e., stationary, in flight, walking). We also recorded any social associations or behaviors observed at any point (i.e., with adult, with sibling, alone, begging, fed by parent, foraging). We used these supplementary observations to determine time to independence for each individual. We defined independence as the last date we observed any begging or feeding behavior and calculated the mean age (i.e., days post-fledging) of independence (±SE) for each species. Birds became more visible as they aged, especially in regard to begging and interacting with adults; therefore, this was a reliable method to capture the time to independence.

We measured local vegetation features of use points after individuals left the area. We attempted to measure all locations but were often constrained by time and then sampled vegetation at every other location for randomly selected birds. We sampled selected habitat characteristics that we hypothesized could most simply model understory and canopy forest structure. 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 stem density/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 >12.5 cm DBH (West 2009) by using the

appropriate expansion factor for each diameter tree for a 10-factor prism. We estimated understory foliage cover 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 (Noon 1981).

Space-Use
We calculated initial dispersal distances and 95% minimum convex polygon (MCP) natal home ranges for comparison with previous studies and because we did not meet minimum sample recommendations for kernel home ranges (i.e., ≥30; Seaman et al. 2011). We used the 95% MCP method to calculate natal (i.e., dependent stage) range sizes for all individuals that survived the dependent postfledging period (19 days for Acadian flycatchers and 23 days for ovenbirds) with radios intact using the adehabitatHR package in R (R Version 3.1.3, www.r-project.org, accessed 9 Mar 2015; Calenge 2006). We limited our natal home range analysis to 1 individual/brood and resampled the data 3 times using sample sizes of 5, 10, 15, 20, and 25 for each individual in R to provide perspective on the influence of sample size on home range estimates. We considered a bird to have dispersed from the natal area if it made a single or several consistent movements away from the natal area without returning (Anders et al. 1998). We measured the distance from the first postdispersal location to the natal range centroid using the point distance tool in ArcGIS 10.1 (Environmental Systems Research Institute, Redlands, CA, USA). We report the mean 95% MCP natal range size, initial dispersal distances, and age at initial dispersal (±SE) for each species.

Movement Analysis
We calculated 2 metrics of fledgling movement for each observation. We calculated linear distance from the nest and we calculated a daily movement rate based on the linear distance between subsequent locations divided by the elapsed time in days (m/day). We used generalized linear mixed models within an information-theoretic framework to evaluate the relationship of the 2 measures of movement to vegetation, condition, age, year, and season (Burnham and Anderson 2002, Bolker et al. 2009). We limited analysis to observations for which we had vegetation data and, because the locations of siblings are not independent, we used observations from 1 individual per brood. We did not include data for the first movement away from the nest to avoid confounding factors or bias from birds escaping researchers after radio attachment. We created an a priori candidate model set with singular and additive combinations of variables of interest and 2 interactions (Appendix A). We included fledgling age (i.e., days out of the nest) in all models to account for changes in movement ability and behavior related to age (Yackel Adams et al. 2001, White and Faaborg 2008, Vitz and Rodewald 2010). We included mass at fledging as a measure of individual condition (Grüebler and Naef-Daenzer 2008, Vitz and Rodewald 2010). We used vegetation characteristics (i.e., understory foliage density (0−2m) + sapling density + saw timber density) at a location to predict the subsequent movement from that location to
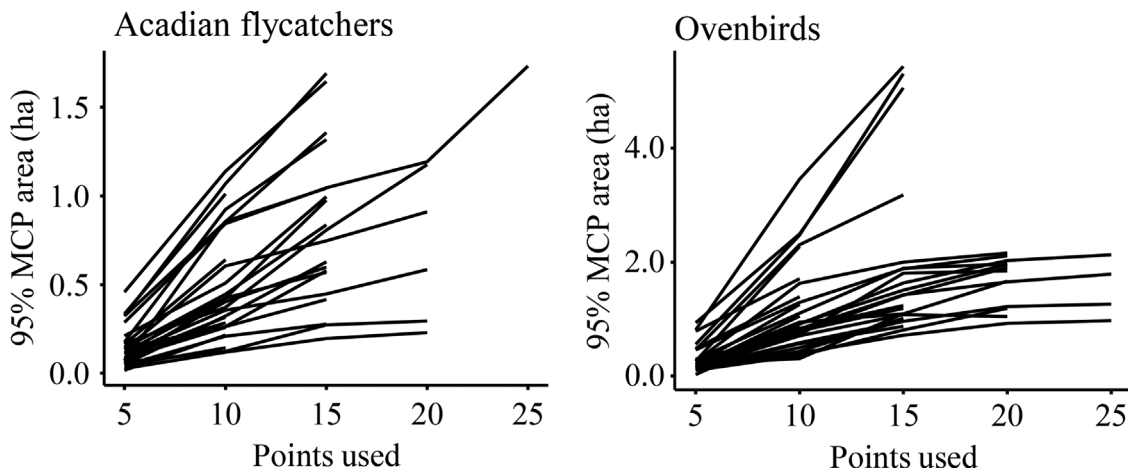
Figure 1. Mean 95% minimum convex polygon (MCP) natal areas (ha) from 3 rounds of resampling of natal relocation data for 30 fledgling Acadian flycatchers and 29 fledgling ovenbirds in central Missouri, USA, 2011–2015.

