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POST-FLEDGING DISPERSAL TIMING AND NATAL RANGE SIZE OF TWO SONGBIRD SPECIES IN AN URBANIZING LANDSCAPE

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Abstract. Little is known about juvenile birds' movements during the post-fledging stage of development, especially in urbanizing landscapes where novel ecological factors such as invasive plants and altered densities of conspecifics might influence fledglings' use of space. In 2008 and 2009 we used radio telemetry to track movements of fledgling Northern Cardinals (*Cardinalis cardinalis*; $n = 45$) and Acadian Flycatchers (*Empidonax virescens*; $n = 31$) in a network of riparian forests embedded within a rural-to-urban gradient of landscapes in central Ohio. A subset of 20 cardinals and 11 flycatchers survived sufficiently long for subsequent analyses of their movement. Natal ranges of juvenile cardinals decreased in size with proximity to fragment edge, and fledglings moved less from nests surrounded by extensive cover of the Amur honeysuckle (*Lonicera maackii*). Conversely, the size of natal ranges of juvenile flycatchers was positively related to honeysuckle cover. During the study period, 70% of the cardinals dispersed from natal sites at an average of 47 ± 2 days after fledging. Dispersal patterns of individual cardinals varied; birds dispersed locally within their natal forest fragment or made extended movements into the surrounding landscape matrix. In our study area the density of cardinals increased with urbanization, and fledglings tended to disperse later from sites of high densities of conspecifics. Collectively, our results suggest that while novel ecological factors associated with urbanization may influence fledglings' movements, patterns are likely species-specific.

Key words: Acadian Flycatcher, dispersal, fledgling, invasive plants, natal range, Northern Cardinal, urbanization.

Sincronización de la Dispersión Posterior al Emplumamiento y del Tamaño del Rango Natal de Dos Especies de Aves Canoras en un Paisaje Urbanizado

Resumen. Se sabe poco sobre los movimientos de las aves juveniles durante el estadio de desarrollo posterior al emplumamiento, especialmente en paisajes urbanizados donde nuevos factores ecológicos como las plantas invasoras y las densidades alteradas de individuos de la misma especie podrían influenciar el uso que hacen del espacio los volantones. En 2008 y 2009 usamos radio telemetría para seguir los movimientos de los volantones de *Cardinalis cardinalis* ($n = 45$) y *Empidonax virescens* ($n = 31$) en una red de bosques ribereños embebidos dentro de un gradiente de paisajes de rural a urbano en el centro de Ohio. Un subgrupo de 20 individuos de *C. cardinalis* y 11 individuos de *E. virescens* sobrevivió el tiempo suficiente como para realizar análisis subsecuentes de sus movimientos. Los rangos de los juveniles de *C. cardinalis* disminuyeron en tamaño con la proximidad al borde del fragmento y los volantones se movieron menos desde los nidos rodeados de una cobertura extensa de *Lonicera maackii*. Por el contrario, el tamaño de los rangos de los juveniles de *E. virescens* se relacionó positivamente con la cobertura de *Lonicera maackii*. Durante el periodo de estudio, 70% de los of juveniles de *C. cardinalis* se dispersaron desde los sitios natales en promedio a los 47 ± 2 días luego del emplumamiento. Los patrones de dispersión de los individuos de *C. cardinalis* variaron; las aves se dispersaron localmente dentro de su fragmento natal de bosque o realizaron movimientos que se extendieron a la matriz de paisaje circundante. En nuestra área de estudio, la densidad de *C. cardinalis* aumentó con la urbanización y los volantones tendieron a dispersarse más tarde desde sitios con alta densidad. En conjunto, nuestros resultados sugieren que si bien los nuevos factores ecológicos asociados con la urbanización pueden influenciar los movimientos de los volantones, los patrones son probablemente específicos para cada especie.

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INTRODUCTION

Despite a growing literature regarding the survivorship and habitat use of juvenile birds (e.g., Anders et al. 1997, Rush and Stutchbury 2008, Vitz and Rodewald 2011), little is known about spatial ecology during the post-fledging stage of development. In particular, the ecological forces governing the size of the natal range and timing of dispersal are poorly understood, especially in urbanizing landscapes where novel ecological factors such as invasive shrubs (Borgmann and Rodewald 2005) and altered densities of territories of conspecifics (Leston and Rodewald 2006) might influence movement patterns.

Daily movements early in the post-fledging period collectively define a bird's natal range, which is the area used prior to the initiation of post-fledging dispersal (Anders et al. 1998). Because fledglings are behaviorally limited and dependent on parents for resources, variation in post-fledging movements has been linked to energetic condition, parental behavior, and territory quality (Naef-Daenzer and Grüebler 2008, Vitz and Rodewald 2010, van Overveld et al. 2011). Specifically, the size of the natal range increases with improvement in a fledgling's condition (Naef-Daenzer and Grüebler 2008) and with reductions in territory quality due to frequent parental excursions beyond the breeding area (van Overveld et al. 2011). Likewise, resource competition can limit the size of adults' territories where densities of conspecifics are high (Haggerty 1998, Stober and Krementz 2006), and fledglings' use of space presumably reflects those constraints. Finally, because moving is energetically costly and predation accounts for most mortality of fledglings (e.g., Anders et al. 1997, Vitz and Rodewald 2011), the natal range should be smaller in areas with rich food resources (Rolstad and Rolstad 1995) or microhabitat features that provide extensive cover (Haggerty 1998, Garza et al. 2005, Springborn and Meyers 2005, Stober and Krementz 2006, Whitaker et al. 2007).

Post-fledging dispersal is the initial movement juveniles make when departing the natal area for future breeding territories (i.e., natal dispersal; Greenwood and Harvey 1982, Anders et al. 1998, Vitz and Rodewald 2010). It can occur as early as 13 days after leaving the nest for small passerines (Nilsson and Smith 1985) and as late as day 137 for large raptors (Ferrer 1993) and is thought to coincide with the transition to independence when the juvenile is no longer behaviorally dependent upon adults (Vega Rivera et al. 1998, White and Faaborg 2008). Upon dispersal, fledglings make long linear movements to one or more areas of concentrated daily use, known as post-dispersal ranges (Anders et al. 1998). While the majority of studies have reported fledglings using only one post-dispersal area (Walls and Kenward 1998, Anders et al. 1998, Lang et al. 2002), for Swainson's Thrush (*Catharus ustulatus*) White and Faaborg (2008) recorded as many as four distinct ranges within the first 9 weeks after fledging.

