POSTFLEDGING SURVIVORSHIP AND HABITAT SELECTION ACROSS A RURAL-TO-URBAN LANDSCAPE GRADIENT

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Abstract.—Despite recent increases in the number of demographic studies of birds in urban environments, the postfledging period remains poorly understood. Because novel ecological factors, including changes in predator abundance and invasive exotic shrubs, are associated with urbanization, we asked (1) how does postfledging survivorship vary across a rural-to-urban landscape gradient and (2) to what extent does Amur Honeysuckle (*Lonicera maackii*), an invasive exotic shrub, influence patterns of survivorship and habitat selection? During the 2008 and 2009 breeding seasons, we placed radiotransmitters on fledgling Northern Cardinals (*Cardinalis cardinalis*; $n = 45$) and Acadian Flycatchers (*Empidonax virescens*; $n = 31$) that occupied riparian forest stands embedded within a rural-to-urban landscape gradient in central Ohio, USA. Predation was the primary cause of fledgling mortality for both species, but cumulative survivorship ($\pm$ SE) for Acadian Flycatchers (0.720 ± 0.097; 22 days) was $1.6 \times$ that of Northern Cardinals (0.440 ± 0.077; 71 days). Survivorship across the entire postfledging period was not associated with urbanization, but during the initial 3 days after fledging, when mortality rates were highest, Northern Cardinal survivorship was positively related to urbanization. Northern Cardinals strongly selected for complex understory vegetation that was positively associated with survivorship, but survival was not related specifically to cover by Amur Honeysuckle. Contrary to assumptions that postfledging survival declines as landscapes urbanize, our results suggest that urban forests may provide suitable habitat for juvenile birds living within metropolitan areas. *Received 24 June 2010, accepted 31 December 2010.*

Key words: fledgling survival, habitat selection, honeysuckle, invasive plants, postfledging, predation, urbanization.

Supervivencia Posterior al Emplumamiento y Selección de Hábitat en un Gradiente de Paisaje Rural a Urbano

Resumen.—A pesar de los incrementos recientes en el número de estudios demográficos sobre aves en ambientes urbanos, el período posterior al emplumamiento todavía es poco comprendido. Debido a que factores ecológicos nuevos (incluyendo los cambios en la abundancia de depredadores y de arbustos exóticos invasores) están asociados con la urbanización, nos preguntamos: (1) ¿cómo varía la supervivencia de los volantones en un gradiente de paisaje rural a urbano?, y (2) ¿en qué grado afecta una especie invasora de arbusto (*Lonicera maackii*) los patrones de supervivencia y selección de hábitat? Durante las temporadas de cría de 2008 y 2009, acoplamos transmisores de radio a volantones de las especies *Cardinalis cardinalis* ($n = 45$) y *Empidonax virescens* ($n = 31$) que ocupaban rodales de bosques ribereños embebidos en un gradiente de paisaje rural a urbano en el centro de Ohio. La depredación fue la causa principal de la mortalidad de los volantones en ambas especies, pero la supervivencia acumulada ($\pm$ EE) de *E. virescens* (0.720 ± 0.097; 22 días) fue 1.6 veces mayor que la de *C. cardinalis* (0.440 ± 0.077; 71 días). La supervivencia a lo largo de todo el período posterior al emplumamiento no se asoció con la urbanización, pero durante los tres primeros días de la incubación, cuando las tasas de mortalidad fueron máximas, la supervivencia de *C. cardinalis* se relacionó positivamente con la urbanización. Los individuos de *C. cardinalis* seleccionaron fuertemente coberturas complejas de vegetación en el sotobosque, que se asociaron positivamente con la supervivencia. Sin embargo, la supervivencia no se relacionó específicamente con la cobertura de *L. maackii*. De modo contrario al supuesto de que la supervivencia posterior al emplumamiento disminuye conforme los paisajes se urbanizan, nuestros resultados sugieren que los bosques urbanos podrían brindar ambientes idóneos para las aves jóvenes que viven en áreas metropolitanas.