evaluate our hypothesis that movements should be smaller from dense cover as measured by vegetation structure. We included ordinal date of fledging (fledge date) in models to help capture changes in the predator community and conspecific adult breeding behaviors (e.g., maintaining territory or preparing for migration). Ordinal date of fledging outperformed other measures of season in preliminary analyses. We tested for an interaction between year and fledge date because differences in movement may be due to weather and climate and predator communities may ebb and flow year to year (Haché et al. 2014). We tested for interactions between fledgling age and fledge date because we predicted that adults fledging young early in the breeding season may maintain territories (thus have shorter fledgling movements), whereas those adults fledging young late in the breeding season may be more transient as they start a pre-migratory molt. We did not include site in models because the addition of site to any model that included other fixed effects of interest did not overcome the 2 AIC_c point penalty for each site parameter. We normalized all continuous variables before conducting analysis. We confirmed non-collinearity of covariates by determining the variance inflation factor was <2.0 for all covariates.

We fit models with a 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, USA). We included individual 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 included lag distance (i.e., previous distance from nest) as a fixed covariate in all models of distance from the nest to account for spatial autocorrelation between successive individual observations. We based inference on the best supported model because other closely ranked models differed from the top model only in the addition of uninformative parameters (i.e., parameters whose contribution to the model AIC_c value did not overcome the 2 AIC_c

point penalty for each parameter; Burnham and Anderson 2002, Arnold 2010).

RESULTS

We attached radio-transmitters to 62 ovenbird fledglings from 48 broods and 45 Acadian flycatcher fledglings from 45 broods. Fledging date ranged from 26 May to 15 July for ovenbirds and 12 June to 5 August for Acadian flycatchers. Ovenbirds weighed 14.52 ± 0.06 (SE) g and Acadian flycatchers weighed 11.36 ± 0.04 g at time of capture. We recorded 541 behavioral observations from 38 Acadian flycatchers and 626 behavioral observations from 43 ovenbirds that were from different broods. We observed fledglings with siblings 40% and 14% of the time for Acadian flycatchers and ovenbirds, respectively. We observed nesting adult Acadian flycatchers primarily in the understory and sub-canopy (J. M. A. Jenkins, University of Missouri,
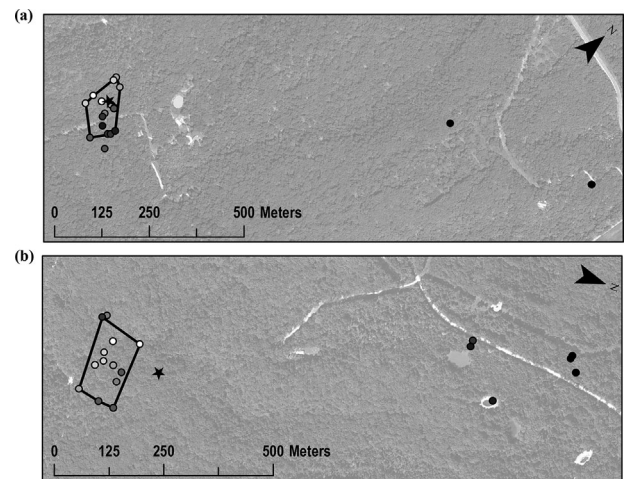

Figure 2. Examples of typical postfledging space-use for Acadian flycatchers (a) and ovenbirds (b) in Missouri, USA forest fragments, 2012–2015. Polygons represent 95% minimum convex polygon (MCP) natal home ranges, stars represent nest sites, and points represent relocations over time (points darken with age).