Because natal dispersal is believed to improve an individual's ability to avoid inbreeding and competition for mates and environmental resources (Dobson and Jones 1985), a substantial literature regarding dispersal ecology has emerged (Clobert et al. 2001). Nevertheless, little is known about the ecological factors that influence the timing of the initial movements of post-fledging dispersal. The ability of an individual to emigrate from its natal area has consequences for future immigration into breeding territories (Ims and Hjermann 2001). Larger individuals and those in better condition disperse earlier (Nilsson and Smith 1985, Ferrer 1992, Lens and Dhondt 1994, but see Currie and Matthysen 1998, Middleton and Green 2008), likely because they are better able to meet the energetic costs of dispersing (Ims and Hjermann 2001) and claim preferred breeding territories (van der Jeugd 2001). Intraspecific competition at the natal site has also been positively associated with dispersal rates in a wide range of taxa (Lambin et al. 2001), though some studies suggest that dispersal of birds is not density dependent (Pasinelli and Walters 2002). Finally, habitat composition at the landscape scale can influence the timing of post-fledgling dispersal (Lens and Dhondt 1994). The influence of microhabitat features is unknown.

In landscapes consisting of remnant forests embedded within varying amounts of urban development, novel factors may also influence fledglings' movements. First, habitat fragmentation and patch size may constrain the size or shape of breeding territories and, by association, the areas used by fledglings (Lambert and Hannon 2000, Mazerolle and Hobson 2004, Bayne et al. 2005, Leonard et al. 2008). Second, landscape structure contributes strongly to invasion by exotic plants (Bartuszevige et al. 2006), and the abundance and extent of invasive species is correlated with proximity to developed areas (Hutchinson and Vankat 1997, Barton et al. 2004, Borgmann and Rodewald 2005). Because fledglings select structurally complex microhabitats that reduce risk of predation (Ausprey and Rodewald 2011, Vitz and Rodewald 2011), invasive plants, such as the Amur Honeysuckle (*Lonicera maackii*), may influence fledglings' movements by altering habitat composition and structural complexity (Mills et al. 1989, Reichard et al. 2001). Finally, species attracted to anthropogenic food resources are more abundant in urban forests (Leston and Rodewald 2006), potentially altering the degree to which fledglings' movements are density dependent.

We studied the spatial ecology of two species of songbirds, the Northern Cardinal (*Cardinalis cardinalis*) and Acadian Flycatcher (*Empidonax virescens*), within an urbanizing landscape in central Ohio. On the basis of the literature and our knowledge of the study system, we hypothesized that the size of the natal home range and timing of post-fledging dispersal should be determined by the combined effect of habitat attributes, social context, and an individual's condition. First, we predicted that the size of the natal range and distance moved from the nest in the natal area should (1) decrease with

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the presence of preferred microhabitat features because of the immediate availability of necessary resources, (2) decrease with the fledgling's and nest's proximity to edge because of spatial constraints associated with habitat fragmentation, (3) decrease with the density of conspecifics' territories because of increased competition, and (4) increase with condition because of the energetic costs associated with movement. Second, we predicted that the timing of post-fledging dispersal should be (1) inversely related to condition at time of fledging, because birds in good condition can better meet the energetic costs associated with dispersal, (2) inversely related to the density of conspecifics' territories at the natal site because of intraspecific competition for resources, (3) directly related to fledging date, because adults are more likely to renest earlier in the breeding season and will have less time to care for previous broods, and (4) directly related to the extent of landscape fragmentation due to habitat discontinuity.

METHODS

STUDY AREA

We conducted research in 26 mature riparian forests located along a rural-to-urban landscape gradient in central Ohio (Franklin and Delaware counties). Fledglings included in this study were tracked at 12 forests for cardinals and 9 forests for flycatchers. Forests were of comparable size, shape, and spatial configuration and were >2 km apart (Rodewald and Shustack 2008). Common trees and woody understory plants included sycamore (*Platanus occidentalis*), boxelder (*Acer negundo*), sugar maple (*A. saccharum*), black walnut (*Juglans nigra*), ash (*Fraxinus* spp.), American hackberry (*Celtis occidentalis*), Amur honeysuckle (*Lonicera maackii*), common spicebush (*Lindera benzoin*), tall pawpaw (*Asimina triloba*), and Ohio buckeye (*Aesculus octandra*). Amur honeysuckle is a dominant understory shrub throughout our study area and increases in extent with the amount of urbanization surrounding each forest fragment (Borgmann and Rodewald 2005).

STUDY SPECIES

We selected the Northern Cardinal and Acadian Flycatcher as study species for a concomitant study regarding the effects of urbanization on fledglings' survivorship (Ausprey and Rodewald 2011), providing us an opportunity to examine the spatial ecology of two species with different life-history strategies. Acadian Flycatchers are migratory, feed exclusively on arthropods, and generally breed in large, undisturbed tracts of mature forests (Whitehead and Taylor 2002). Cardinals do not migrate, feed on a variety of food resources, and breed within a diverse assortment of disturbed and undisturbed habitats (Halkin and Linville 1999). Previous research in our study area indicates that cardinals respond positively, and flycatchers negatively, to urbanization within the surrounding landscape matrix (Rodewald and Bakermans 2006).

FIELD METHODS

We used radio telemetry to track the movements of cardinal and flycatcher fledglings from May to September in 2008 and 2009. Because we were working within forests surrounded by landscapes that ranged from predominantly rural to highly urbanized, we strategically selected cardinal nests so as to obtain a balanced sample of fledglings across the gradient of urbanization (Ausprey and Rodewald 2011). All accessible flycatcher nests were sampled. We monitored nests of the cardinal every 2 or 3 days, those of the flycatcher every 3 or 4 days, until 4 days before the expected time of fledging, after which we monitored nests daily. Because we have observed cardinals to fledge as early as 10 days after hatching, we tagged most nestlings at age day 7 or 8, with the exception of two birds estimated to be 9 or 10 days old. We tagged Acadian Flycatcher nestlings on the day before or on their date of expected fledgling, which usually was day 13 or 14. Because flycatchers tended to leave their nests within 2 hr after being tagged, we attempted to tag nestlings at the latest date possible before fledging, when we estimated that they had reached their maximum development in the nest.