The process of urbanization can profoundly alter a suite of ecological factors that collectively influence bird populations, including food and cover resources (Hutchinson and Vankat 1997, Barton et al. 2004, Borgmann and Rodewald 2005), microclimate (Shochat et al. 2006), and predator populations (Prange and Gehrt 2004, Chace and Walsh 2006, Marzluff et al. 2006, Rodewald et al. 2011).

Nevertheless, in stark contrast to the rich literature on urban bird communities (e.g., Beissinger and Osborne 1982, Rodewald and Bakermans 2006), demographic studies of urban birds remain uncommon, and little is known about the population processes that operate within metropolitan areas (Shochat et al. 2006). The few demographic studies conducted within urban systems to date

have focused on adult survival (Rodewald and Shustack 2008a, b) and reproductive productivity (Rodewald and Shustack 2008 a, b; Chamberlain et al. 2009). Juvenile survival remains relatively unstudied (Whittaker and Marzluff 2009, Jackson 2010, Balogh et al. 2011), leaving a large gap in our understanding of avian population ecology in urban systems.

Because fledgling mortality is high in a wide variety of passerine species in both forested and nonforested landscapes (e.g., Anders et al. 1997, Yackel Adams et al. 2001, Rush and Stutchbury 2008, Vitz 2008), the postfledging period represents a highly sensitive stage of the avian life cycle that likely influences population viability (Anders and Marshall 2005). Daily survivorship generally improves with fledgling age, and birds are most at risk during the first 5 days after fledging (Naef-Daenzer et al. 2001, Cohen and Lindell 2004, Rush and Stutchbury 2008, Vitz 2008), when up to 70% of observed juvenile mortality can occur (King et al. 2006). Although various reproductive, physiological, and environmental factors—such as brood size (Styrsky et al. 2005), body condition (Naef-Daenzer et al. 2001, Vitz 2008), starvation (Sullivan 1989, Jackson 2010), disease (Jackson 2010, I. Ausprey pers. obs.), and exposure (I. Ausprey pers. obs.)—can influence fledgling survivorship, predation has been implicated as the primary cause of mortality (Anders et al. 1997, King et al. 2006, Vitz 2008). Identified predators of fledglings include raptors (e.g., Lindsey et al. 1994, Anders et al. 1997, Yackel Adams et al. 2001, King et al. 2006), snakes (e.g., Anders et al. 1997, Kershner et al. 2004, Vitz 2008, Jackson 2010), Eastern Chipmunks (*Tamius striatus*; Anders et al. 1997, King et al. 2006, Vitz 2008), Raccoons (*Procyon lotor*; Schmidt et al. 2008), and Domestic Cats (*Felis catus*; Vitz 2008, Balogh et al. 2011).

Urban environments pose many risks for fledgling birds, but two ecological factors associated with urbanizing landscapes seem especially influential. First, numbers of known and potential predators are positively associated with urbanization (Sorace 2002, Chamberlain et al. 2009, Rodewald et al. 2011) and may exacerbate predation risk. Domestic cats, in particular, are thought to have devastating impacts on songbirds that live within the urban matrix (van Heezik et al. 2010, Balogh et al. 2011). Second, urban-associated invasions of exotic plants may affect fledgling survivorship by changing vegetation structures in ways that either (1) provide additional cover or (2) act as "ecological traps" (*sensu* Gates and Gysel 1978) that facilitate the access to fledglings by predators. For example, American Robin (*Turdus migratorius*) and Northern Cardinal (*Cardinalis cardinalis*) nests located in exotic plants had lower daily survivorship rates than those in native plants (Schmidt and Whelan 1999a, Borgmann and Rodewald 2004, Rodewald et al. 2010). Because fledglings are known to select landscapes with structurally complex vegetation, such as early-successional forest (Rappole and Ballard 1987, Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2008) and microhabitats rich with shrub cover and abundant saplings (Rush and Stutchbury 2008, Vitz 2008), fledglings also might be expected to select invasive shrubs that provide a perceived level of extensive cover. How invasive plants influence fledgling survivorship is unknown.