Table 1. Summary of model selection results from the best-ranked a priori candidate models of the effects of age, vegetation, season, year, and condition on movement rate of postfledging ovenbirds and Acadian flycatchers in central Missouri, USA, 2012–2015. We present only models within 2 AIC_c of the top model and the null model for comparison.

Model	Deviance	K[a]	ΔAIC_c[b]	w_i[c]
Ovenbirds				
Age + understory foliage density + sapling density + saw timber density	3,935.03	7	0.0	0.42
Null	3,962.97	3	19.7	<0.01
Acadian flycatchers				
Age + fledge date + year + (fledge date × year)	2,969.99	9	0.0	0.37
Age + fledge date + condition + year + (fledge date × year)	2,968.91	10	1.0	0.22
Age + fledge date + year + (age × fledge date) + (fledge date × year)	2,969.50	10	1.6	0.16
Null	3,002.38	3	19.9	<0.01

[a] Number of parameters in a model.
[b] Difference between each model's second-order Akaike's Information Criterion (AIC_c) value and the lowest AIC_c value in the candidate set.
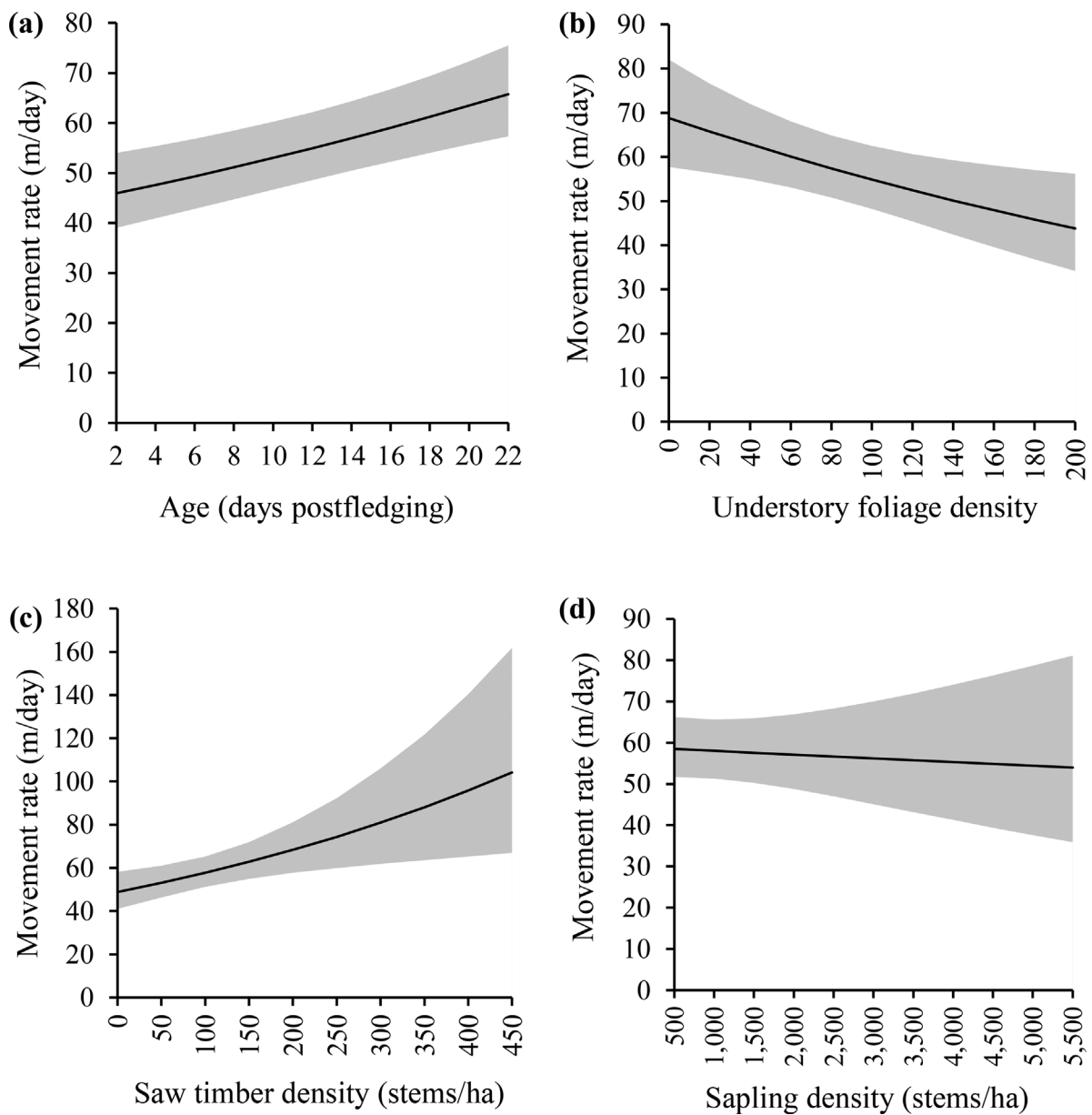[c] Akaike weight of each model in relation to the entire candidate set.