To attach transmitters, we used a modified figure-8 harness made of an elastic blend of cotton and nylon (Rappole and Tipton 1991). To minimize problems associated with lack of independence we randomly selected one nestling of sufficient mass within each nest for tagging. While we acknowledge that avoiding smaller fledglings biases our sample, we were restricted by permits and institutional guidelines for animal care. Cardinal tags weighed on average 5.8% of the fledgling's mass (tag mass: 1.45 g, BD-2, Holohil Systems Ltd.) and had a battery life of 9 weeks (n = 20) and 5 weeks (n = 1). Flycatcher tags weighed on average 4.8% of each fledgling's body mass and had a battery life of 16–21 days (tag mass: 0.47 and 0.6 g, BD-2N, Holohil Systems Ltd.). Transmitters are widely used to assess animals' movements (e.g., Kenward 2001, Millspaugh and Marzluff 2001) and have been shown to have little effect on an individual's condition (Rae et al. 2009) or behavior (Naef-Daenzer 1993, but see Barron et al. 2010). In addition, we resighted two cardinals without their transmitters a year after they had been tagged, indicating that they had successfully dropped their tags.

All nestlings from each nest received one numeric U.S. Geological Survey aluminum band and three colored plastic bands and were weighed with a Pesola spring scale (0.05-g accuracy) immediately after removal from the nest. Processing time from the point of removal of the first nestling to the replacement of the last nestling varied between 15 and 60 min depending on the number of nestlings.

While relocating tagged fledglings every 1 or 2 days, we visually confirmed their identity through radio telemetry and by resighting color bands. At each relocation point we recorded coordinates with WAAS-enabled Garmin 12 XL and DeLorme pn-40 GPS units (average error ±6.5 m).

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We recorded coordinates only when we had determined the individual's precise location, either through visual detection or change in transmitter signal. We tracked fledglings until we no longer detected a signal. Because the battery life of transmitters on flycatchers was similar to those birds' expected dispersal date (3–4 weeks after fledging; Whitehead and Taylor 2002), we did not assume that a fledgling had dispersed from the natal area if the signal disappeared. For cardinals we assumed that the transmitters failed if we (1) relocated an individual with a dead tag, (2) detected weak signals 1 or 2 days before disappearance, or (3) if the signal died within 1 week of expected battery failure.

We used a modified version of the James and Shugart (1970) method to assess microhabitat use within 0.04-ha circles centered at points where birds were visually relocated and at nest sites. We estimated percent cover of Amur honeysuckle and native shrubs and counted the number of saplings (3–8 cm dbh) and mature trees (>8 cm dbh) at relocation points, daily for flycatchers and, because of time constraints, every 2 or 3 days for cardinals.

We estimated the density of cardinal territories from spot-map surveys (Bibby et al. 2000) within one 2-ha grid at each site. Ten weekly surveys were completed from May through July in 2008 and 2009 and were designed to detect every cardinal within the grid.

We used an index of urbanization to quantify the extent of urbanization in the landscape surrounding forest fragments with nestlings. We quantified the landscape composition within a radius of 1 km surrounding each forest by analyzing digital orthophotos (2002–04) and building data from Franklin and Delaware counties. Other studies have shown strong associations between bird communities and this 1-km scale (Tewksbury et al. 1998, Saab 1999, Rodewald and Yahner 2001). The first principal component from a principal components analysis examining developed features explained 80% of the variation among sites (eigenvalue 3.99) (Rodewald and Shustack 2008). Factor 1, the "urban index," loaded positively for number of buildings (0.92), percent road cover (0.94), pavement (0.90), and lawn (0.88) but negatively for percent agricultural cover (–0.83) (Rodewald and Shustack 2008). In our study area forest fragments are better defined by their width than by their area because they are generally long, linear, and connected rather than discrete patches. Because the urban index was not correlated with forest width, we did not confound habitat area with urbanization (Rodewald and Shustack 2008).

STATISTICAL ANALYSES

Natal-range analysis. To facilitate comparison with studies that had used both minimum convex polygons (MCPs) and kernel-density estimators (KDE), we calculated natal ranges of the cardinal by both methods. Because MCPs are sensitive to outliers (Kernohan et al. 2001), we calculated 95% MCPs with the "area added" function within the Home Range Tools for ArcGIS (Rodgers et al. 2007). This function removes points that contribute the largest amount of area to the MCP until the requested percentage of points is reached (Rodgers and Kie 2011). As most of the MCP boundaries of cardinal ranges overlapped adjacent habitat that fledglings did not use (e.g., manicured grass), we also manually adjusted the MCP boundaries to include only forested and shrub habitat. We also calculated natal ranges with KDE because MCPs may produce spurious results and are considered less accurate (Laver and Kelly 2008, but see Wauters et al. 2007). In estimating fixed kernel densities, we used likelihood cross-validation (CVh) rather than least-squares cross-validation (LSCVh) for smoothing because the latter method can undersmooth data in samples <50 (Horne and Garton 2006). For fledglings that dispersed from the natal area, we defined the natal range by all points where we recorded the fledgling prior to its dispersal. Using the program Animal Space Use 1.3 (Horne and Garton 2009), we calculated a unique smoothing factor for each individual by likelihood cross-validation and on the basis of that factor estimated the 95% and 50% fixed-kernel densities in R with the function "kernelUD" (package "adehabitatHR"; Calenge 2006). Additionally, we delineated the edges of forest fragments bordering habitat we assumed to be unsuitable for cardinals, such as lawns, residential neighborhoods and other developed features. By including this spatial information in the KDE function as a "boundary" (Benhamou and Cornelius 2010) we were able to contract the estimated utilization distributions to areas of expected use (i.e., riparian forest). We considered our bounded KDE estimates to be the most biologically meaningful interpretation of the size of the natal range and used them in our subsequent analyses. See Tables 1 and 2 for natal ranges as estimated by all analytical techniques.

For the flycatcher we calculated natal ranges with 95% MCPs only since sample sizes were too small for KDE ($n < 30$; Kernohan et al. 2001). We view these estimates as conservative since interval analysis for 95% MCPs with the ArcView Animal Movement Extension version 2 (Hooge and Eichenlaub 2000) indicated that natal ranges of neither the cardinal nor the flycatcher reached an asymptote. This is likely due to two reasons. First, our sample size was limited to the life of the transmitter (<21 days for flycatchers), because we did not want to risk autocorrelation within ranges by sampling fledglings more than once a day or additional members of family groups. Second, fledgling birds are developing behaviorally and likely expand their natal ranges as their flight capabilities improve. Hence the assumption that increased sampling leads to stable natal-range sizes (as in traditional home-range analyses) may not be valid, especially if fledglings eclipse parental territory boundaries when approaching independence. Given these considerations and the fact that the intensity of our sampling of individual flycatchers was similar (Table 2) and was not correlated to

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TABLE 1. Estimates of natal range (ha) derived by the minimum convex polygon (MCP) technique and kernel-density estimation for the Northern Cardinal in central Ohio, 2008–2009. See Methods for description of the specific analytical techniques.