We studied how postfledging survivorship of two songbird species varied along a rural-to-urban landscape gradient. In addition, we examined how Amur Honeysuckle (*Lonicera maackii*), an exotic invasive shrub that is positively associated with urban land uses in our study area (Borgmann and Rodewald 2005),

might influence patterns of habitat use and survival. On the basis of the literature and previous experience with the study system, we made the following three predictions: (1) fledgling survivorship declines with increasing urbanization surrounding riparian forests, presumably because of increased abundance of predators; (2) because fledglings are attracted to structurally complex habitats, they preferentially use microhabitats with extensive honeysuckle cover; and (3) use of honeysuckle affects survivorship by either (a) increasing predation risk, possibly by drawing fledglings closer to the ground, or (b) deterring predation, presumably by providing protective cover.

Methods

Study area.—We conducted research in 26 mature riparian forest stands located within the Columbus metropolitan area of Franklin and Delaware counties, Ohio. Fledglings were tracked in 21 of these sites during May–September in 2008 and 2009. Forests were of similar size, shape, and spatial configuration and were at least 2 km apart (Rodewald and Shustack 2008b). Plant communities consisted of a diversity of trees and woody understory plants, including American Sycamore (*Platanus occidentalis*), Boxelder (*Acer negundo*), Sugar Maple (*A. saccharum*), Black Walnut (*Juglans nigra*), ash (*Fraxinus* spp.), Common Hackberry (*Celtis occidentalis*), Amur Honeysuckle, Northern Spicebush (*Lindera benzoin*), Pawpaw (*Asimina triloba*), and Yellow Buckeye (*Aesculus flava*).

Landscape composition within a 1-km-radius circle surrounding each site was quantified by analyzing digital orthophotos (2002–2004) 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, Rodewald and Bakermans 2006). The first principal component of a principal component analysis examining developed features explained 80% of the variation among sites (eigenvalue = 3.99) (Rodewald and Shustack 2008b). Factor 1, referred to here as the "urban index," loaded positively for number of buildings (0.92), percent road cover (0.94), pavement (0.90), and lawn (0.88), but loaded negatively for percent agricultural cover (–0.83) (Rodewald and Shustack 2008b). Hence, as the extent of built land and other urban land uses expand, the urban index increases from negative (rural) to positive (urban) values, representing a gradient of change in landscape composition surrounding each site. Because the urban index was not correlated with riparian forest width, habitat area and the extent of urbanization were not confounded (Rodewald and Shustack 2008b).

Study species.—The Northern Cardinal (hereafter "cardinal") is an "urban adapter," a synanthropic species that is present in higher densities in urban than in rural forests during the breeding (1.7 × higher) and nonbreeding (4.0 × higher) seasons (Leston and Rodewald 2006). Moreover, adult annual survivorship, productivity, and body condition of cardinals are similar between rural and urban sites, which suggests that urbanization does not affect fitness (Rodewald and Shustack 2008a). Conversely, Acadian Flycatchers (*Empidonax virescens*; hereafter "flycatchers") are "urban avoiders": they are less abundant (Bakermans and Rodewald 2006), settle and initiate breeding later (Rodewald and Shustack 2008b, Shustack and Rodewald 2010), and produce fewer young (Rodewald and Shustack 2008b) in urban than in rural forests.

Field methods.—We used radiotelemetry to track the fate and movements of fledgling cardinals and flycatchers. We strategically targeted nests for radiotransmitter use in order to sample as much of the rural-to-urban gradient as possible, although some targeted nests were not sampled because of their height or position over water. Nests were monitored every 2–3 days for cardinals and every 3–4 days for flycatchers until 4 days before the expected time of fledging, whereupon nests were monitored daily. Because cardinal nestlings may fledge as early as day 10 posthatching in our system, we attached radiotransmitters to most nestlings at 7–8 days of age, with the exception of two birds estimated to be 9–10 days old. Transmitters were applied to nestling Acadian Flycatchers on the day before or on their expected fledgling date (about 13–14 days of age). Because most flycatchers left the nest within 2 h after transmitter application, we attempted to attach transmitters at the maximum body size and age possible before a visit would lead to premature fledging.