Figure 3. Predicted daily movement rates of postfledging ovenbirds based on the best-supported model relating age (a), understory foliage density (b), saw timber density (c), and sapling density (d) to daily movement rate in Missouri, USA, 2012–2015. Estimates are reported for the dependent period (a), and for the observed range of each vegetation variable (b–d) while other covariates are held at their means. Shaded areas represent 95% confidence intervals.

personal observation) and postfledging Acadian flycatchers in the understory and sub-canopy (50% of observations) and overstory canopy (40% of observations). We observed postfledging ovenbirds mainly on the ground (76% of observations) or in the low understory (22% of observations). Surviving ovenbirds were monitored for 27.47 ± 2.81 days (max. $= 49$, min. $= 23$) and Acadian flycatchers for 27.11 ± 1.57 days (min. $= 15$, max. $= 46$). Ovenbird fledglings were independent from adults 23.14 ± 1.04 days after fledging, whereas Acadian flycatchers were independent 19.52 ± 1.21 days after fledging.

We calculated size of natal areas for 30 Acadian flycatchers and 29 ovenbirds from different broods that survived to independence with radios intact (Appendix B). We consider these estimates to be conservative because neither species' natal area completely reached an asymptote based on resampling with the available sample sizes (Fig. 1). We limited our summary of natal areas to the 20 Acadian flycatchers and 23 ovenbirds that had ≥ 15 locations because our asymptotic analysis indicated home range size was dependent upon the number of locations but some individuals appeared to reach an asymptote at >15 locations (Fig. 1). The mean Acadian flycatcher natal area (0.97 ± 0.12 ha, range $= 0.23-1.77$ ha) was 55% smaller than the mean ovenbird natal area (2.14 ± 0.32 ha, range $= 0.79-6.22$ ha).

Acadian flycatcher daily movements (46.38 ± 45.62 m) were 28% shorter than ovenbird movements (63.85 ± 53.66 m). Even though ovenbirds were not capable fliers at fledging, their initial movements away from the nest were on average twice as long as volant Acadian flycatcher initial movements. Newly fledged ovenbirds and Acadian flycatchers were found 57.73 ± 9.30 m (range $= 9-150$ m)

Table 2. Estimated coefficients (β), standard error (SE), and confidence intervals (CI) from the top candidate model of the effects of age, vegetation, season, year, and condition on movement rate of postfledging ovenbirds and Acadian flycatchers in Missouri, USA, 2012−2015.

Effect	β	SE	95% CI Lower	95% CI Upper
Ovenbirds				
Intercept	4.06	0.06	3.94	4.19
Age	0.17	0.04	0.09	0.26
Saw timber density	0.12	0.04	0.03	0.20
Understory foliage density	−0.12	0.05	−0.22	−0.03
Sapling density	−0.01	0.04	−0.09	0.06
Acadian flycatchers				
Intercept	3.87	0.09	3.69	4.05
Age	0.21	0.05	0.12	0.29
Year-2013	−0.26	0.11	−0.48	−0.03
Year-2014	0.14	0.11	−0.08	0.36
Fledge date	−0.19	0.07	−0.33	−0.06
Fledge date × year-2013	0.44	0.10	0.25	0.64
Fledge date × year-2014	0.12	0.12	−0.11	0.36

and 26.57 ± 3.90 m (range $= 9-102$ m) from the nest the day after fledging, respectively. We recorded distinct postfledging dispersals for 10 Acadian flycatchers and 8 ovenbirds. Ovenbird postfledging dispersal distances were 26% shorter than Acadian flycatcher postfledging dispersal distances (Fig. 2). Acadian flycatcher postfledging initial dispersals were 840 ± 155 m from natal area centroids and took place 28.50 ± 2.52 days postfledging. Ovenbird initial postfledging dispersals were 618 ± 79 m and took place 29.75 ± 3.34 days postfledging.