Bird	n[a]	95% Kernel	95% Kernel bounded	50% Kernel	50% Kernel bounded	95% MCP	95% MCP bounded
30	35	1.45	1.01	0.40	0.33	0.64	0.64
151	39	3.40	2.48	0.56	0.51	1.45	1.20
191	34	2.32	1.50	0.45	0.35	0.68	0.53
340	49	3.62	3.62	0.79	0.79	1.43	1.43
379	37	1.33	1.33	0.30	0.30	0.84	0.84
390	27	0.43	0.27	0.11	0.08	0.18	0.14
440	31	1.37	1.11	0.26	0.24	0.31	0.31
471	34	6.75	6.45	1.46	1.47	2.74	2.74
472	38	2.22	2.22	0.54	0.54	1.33	1.33
510	25	2.75	2.10	0.53	0.50	0.67	0.65
559	30	1.67	1.29	0.34	0.30	0.54	0.52
590	45	3.75	1.82	0.79	0.37	1.07	0.84
600	37	1.84	1.63	0.43	0.43	1.07	1.07
620	37	1.47	1.22	0.37	0.32	0.74	0.65
649	36	2.13	1.67	0.42	0.35	0.80	0.80
671	40	1.24	1.03	0.27	0.19	0.49	0.45
730	35	1.83	1.81	0.35	0.38	0.93	0.33
790	49	4.42	3.94	0.66	0.64	1.78	1.75
829	42	0.92	0.76	0.21	0.19	0.38	0.27
850	36	1.60	1.10	0.31	0.20	0.58	0.43
Mean	37	2.33	1.92	0.48	0.42	0.93	0.85
(SE)	(1)	(0.32)	(0.30)	(0.06)	(0.06)	(0.13)	(0.13)

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

TABLE 2. Estimates of natal range (ha) derived by the minimum convex polygon (MCP) technique for the Acadian Flycatcher in central Ohio, 2008–2009. See Methods for description of the specific analytical techniques.

Bird	n[a]	95% MCP
477	22	2.67
478	21	2.29
518	22	1.79
538	20	1.39
658	20	1.49
699	19	0.99
718	17	3.67
739	22	1.95
759	22	2.08
839	18	1.94
859	19	0.74
Mean	20	2.33
(SE)	(0.5)	(0.17)

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

natal-range size ($r = –0.08$, $P = 0.81$), we decided that our natal-range estimates were suitable for subsequent analysis.

Dispersal analysis. Past studies have identified the timing of post-fledging dispersal by either qualitatively describing sudden large movements (Anders et al. 1998, White and Faaborg 2008) or by selecting a threshold beyond which birds are considered to have dispersed (King and Belthoff 2001, Vitz and Rodewald 2010). Qualitative assessments are sufficient when individuals make obvious large movements from the natal area, but subtle shifts in area used may not be noticeable. Likewise, imposing a threshold common to all individuals may obscure individual variation in dispersal behavior.

We first assessed juveniles' movements qualitatively by visually identifying single or sequential movements that were relatively long. We considered a bird to have dispersed if it left the natal area and never returned (Belthoff and Richison 1989, Anders et al. 1998, White and Faaborg 2008). Using the program SegReg, we then quantitatively assessed dispersal movements through segmented regression analyses of distance from the nest and density of relocation points on days after fledging. SegReg (Oosterbaan 2008) fits a set of predefined trend lines with breakpoints and selects the trend that maximizes the coefficient of explanation E. When the trend is linear without a breakpoint, E is equivalent to the correlation coefficient R^2. With segmented regression E becomes a better measure of explained variation because it takes into account the estimated

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breakpoint. A segmented trend is considered a better fit than a linear trend when E exceeds the value of R^2 and is proven to be a significantly better estimation of explained variation according to F-tests for goodness of fit (Oosterbaan 2002, 2005, 2008). We used distance from nest and density of relocation points as dependent variables because our observations in the field suggested that fledglings moved farther from the nest and used a larger area with age. We calculated density of relocation points by estimating 95% fixed-kernel densities for the entire post-fledging range of each bird. The qualitative and quantitative methods yielded the same dispersal dates within 1 or 2 days for 11 of the 13 birds that dispersed (Table 3). The segmented regression analysis calculated a premature breakpoint for one of the remaining birds and failed to detect a breakpoint for the second. Because the dispersal patterns of these two birds seemed visually obvious, we relied upon the qualitative method to determine dispersal timing.

We calculated distances between natal and dispersal areas by using the Spider Diagram tool in the ArcView Animal Movement Extension version 2 (Hooge and Eichenlaub 2000). From the center of each natal range we calculated the distance to each dispersal point and then averaged all distances per distinct dispersal area to arrive at an average dispersal distance. We considered areas where juveniles spent at least 3 days after dispersing distinct dispersal areas (White and Faaborg 2008). Because of the brevity of the transmitter batteries' life we did not calculate the timing of the flycatchers' dispersal. We used the same methods to calculate the average distance between nest sites and fledglings' locations within the natal range. We used a Wilcoxon rank-sum test to compare dispersal distances between fledglings that dispersed locally and those that made extended movements ($P < 0.05$ considered statistically significant).

We calculated the extent of habitat fragmentation surrounding each natal forest fragment in ArcGIS 9.x by using aerial photos to digitize all forest and shrub habitat within a 1-km radius of the nest site.

Analysis of ecological factors. When examining the associations between natal-range size, distance moved from the nest, dispersal timing, and a suite of ecological factors, we used an information-theoretic framework that compares the relative weight of evidence for multiple models with Akaike's information criterion (AIC_c) corrected for small sample sizes (Burnham and Anderson 2002). Models included (1) mass, because fledglings' movements can vary with their condition (Naef-Daenzer and Grüebler 2008, Vitz and Rodewald 2010), (2) microhabitat structures (honeysuckle cover and number of saplings <8 cm dbh), because fledglings select for structurally complex microhabitats (e.g., Rush and Stutchbury 2008, Ausprey and Rodewald 2011, Vitz and Rodewald 2011), (3) territory density, because adults' territory size (Haggerty 1998) and dispersal rates (Lambin et al. 2001) can vary with density, (4) distance from the fledgling to the edge of the natal forest fragment, because habitat fragmentation can constrain territory size and shape (e.g., Bayne et al. 2005), (5) dispersal distance, (6) date of fledging, (7) extent of fragmentation in the surrounding landscape, because dispersal timing can vary with landscape composition (Lens and Dhondt 1994), and (7) the urban index. For the cardinal, we did not include distance from the nest to the fragment edge because it was highly

TABLE 3. Estimates of day of dispersal of Northern Cardinals in central Ohio, 2008–2009, by qualitative (visual) and quantitative (segmented regression analysis) methods. The day of final dispersal was determined by visual estimation (V) or results from the segmented regression analysis of distance from nest on day (N) or of relocation-point density on day (D). See Methods for description of the segmented regression analysis.