We used a modified figure-8 harness made of a cotton-nylon elastic blend to attach transmitters (Rappole and Tipton 1991). To avoid issues surrounding lack of independence, we randomly selected one nestling within each nest to receive a transmitter. For cardinals, we used two different models of transmitters that weighed, on average, 5.8% of the nestling's mass (transmitter mass: 1.45 g; BD-2, Holohil Systems, Carp, Ontario) and had battery lives of 9 weeks ($n = 43$) and 5 weeks ($n = 2$). Flycatcher transmitters weighed, on average, 4.8% of the nestling's body mass and had a battery life of 16–21 days (transmitter mass: 0.47 g and 0.6 g; BD-2N, Holohil Systems). Only nestlings that were of sufficient mass to carry a transmitter were selected (transmitter <6% of body mass). Transmitters are widely used to assess animal movements (e.g., Kenward 2001, Millspaugh and Marzluff 2001) and have been shown to have little effect on individual condition (Rae et al. 2009) or behavior (Naef-Daenzer 1993; but see Barron et al. 2010). We did not attempt to remove transmitters, but two cardinals were identified without them a year after application, which indicated that they had successfully dropped their transmitters.

All nestlings from each nest received one numeric federal band and three colored plastic bands. Immediately after removal from the nest, we weighed each nestling with a Pesola spring scale (accuracy 0.05 g). Processing time, from the point of removing the first nestling to the replacement of the last nestling, varied between 15 and 60 min depending on the number of nestlings.

During relocation events every 1–2 days, we visually confirmed the identity of tagged fledglings through radiotelemetry homing techniques and by resighting color bands. At each relocation point, we recorded the plant species used and visually estimated height of the individual at first detection (to the nearest meter). To avoid detection bias due to observer-influenced behavior we recorded this information only for fledglings that had not moved in response to our presence.

We considered a fledgling to be depredated if (1) remains were found with the transmitter or leg bands; (2) blood, scat, or scent was detected on or near the transmitter; (3) tooth or beak marks were imprinted in the transmitter housing; (4) the transmitter was buried; or (5) the transmitter or leg bands were found in association with a likely predator. If we found no direct evidence of predation but failed to detect the fledgling during hour-long searches on the relocation day and the following day, we also concluded that the fledgling had been depredated. This assumption was based on extensive field observations that indicated that most mortality occurred early during the postfledging period, when fledglings are dependent on parents and exhibit behavioral cues (e.g., loud begging) obvious to a trained observer, and was invoked for only 5 individuals that disappeared within the first week postfledging.

We measured microhabitat characteristics at relocation points daily for flycatchers. For cardinals, we sampled relocation points daily during the first 5 days postfledging and every 2–3 days thereafter. Logistical constraints prevented us from sampling the entire 9-week study period. We surveyed vegetation only at points where the bird was visually located. Vegetation was assessed using a modified version of the James and Shugart (1970) method within a 0.04-ha circle centered at the relocation point and at a randomly derived paired plot 50 m away, as well as at nest sites. We visually estimated the average cover (nearest 10%) of the forest canopy, native shrub layer, honeysuckle shrubs, and Multiflora Rose (*Rosa multiflora*) and other invasive shrubs, and we counted numbers of woody stems >3 cm diameter at breast height (DBH). Stem counts were grouped into four classes: saplings (3–8 cm DBH), small trees (8–23 cm DBH), medium trees (23–38 cm DBH), and large trees (>38 cm DBH). For each cover variable, we averaged estimates collected at four quadrants per plot. Because of logistical constraints, plots were sampled by different observers. We attempted to minimize variation among observers by frequently calibrating and checking estimates in the field.