We used 395 and 316 movement observations in our ovenbird and Acadian flycatcher daily movement rate models, respectively. The best-supported model of daily
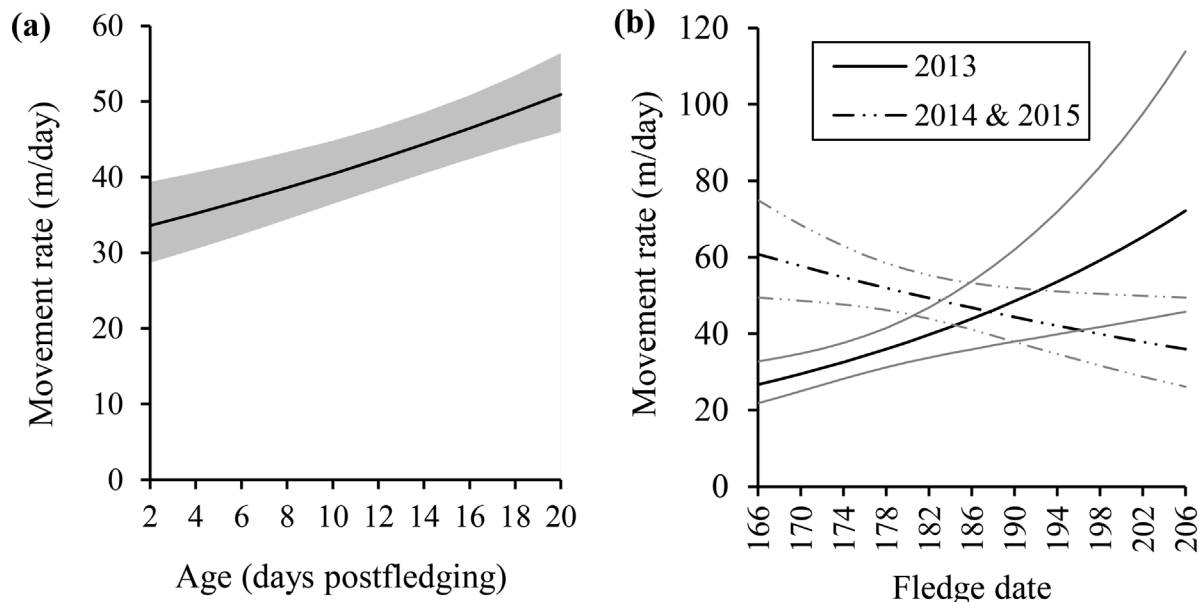

Figure 4. Predicted daily movement rates of postfledging Acadian flycatchers based on the best-supported model relating age (a) and the interaction of fledge date and year (b) to daily movement rate in Missouri, USA 2013−2015. Estimates are reported for the range of dates recorded. For (a), fledge date is held at the mean, and year was held at observed frequencies. The 95% confidence intervals for beta estimates of 2014 and 2015 were not significantly different so estimates were created for 2014 and 2015 combined. Shaded area (a) and gray lines (b) represent 95% confidence intervals.

movement rates for ovenbirds included age, foliage density (0–2 m), sapling density, and saw timber density and had a model weight of 0.42 (Table 1). Ovenbird daily movement rates were positively related to age and saw timber density, negatively related to understory foliage density, and were not related to sapling density (Fig. 3, Table 2). The best-supported model of Acadian flycatcher daily movement rates included age, fledge date, year, and an interaction of fledge date and year and had a model weight of 0.37 (Table 1). Two additional models had a $\Delta AIC_c < 2$, but they did not add any informative variables to the top model (Table 1). Acadian flycatcher movement rates were positively related to age and varied by season and year (Fig. 4, Table 2).