	Visual	Distance from nest		Point density			
Bird	Dispersal day	Breakpoint day	E	Breakpoint day	E	Final dispersal day	Criteria used
30	54–56	45.8	0.80	54.2	0.47	55	V, D
151	51–52	51.3	0.68	—	0.51	52	V, N
191	43–44	43	0.96	41.3	0.60	44	V, N
340	53–54	48	0.88	—	0.69	54	V
390	34–35	34.2	0.50	22.7	0.40	35	V, N
440	35–36	35.2	0.99	34.1	0.64	36	V, N
471	37–38	23.1	0.66	—	—	38	V
472	43–46	45.1	0.86	41.3	0.71	46	V, N
510	33–35	—	—	35.7	0.62	35	V, D
647	46–47	45.5	0.93	41.3	0.41	47	V, N
671	45–46	45	0.74	25.2	0.41	46	V, N
730	41–42	41.5	0.91	24.2	0.54	42	V, N
850	49–50	48.6	0.60	24.2	0.53	50	V, N

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correlated with the fledgling's proximity to edge ($r = 0.91$). No predictor variables within each model set were strongly correlated ($r < 0.40$). We considered the model with lowest AIC_c value the best and competing models (<2 ΔAIC_c from the top model) equally plausible given the data. Akaike weights (w_i, weight of evidence for each model) indicated the relative support for each model and represented the likelihood that any given model was the true best model. Variables were square-root or log transformed as needed to meet assumptions of normality. Because we were working with small sample sizes, we were concerned that extreme outliers would bias results. We used Cook's distance to quantify the leverage of points within each model and considered deleting points where (1) $D_i > 0.50$ and (2) the outlier was obscuring a clear relationship or creating a doubtful association. We deleted two points, one in the dispersal-timing model set for cardinals and one in the natal-range model set for flycatchers. In both cases biological circumstances unique to each individual likely explained their behavior as outliers: the flycatcher fledged in a forest fragment where an unusually high density of adults' territories likely constrained its natal range, and the cardinal was the only individual to fledge from a nest located outside the forest fragment containing its natal range (nest <20 m from edge). AIC_c values and other statistics were derived from generalized linear models constructed in R (function glm). All means are reported with estimates of standard error (± SE).

RESULTS

We tagged 45 fledgling cardinals (24 in 2008 and 21 in 2009) and 31 fledgling flycatchers (13 in 2008 and 18 in 2009). High predation rates and malfunctioning transmitters reduced the sample of individuals available for movement analyses to 21 cardinals and 11 flycatchers. We tracked cardinals for 42–71 days and flycatchers for 17–22 days after fledging, depending on transmitter life, dispersal movements, and logistical constraints. One cardinal dropped its tag prematurely at day 40 after fledging and was censored from subsequent analyses. Cardinal nests and fledglings were twice as close to the edge of the natal forest fragment as those of flycatchers (nest: $t_{17.5} = 3.0$, $P = 0.01$; fledgling: $t_{15.8} = 3.0$, $P = 0.01$).

NATAL RANGE

Variation in the size of cardinals' natal range (bounded 95% KDE; Table 1) was best explained by the model including the fledgling's distance from edge, which held a weight of evidence (w_i) of 0.98 (Table 4). Natal-range size was positively associated with fledglings' distance to the edge of the natal forest fragment ($\beta = 0.2$, 95% CI = 0.1–0.3; Fig. 1). Distance from the nest to the natal range was best explained by the urban index ($w_i = 0.43$) and the amount of honeysuckle surrounding the nest ($w_i = 0.27$; Table 5). This distance was negatively associated with the extent of urbanization in the surrounding landscape ($\beta = –0.8$, 95% CI = –1.4 to –0.1) and

TABLE 4. Models of ecological factors explaining variation in natal ranges of the Northern Cardinal (bounded 95% KDE; $n = 20$) and Acadian Flycatcher (95% MCP; $n = 10$) in central Ohio, 2008–2009. Models include mass of fledglings at time of tagging (mass), density of breeding territories of the cardinal within the natal fragment of forest (density), average percent cover of honeysuckle shrubs at relocation plots (honeysuckle), tree density at relocation plots (trees), sapling density at relocation plots (saplings), the distance of fledglings from the fragment edge (edge), and the index of urbanization (urban index). K, number of parameters; ΔAIC_c, distance from top model; w_i, model weight.

	K	ΔAIC_c	w_i
Northern Cardinal			
Edge	3	0[a]	0.99
Null	2	12.01	0
Density	3	12.97	0
Honeysuckle	3	13.74	0
Saplings	3	14.38	0
Mass	3	14.52	0
Urban index	3	14.8	0
Acadian Flycatcher			
Honeysuckle	3	0[b]	0.83
Null	2	4.91	0.07
Trees	3	6.65	0.03
Saplings	3	6.78	0.03
Urban index	3	7.74	0.02
Mass	3	8.71	0.01
Edge	3	8.84	0.01

[a]The AIC_c value for the top model was 29.27.
[b]The AIC_c value for the top model was 94.86.