Analysis.—Because we wanted to understand the relative performance of a suite of biologically relevant factors in explaining survivorship, we used known-fate models in Program MARK (White and Burnham 1999) rather than the Kaplan-Meier product estimator. We used an information-theoretic framework that compares relative weight of evidence for multiple models using Akaike's information criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). The model with the lowest AIC_c value was considered best, and competing models (<2 ΔAIC_c from the top model) were considered equally plausible given the data. Akaike weights (ω_i, weight of evidence for each model) indicated the relative support for each model and represented the likelihood that any given model was the most parsimonious model.

We first constructed a set of time-dependent models to identify the most appropriate temporal pattern of survivorship. The time-dependent model set for cardinals included fully time-dependent and constant survivorship models and models containing two survival periods (days 1–3 and 4–71), three survival periods (days 1–3, 4–7, and 8–71), four survival periods (days 1–3, 4–7, 8–14, and 15–71), and five survival periods (days 1–3, 4–7, 8–14, 15–21, and 22–71). These periods were selected on the basis of their correspondence to mobility stages of cardinals. Cardinals have limited flight capabilities immediately after leaving the nest (Halkin and Linville 1999), have improved but limited capabilities by the end of the first week after fledging, exhibit extensive flight ability during their second week (Wanamaker 1942), are similar to adults in flight ability by the third week, and can forage independently during the fourth week (Halkin and Linville 1999). The time-dependent model set for flycatchers included fully time-dependent and constant survivorship models and models containing two survival periods (days 1–7 and 8–21), and three survival periods (days 1–7, 8–14, and 15–22). We did not include a survival period less than day 7, because flycatchers are more developed than cardinals upon

fledging and exhibit advanced flight abilities comparable to adults by the second week. We included the third week as a survival period because we and others (Whitehead et al. 2002) have observed independent birds fly-catching by 3 weeks of age.

Next, we used the top temporal model from the first survival analysis as the null model in a subsequent analysis of individual and habitat variables. Here, we constructed a second set of *a priori* models to explain fledgling survivorship. We included (1) year; (2) fledgling mass at time of transmitter attachment, because prior studies have found positive associations between survivorship and body condition (Naef-Daenzer et al. 2001, Vitz 2008); (3) fledging date, because fledgling survivorship can vary seasonally (Vitz 2008); and (4) several variables describing microhabitat structure at relocation points, because survivorship has been positively associated with understory stem densities (Rush and Stutchbury 2008, Vitz 2008). Microhabitat variables included the amount of honeysuckle and native shrub cover and numbers of woody stems within four size classes commonly used to describe forest structure in avian field studies (James and Shugart 1970, Martin et al. 1997). We also included an interaction term between time and the urban index, because associations between urbanization and survival may change with fledgling age. Habitat variables were averaged across all relocation points for a given individual. Because fledglings may have selected different microhabitat structures as they developed, we used one-way analyses of variance to compare differences in each microhabitat structure across the five survivorship periods. Habitat variables were first square-root or arcsine-square-root transformed to approach normality, and the individual bird was treated as the replicate to avoid pseudoreplication across vegetation sampling units. For cardinals, there was no change in honeysuckle ($F = 0.13$, df = 4 and 131, $P = 0.97$) or native shrub cover ($F = 0.42$, df = 4 and 131, $P = 0.80$), and no change in numbers of trees 3–8 cm DBH ($F = 1.10$, df = 4 and 131, $P = 0.36$), 23–38 cm DBH ($F = 0.11$, df = 4 and 131, $P = 0.53$), or ≥38 cm DBH ($F = 0.50$, df = 4 and 131, $P = 0.73$) among the five survival periods. The average number of trees 8–23 cm DBH was significantly different across survival periods ($F = 3.42$, df = 4 and 131, $P = 0.01$), but Tukey's HSD post hoc test for multiple comparisons showed no significant pairwise differences. For flycatchers, there was no change in honeysuckle ($F = 1.81$, df = 3 and 91, $P = 0.15$) or native shrub cover ($F = 0.75$, df = 3 and 91, $P = 0.52$), or number of trees 3–8 cm DBH ($F = 2.28$, df = 3 and 91, $P = 0.08$), trees 8–23 cm DBH ($F = 0.70$, df = 3 and 91, $P = 0.55$), trees 23–38 cm DBH ($F = 0.16$, df = 3 and 91, $P = 0.92$), or trees ≥38 cm DBH ($F = 0.74$, df = 3 and 91, $P = 0.53$) among the four survival periods. For each species, we also ran a second set of habitat-association models to examine fledgling mortality during the period of highest vulnerability due to limited flight abilities, which were days 1–3 for cardinals and days 1–7 for flycatchers. All model sets used the logit link function.