We used 266 ovenbird locations and 317 Acadian flycatcher locations in our models predicting distance from the nest. The best supported model of ovenbird distance from the nest included age, fledge date, and an interaction of age and fledge date with a model weight of 0.43 (Table 3). The best supported model of Acadian flycatcher distance from the nest included age and had a model weight of 0.18. Five additional models had $\Delta AIC_c < 2$ and included the additional parameters fledge date × age, mass at fledging, and year but we did not consider these further because the contribution of those parameters did not overcome the 2 AIC_c point penalty for each additional parameter (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. 5, Table 4). Individuals accounted for a greater percentage of the random-effect variance in the response of movement from the nest compared to the response of daily movement rate, and contributed more variance in ovenbird movement models (distance to nest = 20%, movement rate = 12%) than in Acadian flycatcher models (distance to nest = 15%, movement rate = 3%).

DISCUSSION

Habitat structure and behavioral development (age) were most closely related to movements of postfledging birds. We hypothesized that birds would move shorter distances once they reached vegetation that offered foraging opportunities while providing cover from predators. Our finding that ovenbirds moved shorter distances from locations with dense understory, a vegetation characteristic positively associated with their resource selection (Streby and Andersen 2013, Jenkins 2016) and survival (King et al. 2006, Vitz and Rodewald 2011), supports this prediction. We did not find strong effects of vegetation density on daily movement patterns for postfledging Acadian flycatchers; however, we observed a vertical expansion in postfledging foraging space-use that may have confounded the limitations of our 2-dimensional analysis. Ausprey and Rodewald (2013) reported that Acadian flycatchers in riparian forests expanded natal areas as honeysuckle (*Lonicera maackii*) cover increased and suggested that unrestricted foraging space was more valuable postfledging than cover from predation.

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). We did not find support for a relationship between mass at fledging and movement distances; however, by including only initial mass at fledging in an analysis that included all postfledging ages, we were 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 fledgling ovenbirds and worm-eating warblers and reported 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. The relationship between condition at fledging and postfledging survival are also variable in the literature, with studies reporting positive effects or no effect (Dhondt 1979, Anders et al. 1997, Naef-Daenzer et al. 2001, Vitz and Rodewald 2011, Haché et al. 2014). The inconsistent effect of mass on daily movements and survival may indicate that poor initial condition is only noteworthy when resources are scarce or long-distance movements to find quality postfledging habitat are required.

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 to nest for postfledging ovenbirds and Acadian flycatchers in central Missouri, USA, 2012–2015. All nest distance models had a lag distance covariate (i.e., previous distance from nest) to account for spatial autocorrelation. We present only models within 2 AIC_c of the top model and the null model for comparison.

Model	Deviance	K[a]	ΔAIC_c[b]	w_i[c]
Ovenbirds				
Age + fledge date + (age × fledge date)	2,933.02	7	0.0	0.43
Null	3,018.22	4	78.9	<0.01
Acadian flycatchers				
Age	3,329.87	5	0.0	0.18
Age + fledge date + (age × fledge date)	3,325.88	7	0.2	0.16
Age + condition	3,329.31	6	1.5	0.08
Age + fledge date + condition + (age × fledge date)	3,325.23	8	1.6	0.08
Age + fledge date + condition + year + (age × fledge date)	3,325.23	8	1.6	0.08
Age + fledge date + year + (age × fledge date)	3,323.43	9	2.0	0.07
Null	3,445.95	4	114.0	<0.01