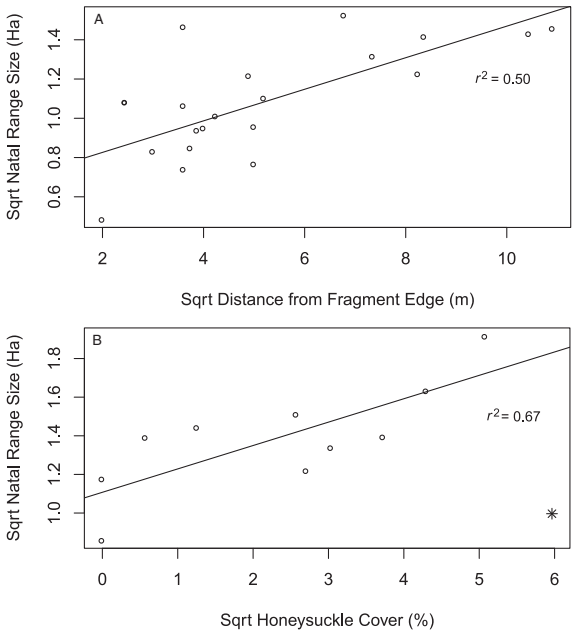


FIGURE 1. Ecological factors associated with variation in the size of natal ranges of fledgling Northern Cardinals (A; $n = 20$; bounded 95% kernel density estimate) and Acadian Flycatchers (B; $n = 10$; 95% minimum convex polygon) in central Ohio, 2008–2009. The outlying flycatcher ($D_i > 0.50$) removed from the analysis is marked with an asterisk (*).

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TABLE 5. Models of ecological factors explaining variation in the average distance moved from the nest to the natal range for the Northern Cardinal (n = 20) and Acadian Flycatcher (n = 11) in central Ohio, 2008–2009. Models include mass of fledgling at time of tagging (mass), density of breeding territories of the cardinal within the natal fragment of forest (density), average percent cover of honeysuckle shrubs at the nest site (honeysuckle nest), sapling density at the nest site (sapling nest), tree density at the nest site (trees nest), the distance of the nest from the fragment edge (nest edge), and the index of urbanization (urban index). K, number of parameters; ΔAIC_c, distance from top model; w_i, model weight.

	K	ΔAIC_c	w_i
Northern Cardinal			
Urban index	3	0[a]	0.43
Honeysuckle nest	3	0.91	0.27
Null	2	3.17	0.09
Density	3	3.95	0.06
Nest edge	3	3.97	0.06
Mass	3	4.32	0.05
Sapling nest	3	4.91	0.04
Acadian Flycatcher			
Null	2	0[b]	0.36
Urban index	3	0.09	0.34
Trees nest	3	3.26	0.07
Honeysuckle nest	3	3.49	0.06
Nest edge	3	3.54	0.06
Mass	3	3.63	0.06
Sapling nest	3	3.71	0.06

[a]The AIC_c value for the top model was 72.52.
[b]The AIC_c value for the top model was 45.43.

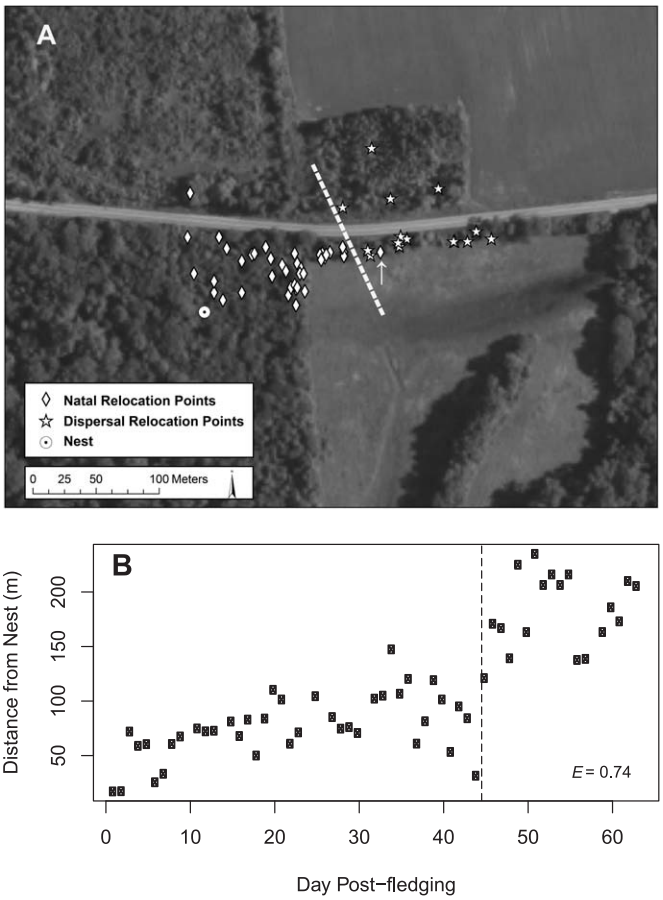


FIGURE 2. (A) Example of local post-fledging dispersal by a fledgling Northern Cardinal in central Ohio (2008) and (B) the relationship between distance moved and the fledgling's age with the calculated breakpoint (dashed vertical line) from segmented regression analysis. The coefficient of explanation (E) describes the amount of variation explained by the model. The regression breakpoint (vertical line) corresponds to the dashed line on the map. This individual made one exploratory movement 11 days prior to dispersing (arrow on the map).

percent cover of honeysuckle at the nest (β = –0.2, 95% CI = –0.4 to –0.01). Honeysuckle cover where cardinal fledglings were relocated was positively related to cover at nest sites (β = 0.7, 95% CI = 0.1–1.3) but not to the fledgling's distance from the fragment edge (β = –0.2, 95% CI = –0.8–0.4). Honeysuckle cover at nest sites was not related to distance from nest to the fragment edge (β = –0.1, 95% CI = –0.7–0.4).

For the flycatcher, natal-range size was best explained by honeysuckle cover, which held a weight of evidence of 0.83 (Table 4). Natal-range size was positively associated with increased honeysuckle cover (β = 12.1, 95% CI = 4.1–20.2; Fig. 1). Distance from the nest to fledglings' locations in the natal range was not explained well by any model (Table 5).

POST-FLEDGING DISPERSAL

We detected post-fledging dispersal movements by 13 of 20 (65%) cardinals. Of the remaining seven individuals, three made extended dispersal-like movements upon reaching a specific age post-fledging but then returned frequently to the natal range. Fledglings dispersed from the natal area an average of 47 ± 2 days (range 35–55 days) after fledging in either local or extended movements. Birds that dispersed locally did so within their natal forest fragment (n = 8; Fig. 2), whereas birds making extended movements dispersed to new forest fragments or within the surrounding landscape matrix (n = 5; Fig. 3). Birds making extended movements dispersed significantly farther (median 594 m, range 349–985 m) than did birds dispersing locally (median 171 m, range 93–569 m; U = 58.0, P = 0.03). Of the birds that dispersed, 11 moved to a single dispersal area, one moved to two, and one moved to three. Six of the fledglings that dispersed made exploratory movements into their future dispersal area prior to dispersing. Five birds made one movement (3, 5, 10, 11, and 12 days before dispersing) and one made two movements 3 and 4 days prior to dispersal. Of the birds that had dispersed prior to transmitter failure, the model including conspecific territory density best explained variation in dispersal date, carrying a weight of 0.69 (Table 6). Birds in forests with higher densities of conspecifics dispersed later than did those in forests with lower densities (β = 1.3, 95% CI = 0.4–2.2).