To quantify the difference in fledgling position between detections in honeysuckle versus all other plants, we performed a binomial logistic regression analysis using generalized estimating equations (GEE) in R (package geepack; Højsgaard et al. 2005), which account for correlation across detections for each individual bird (Zuur et al. 2009). We assumed a compound correlation structure ("exchangeable"); individual fledgling position was moderately correlated for cardinals ($\alpha = 0.236$) and slightly correlated for flycatchers ($\alpha = 0.086$).

We examined the extent to which fledglings selected specific microhabitat features with a discriminant function analysis (DFA; PROC CANDISC, SAS Institute 2010) performed on the same habitat variables used in the survival analysis. Prior to analysis, variables were either square-root or arcsine-square-root transformed to approximate normal distributions. The univariate Levene's test was used to examine homogeneity of variance within each discriminating variable, which is an assumption of DFA (McGarigal et al. 2000). Because habitat variables were not strongly correlated, all were included in the DFA. Individual birds were considered replicates to avoid pseudoreplication across vegetation sampling units.

Results

Fledglings.—In 2008 we placed transmitters on 24 cardinals and 13 flycatchers from 23 and 11 nests, respectively. In 2009 we placed transmitters on 21 cardinals and 18 flycatchers from 21 and 17 nests, respectively. Because few flycatcher nests were successful in our system, we attached a transmitter to a second fledgling from two flycatcher nests in 2008 and one nest in 2009. A second fledgling cardinal from one nest in 2008 also had a transmitter attached because the first fledgling was depredated within the first day, and we were able to easily capture a sibling near the nest during the first day postfledging.

Fledgling mortality.—Twenty-three of 45 fledgling cardinals (51%) died during the study, with predation accounting for 83% of total fledgling mortality. Five of the 31 flycatchers (16%) suffered mortalities, all of which were attributed to predation. Identified or likely predators included Red Foxes (*Vulpes vulpes*), Coyotes (*Canis latrans*), and American Red Squirrels (*Tamiascurus hudsonicus*). We encountered additional mortality events for three individuals that were not included in the survival or habitat selection analyses: a banded sibling of a transmittered cardinal and two fledgling flycatchers with transmitters that fledged prematurely during a pilot study in June 2008. The cardinal was killed by a car 30 days after fledging, and the flycatchers were depredated by a Broad-winged Hawk (*Buteo platypterus*) and a Domestic Cat.

Fledgling survivorship.—Cumulative survivorship and daily survival rates varied temporally for both cardinals and flycatchers (Fig. 1). The top model explaining cardinal survivorship calculated a cumulative survivorship value (± SE) of 0.440 ± 0.077 over
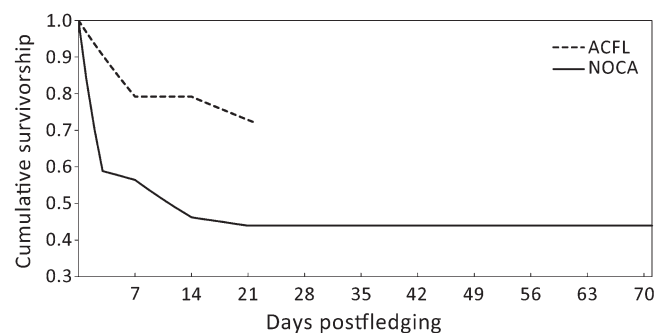
Fig. 1. Cumulative survivorship, using daily survivorship estimates from the top-ranked time model for fledgling Northern Cardinals (NOCA; $n = 45$) and the second-ranked time model for Acadian Flycatchers (ACFL; $n = 31$) in central Ohio, 2008–2009.