[a] Number of parameters in a model.
[b] Difference between each model's second-order Akaike's Information Criterion (AIC_c) value and the lowest AIC_c value in the candidate set.
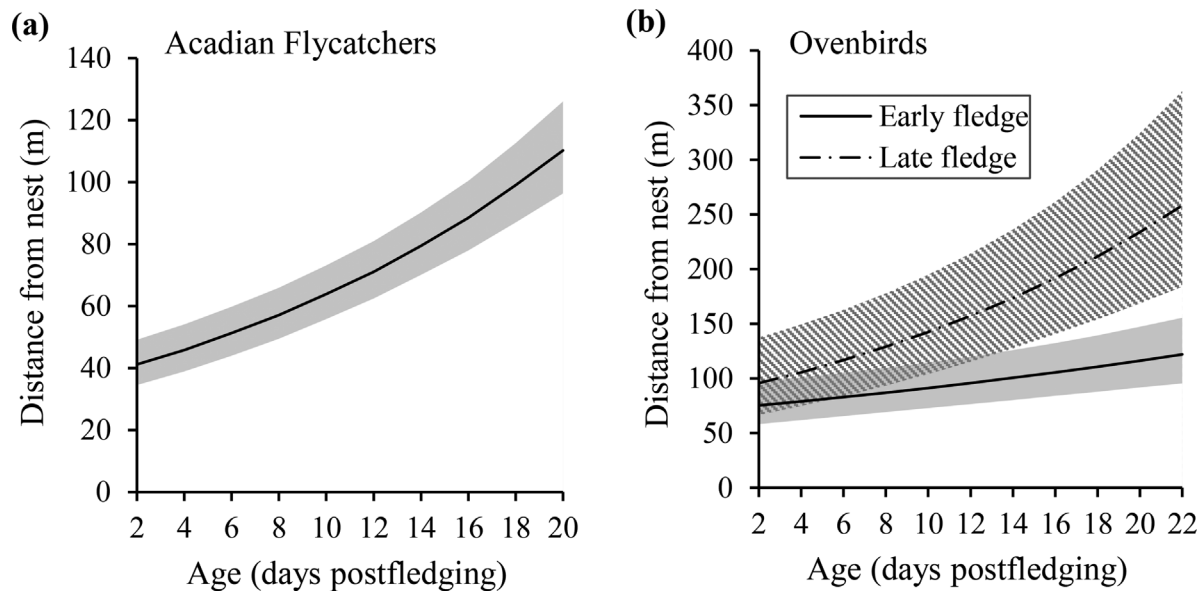[c] Akaike weight of each model in relation to the entire candidate set.

Figure 5. Predicted distance from the nest for postfledging Acadian flycatchers as related to age (a) and for postfledging ovenbirds for early (10th percentile) and late (90th percentile) fledging birds (b) in Missouri, USA, 2012–2015. Estimates are based on the best supported model and 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.

Fledgling movements were related to season and to year. This relationship may have implications for understanding trade-offs in the timing of nesting and postfledging survival or to the potential effects of changing climate on breeding season ecology. Ovenbirds that fledged later in the season moved greater distances from the nest at each age than those fledging earlier. This increase in average movement over the season may reflect increased movement pressure from adult ovenbirds as migration approaches to move to areas that provide high densities of food resources while providing structural protection from predators as they undergo pre-migratory molt, or may suggest that food resources were reduced later in the season, forcing birds to move more. Authors of mist-net and telemetry studies reported mature-forest breeding adults

and juveniles, often mid-molt, using dense nonbreeding areas (e.g., clear-cuts, forest edges, forest openings) postfledging (Anders et al. 1998, Vega Rivera et al. 1998, Pagen et al. 2000, Marshall et al. 2003). Acadian flycatcher seasonal effects differed between 2013 and 2014–2015. The study region experienced a severe drought in 2012 with mean temperatures 2.8° above and precipitation 14.5 cm below the long-term average (Missouri Climate Center 2015). The observed inverse response to fledging date between years may illustrate that the drought had lasting effects on 2013 flycatcher behavior, available food resources, or predator densities, which we were unable to detect with our vegetation surveys or survival analysis (Jenkins et al. 2016), demonstrating the potential importance of considering movements and behavior in addition to survival.

Postfledging ovenbirds and Acadian flycatchers reached independence and started initial dispersals from natal ranges at similar ages post-hatch, even though ovenbirds fledged 5–6 days earlier. This suggests that these birds, although variable in nesting and foraging behavior, need similar amounts of time to behaviorally mature. Movements in our forest fragments may have been restricted by the proximity of edges with open areas. Our mean natal area and postfledging dispersal distances for ovenbirds were approximately 50% smaller than mean natal areas (5.0 ha) and postfledging dispersal distances (1,314 m) for ovenbirds in Ohio, USA contiguous forest (Vitz and Rodewald 2010). Mean dispersal movements of ovenbirds from 2 large tracts of mature forest in Minnesota, USA (849–1,113 m; Streby and Andersen 2012) were also longer than observed in our mature forest fragments. To our knowledge, we are the first to publish initial postfledging dispersal distances for Acadian flycatchers. Acadian flycatcher mean natal areas were within the mid-range of reported values

Table 4. Estimated coefficients (β), standard error (SE), and confidence intervals (CI) from the top candidate model of the effects of age, vegetation, season, year, and condition on distance to nest for postfledging ovenbirds and Acadian flycatchers in central Missouri, USA, 2012–2015. All nest distance models had a lag distance covariate (i.e., previous distance from nest) to account for spatial autocorrelation.