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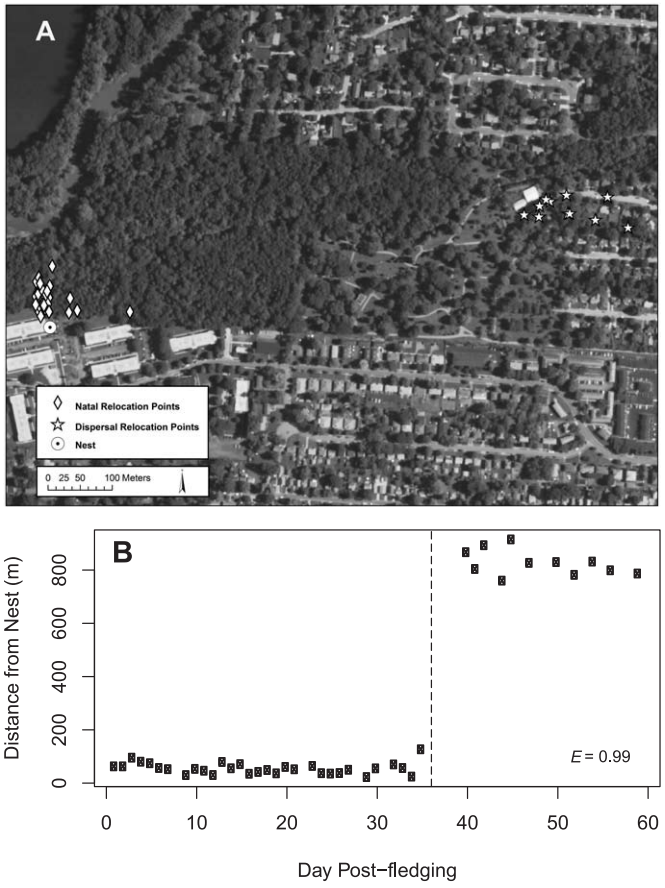


FIGURE 3. (A) Example of extended post-fledging dispersal by a fledgling Northern Cardinal in central Ohio (2008) and (B) the relationship between distance moved and the fledgling's age with the calculated breakpoint (dashed vertical line) from segmented regression analysis. The coefficient of explanation (*E*) describes the amount of variation explained by the model.

TABLE 6. Models of ecological factors explaining variation in timing of post-fledging dispersal of the Northern Cardinal in central Ohio, 2008–2009 ($n = 19$). Models include mass of fledglings at time of tagging (mass), density of the cardinals' breeding territories within the natal fragment of forest (density), the average distance of the fledglings from the fragment edge (edge), the final dispersal distance (dispersal distance), the extent of habitat fragmentation surrounding the natal fragment (site fragmentation), day of fledging, and index of urbanization (urban index). *K*, number of parameters; ΔAIC_c, distance from top model; w_i, model weight.

	K	ΔAIC_c	w_i
Density	3	0[a]	0.69
Null	2	3.48	0.12
Dispersal distance	3	5.39	0.05
Fledging day	3	5.42	0.05
Urban index	3	5.9	0.04
Mass	3	6.74	0.02
Site fragmentation	3	6.89	0.02
Edge	3	7.11	0.02

[a]The AIC_c value for the top model was 19.01.

DISCUSSION

Habitat attributes seemed to have the strongest influence on fledgings' movements, though social context also explained movements of cardinals. Consistent with our prediction, the extent of fledglings' movement was inversely related to preferred habitat attributes. Of the cardinal, a species preferring urban landscapes and a dense understory (Leston and Rodewald 2006), fledglings moved less from nest sites that were (1) surrounded by extensive honeysuckle cover or (2) located in heavily urbanized landscapes. Proximity to the fragment's edge, which is often associated with dense vegetation, also contributed to the size of the eventual natal range. In contrast, Acadian Flycatchers, which prefer more open understories and avoid honeysuckle (Bakermans and Rodewald 2006, Rodewald 2012), expanded their natal ranges as honeysuckle cover increased. Cardinals dispersed later from natal sites where densities of that species' territories were higher (i.e., the more highly preferred areas).

To the best of our knowledge we provide the first evidence that, as with breeding territories, natal ranges and fledglings' movements are inversely related to habitat "quality," as perceived by different species. Although variation in the size of birds' territories has been attributed to physiological (Naef-Daenzer and Grüebler 2008), social (Sillett et al. 2004, Pons et al. 2008), and habitat factors (e.g., Smith and Shugart 1987), territory size is often reported to vary inversely with food availability (Rolstad and Rolstad 1995, McLoughlin and Ferguson 2000, but see Franzblau and Collins 1980), and habitat features can indicate present or future food resources (Smith and Shugart 1987, Marshall and Cooper 2004, Stober and Krementz 2006). The inverse relationship between natal-range size and honeysuckle cover for the Acadian Flycatcher suggests that fledglings perceived habitat quality as a function of food availability rather than extent of protective cover (i.e., a denser understory restricted foraging space). This scenario is consistent with previous work in our study area that demonstrated the flycatcher's strong preference for nesting in areas with open understory and abundant arthropods (Bakermans and Rodewald 2006) as well as a negative relationship between reproductive output and honeysuckle cover (Rodewald 2012).

Conversely, the inverse relationship between the cardinal's movements and honeysuckle cover at nest sites likely reflects both that species' propensity to have smaller breeding territories in areas with dense shrub cover (Connor et al. 1986) and fledgling cardinals selecting for structurally complex microhabitats that promote survivorship (Ausprey and Rodewald 2011). In particular, spatial patterns in vegetation density, particularly as related to exotic shrubs, may explain why fledglings' position with respect to fragment edge, rather than honeysuckle cover itself, best explained variation

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in natal-range size. Invasive plants tend to dominate edges of forest fragments (Brothers and Springarn 1992, Yates et al. 2004, but see Bartuszevige et al. 2006), and cardinals may have been attracted to edge-associated thickets. If these thickets created abrupt changes between dense edge habitats and interior forests with relatively open understories then cardinals' movements would have been further restricted, resulting in the smaller natal ranges we observed for cardinals near fragment edges. The strong negative association between distance moved and urbanization is also likely related to extent of honeysuckle at the site level. In our study area, as landscapes surrounding forest fragments urbanize, cover of the invasive exotic Amur honeysuckle increases (Borgmann and Rodewald 2005). Hence fledglings at more urban sites likely had access to more densely and uniformly distributed honeysuckle that provided more protective cover and so moved less.