TABLE 1. Survivorship time models for fledgling Northern Cardinals and Acadian Flycatchers, created by known-fate models in Program MARK, using Akaike's information criterion corrected for small sample sizes (AIC_c). k is the number of parameters in each model, and ΔAIC_c is the difference between each model and the best-fitting one. Daily survivorship rates change between two (t2), three (t3), four (t4), and five (t5) survival periods, remain constant across all time intervals for model φ., and vary daily for model "t daily."

Model	AIC_c	ΔAIC_c	ω_i	k
Northern Cardinals ($n = 45$)				
φ_{t5}	162.482	0.000	0.658	5
φ_{t4}	163.895	1.413	0.325	4
φ_{t2}	170.525	8.043	0.012	2
φ_{t3}	172.231	9.749	0.005	3
$\varphi.$	226.224	63.742	0.000	1
$\varphi_{t\ daily}$	289.183	126.701	0.000	71
Acadian Flycatchers ($n = 31$)				
φ_{t2}	69.562	0.000	0.462	2
φ_{t3}	69.725	0.163	0.426	3
$\varphi.$	72.383	2.821	0.113	1
$\varphi_{t\ daily}$	99.407	29.845	0.000	22

TABLE 2. Survivorship models for fledgling Northern Cardinals and Acadian Flycatchers that incorporate biological covariates, created by known-fate models in Program MARK, using Akaike's information criterion corrected for small sample sizes (AIC_c). k is the number of parameters in each model, and ΔAIC_c is the difference between each model and the best-fitting one. Models include the best-fitting time model, average numbers of saplings (3–8 [cm DBH]), small trees (8–23), medium trees (23–38), and large trees (≥ 38), average percent cover of honeysuckle shrubs (honey) and native vegetation <4 m (native), fledgling mass at time of tagging (mass), fledgling mass at time of tagging restricted to the first time interval (mass1), fledging date (julian), year, the urban index (urban), and an interaction between survival period and the urban index (t5 * urban).

Model	AIC_c	ΔAIC_c	ω_i	k
Northern Cardinals ($n = 43$)				
$\varphi_{t5 + 3-8}$	152.380	0.000	0.229	6
$\varphi_{t5 + 8-23}$	153.677	1.297	0.120	6
$\varphi_{t5 + urban + 3-8}$	153.770	1.390	0.114	7
$\varphi_{t5 + 23-38}$	154.036	1.656	0.100	6
φ_{t5}	154.676	2.296	0.073	5
$\varphi_{t5 + native}$	154.891	2.511	0.065	6
$\varphi_{t5 + year}$	155.295	2.915	0.053	6
$\varphi_{t5 + \geq 38}$	155.558	3.178	0.047	6
$\varphi_{t5 + mass1}$	156.375	3.995	0.031	6
$\varphi_{t5 + urban}$	156.441	4.061	0.030	6
$\varphi_{t5 + julian}$	156.569	4.189	0.028	6
$\varphi_{t5 + honey}$	156.662	4.282	0.027	6
$\varphi_{t5 + mass}$	156.679	4.298	0.027	6
$\varphi_{t5 + urban + native}$	156.704	4.324	0.026	7
$\varphi_{t5 * urban}$	157.360	4.980	0.019	10
$\varphi_{t5 + urban + honey}$	158.465	6.085	0.011	7
Acadian Flycatchers ($n = 31$)				
$\varphi_{t3 + \geq 38}$	65.644	0.000	0.354	4
$\varphi_{t3 + 8-23}$	66.143	0.499	0.276	4
$\varphi_{t3 + 3-8}$	68.824	3.180	0.072	4
$\varphi_{t3 + year}$	69.540	3.896	0.050	4
φ_{t3}	69.725	4.081	0.046	3
$\varphi_{t3 + honey}$	70.134	4.490	0.038	4
$\varphi_{t3 + julian}$	70.764	5.120	0.027	4
$\varphi_{t3 + urban + 3-8}$	70.875	5.231	0.026	5
$\varphi_{t3 + 23-38}$	71.451	5.807	0.019	4
$\varphi_{t3 + mass}$	71.548	5.904	0.019	4
$\varphi_{t3 + mass1}$	71.712	6.068	0.017	4
$\varphi_{t3 + native}$	71.732	6.088	0.017	4
$\varphi_{t3 + urban}$	71.761	6.117	0.017	4
$\varphi_{t3 + urban + honey}$	72.129	6.485	0.014	5
$\varphi_{t3 + urban + native}$	73.783	8.139	0.006	5
$\varphi_{t3 * urban}$	75.825	10.181	0.002	6