			95% CI	
Effect	β	SE	Lower	Upper
Ovenbirds				
Intercept	4.87	0.07	4.72	5.02
Lag distance	0.18	0.05	0.09	0.27
Age	0.33	0.04	0.26	0.40
Fledge date	0.19	0.08	0.04	0.34
Age × fledge date	0.08	0.04	0.01	0.15
Acadian flycatchers				
Intercept	4.44	0.06	4.31	4.57
Lag distance	0.35	0.05	0.25	0.44
Age	0.49	0.04	0.40	0.57

for Acadian flycatchers in Ohio riparian forests (Ausprey and Rodewald 2013). Longer postfledging dispersal movements may have gone undetected if final destinations were outside the study area, especially if birds moved onto private land inaccessible by road.

MANAGEMENT IMPLICATIONS

Habitat features are useful in predicting the postfledging movements of ovenbirds. We were able to isolate these habitat effects with greater precision by also including behavioral development (age) and season in movement models. We provide limited support for the hypothesis that postfledging birds move less when in areas with more cover, which presumably leads to greater survival. We recommend that researchers use models of daily movement rate rather than natal area to further test resource quality hypotheses during the postfledging period or other periods where individual behavior and ability change with time. We provide additional support for the need to consider postfledging habitat needs in addition to nesting habitat when managing songbird breeding habitat.

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APPENDIX A

A priori candidate model set for generalized linear mixed models of daily movement rates and distance to nest for postfledging Acadian flycatchers and ovenbirds in Missouri, USA, 2012−2015. We added an additional lag distance term (i.e., previous distance from nest) to all nest distance models to account for spatial autocorrelation.

Model
Intercept (null)
Age
Age + fledge date
Age + condition
Age + vegetation
Age + year
Age + fledge date + condition
Age + fledge date + year
Age + fledge date + vegetation
Age + condition + vegetation
Age + condition + year
Age + vegetation + year
Age + fledge date + condition + year
Age + fledge date + condition + vegetation
Age + condition + vegetation + year
Age + fledge date + condition + vegetation + year
Age + fledge date + (age × fledge date)
Age + fledge date + condition + (age × fledge date)
Age + fledge date + year + (age × fledge date) + (fledge date × year)
Age + fledge date + year + (fledge date × year)
Age + fledge date + year + (age × fledge date)
Age + fledge date + vegetation + (age × fledge date)
Age + fledge date + condition + year + (age × fledge date)
Age + fledge date + condition + year + (fledge date × year)
Age + fledge date + condition + year + (age × fledge date) + (age × year)
Age + fledge date + condition + vegetation + (age × fledge date)
Age + fledge date + condition + vegetation + year + (fledge date × age)
Age + fledge date + condition + vegetation + year + (fledge date × year)
Age + fledge date + condition + vegetation + year + (fledge date × age) + (fledge date × year)

APPENDIX B

Estimates of natal area (ha) derived by the minimum convex polygon (MCP) method for Acadian flycatchers and ovenbirds in central Missouri, USA, 2011−2015.

Species					
Acadian flycatcher			Ovenbird		
Bird	n^{a}	95% MCP	Bird	n^{a}	95% MCP
1	22	0.24	1	24	0.79
2	21	0.32	2	29	1.39
3	17	0.98	3	21	1.98
4	20	1.18	4	21	2.16
5	19	0.61	5	15	5.44
6	17	0.29	6	25	1.79
7	20	0.91	7	20	1.97
8	14	0.35	8	15	5.06
9	22	0.55	9	29	1.03
10	9	1.05	10	24	1.55
11	18	1.76	11	25	2.13
12	19	1.77	12	22	1.99
13	16	0.74	13	18	1.01
14	17	1.66	14	24	1.12
15	16	1.67	15	19	1.35
16	15	0.84	16	18	1.34
17	11	0.33	17	14	2.75
18	19	1.29	18	13	2.13
19	11	0.83	19	18	1.16
20	14	0.67	20	17	3.92
21	15	0.57	21	12	1.83
22	12	0.23	22	15	0.97
23	12	0.39	23	12	1.20
24	13	1.52	24	13	1.59
25	5	0.08	25	17	1.00
26	19	0.72	26	10	0.86
27	18	1.08	27	21	2.00
28	16	0.45	28	20	1.90
29	26	1.73	29	19	6.22
30	14	0.36			

[a] Number of points from which the natal area was calculated.