While movements of cardinals within their natal range appear related to habitat, the timing of dispersal movements beyond the natal range may have been associated with social information regarding the quality of local food resources. Fledglings delayed dispersal in areas where the density of cardinal territories was high and may have used population density as a social cue indicating the quality of habitats (e.g., Forsman et al. 2009). Although we did not find a direct relationship between dispersal timing and urbanization, in our area the density of the cardinal population increases with urbanization, likely in response to anthropogenic food resources (Leston and Rodewald 2006). Hence urbanization may have indirectly influenced fledglings' dispersal timing via urban-associated adjustments in territorial behavior and food resources.

Our results also suggest that nonmigratory species, given their tendency to delay post-fledging dispersal, lack the energetic and temporal constraints associated with migration. Cardinals' dispersal movements were 2 to 3.5 weeks later than those of several previously studied migratory species, including the Wood Thrush (*Hylocichla mustelina*; 23–32.5 days post-fledging; Anders et al. 1998, Vega Rivera et al. 1998, Lang et al. 2002), Worm-eating Warbler (*Helmitheros vermivorum*; 21.8 days; Vitz and Rodewald 2010), and Ovenbird (*Seiurus aurocapilla*; 29.2 days; Vitz and Rodewald 2010). While the life of the transmitter battery limited our ability to detect dispersal of the Acadian Flycatcher, one individual moved 1 km south of its natal area 21 days after fledging, which is consistent with other studies of this species reporting dispersal movements 3–4 weeks after fledging (Whitehead and Taylor 2002). Unlike migratory species in which both juveniles and adults disperse relatively long distances (Paradis et al. 1998, Sutherland et al. 2000), juvenile cardinals generally move no more than 100 km from their natal ranges, and many individuals remain within a few kilometers of their nest site (Halkin and Linville 1999). Likewise, whereas some cardinal fledglings we studied dispersed abruptly to novel locations within the surrounding landscape matrix, the majority of individuals either dispersed near their natal ranges or failed to disperse within the life of their transmitters. Since in some species fledglings' mortality has been linked in part to post-fledgling dispersal (Sullivan 1989, Anders et al. 1997, Davies and Restani 2006), delaying or altogether avoiding long-distance movements would be advantageous for species not obliged to migrate.

Because fledglings are behaviorally dependent on their parents before reaching independence, their movements are influenced by parental behavior as well. Adults frequently move their broods beyond exclusive breeding territories (White and Faaborg 2008, Matthysen et al. 2010), especially when habitat quality is poor (van Overveld et al. 2011), and these movements subsequently influence where (Matthysen et al. 2010) and when (White and Faaborg 2008) fledglings disperse. Such parental factors may also partially explain why our estimates of the sizes of the natal ranges (95% MCP) of the cardinal and Acadian Flycatcher are 5 to 10 times and 2.5 to 5 times smaller, respectively, than those reported for fledglings of several mature-forest species, including the Wood Thrush (4.46–9.5 ha; Anders et al. 1998), Worm-eating Warbler (10.6 ha; Vitz and Rodewald 2010), and Ovenbird (5.02 ha; Vitz and Rodewald 2010). More research that explicitly examines behavioral interactions among fledglings and adults is needed, especially as fledglings approach independence and disperse. In particular, testing the assumption that fledglings are not yet behaviorally independent before dispersing is warranted since only one study to date has integrated behavioral and spatial data within the context of post-fledging ecology (White and Faaborg 2008).

Despite our observing dispersal movements by the majority of fledgling cardinals we tracked, our data are limited by three important caveats. First, our analysis is restricted to those individuals that dispersed within the lifespan of their transmitters. Because we failed to resight all but two tagged fledglings during subsequent breeding seasons, stationary individuals likely dispersed after our study concluded. Second, we were unable to make systematic behavioral observations while relocating fledglings and confirm that those fledglings dispersed upon achieving independence. Given that some individuals can reach behavioral independence prior to dispersing (White and Faaborg 2008), our natal ranges may not have been exclusively used by dependent fledglings. Finally, dispersal distances can vary dramatically by sex (Quinn et al. 2011), and we were unable to determine the sex of cardinal fledglings in the field.

To the best of our knowledge this is the first attempt at using segmented regression analysis to quantify animal dispersal movements. Although we were able to identify dispersal movements through traditional qualitative methods, segmented regression analysis provided an added quantitative approach. This was especially useful for confirming the

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dispersal movements of individuals that made local movements to dispersal territories near the natal range. We caution, however, that use of segmented regression analysis requires intimate knowledge of the subjects' movement patterns, especially when the dependent regression variable is selected. For example, distance from nest might not be a useful dependent variable for species making "wandering" natal movements (Anders et al. 1998, White and Faaborg 2008), because the analysis might identify breakpoints between centers of activity prior to the true dispersal movement. In our study, we required the technique be corroborated on two dependent variables in addition to qualitative assessments to successfully identify timing of dispersal of 11 of 13 (85%) of the dispersed individuals. That the segmented regression analysis failed for two individuals indicates that qualitative methods used historically to identify dispersal dates (e.g., White and Faaborg 2008) should still be used in concert with quantitative methods.

This study adds to the conceptual and methodological body of knowledge of post-fledging ecology in three ways. First, we show that, as with size of breeding territories, the size of natal ranges may be a function of habitat attributes and is apparently inversely related to the perceived or actual quality of the habitat according to species-specific habitat preferences. Therefore, invasive species, like Amur honeysuckle in our system, have the potential to affect the movement ecology of young birds. For the cardinal, the inverse relationship between natal-range size and preferred habitat attributes suggests that managers working in fragmented landscapes or small habitat patches may be able to provide sufficient amounts of post-fledging habitat through local habitat management. Second, fledglings and/or their parents may use social cues to guide their movements, which is consistent with the idea that social information influences habitat selection (Forsman et al. 2009, Nocera and Betts 2010). This is especially relevant in urbanizing landscapes where anthropogenic food subsidies may alter avian distributions (Leston and Rodewald 2006). Third, new analytical techniques, such as segmented regression analysis, can serve as useful tools for defining fine-scale dispersal movements. Further research is needed for an understanding of how life-history traits and natural history shape the movement ecology and dispersal behavior of post-fledging birds.

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