five periods (Table 1) during the first 71 days postfledging. Daily survival rates of cardinals were lowest during days 1–3 (0.838 ± 0.036) and varied among days 4–7 (0.990 ± 0.010), days 8–14 (0.972 ± 0.014), days 15–21 (0.993 ± 0.007), and days 22–71 (1.000 ± 0.000). Flycatcher survivorship was best explained by two models that incorporated two and three periods (Table 1). We chose the second-ranked model as most appropriate, because inclusion of a third period was more consistent with field observations of behavioral development during the third week postfledging, and it had a similar weight ($\omega_i = 0.426$) as the top-ranked model ($\omega_i = 0.462$). Cumulative survivorship ($\pm$ SE) of flycatchers was 0.720 ± 0.097 over 22 days. Daily survival rates were lowest during the first week postfledging (0.967 ± 0.013) and remained fairly constant during the second (1.000 ± 0.000) and third weeks (0.988 ± 0.012).

The most important variables explaining survivorship of cardinals over the length of the 71-day postfledging period were tree size classes 3–8, 8–23, and 23–38 cm DBH, which collectively had a weight of evidence of 0.449 (Table 2). The model containing both urbanization and saplings was also highly ranked, but the relationship between survivorship and urbanization was not significant ($\beta = 0.197$, 95% CI: -0.288 to 0.683). Survival of cardinals improved with increasing numbers of saplings ($\beta = 0.557$, 95% CI: 0.003–1.111) and tended to improve as small trees increased ($\beta = 0.492$, 95% CI: -0.086 to 1.070) and medium-sized trees decreased in abundance ($\beta = -0.422$, 95% CI: -0.912 to 0.067). During the first 3 days postfledging, cardinal daily survivorship increased from 0.73 to 0.95 as the number of saplings within the sampling plot increased from zero to 46. Interestingly, when we restricted analysis to the most vulnerable period (days 1–3), the urban index was included in the top model set (Table 3). When controlling for the number of saplings, survival increased as the surrounding landscape became more urbanized ($\beta = 0.625$, 95% CI: 0.004–1.247; Fig. 2). Cumulative survival was 59% higher for fledglings in the most urban sites than for those in the most rural sites during the first 3 days postfledging.

Survivorship of flycatchers over the 22-day postfledging period was best explained by numbers of small and large trees, which were in models having a cumulative weight of evidence of 0.660 (Table 2). Numbers of large trees were negatively associated with flycatcher survivorship ($\beta = -0.720$, 95% CI: -1.233 to -0.207), whereas the number of small trees was positively associated with survivorship ($\beta = 1.306$, 95% CI: 0.027–2.585). Results were similar when the analysis was restricted to the initial period (1–7 days postfledging).

Table 3. Survivorship models for Northern Cardinals ($n = 43$) restricted to the first survival period. Model construction is the same as described in Table 2.

Model	AIC_c	ΔAIC_c	ω_i	k
$\varphi_{t1 + urban + 3-8}$	85.803	0.000	0.245	4
$\varphi_{t1 + 8-23}$	87.281	1.478	0.117	3
$\varphi_{t1 + urban}$	87.867	2.064	0.087	3
$\varphi_{t1 + 3-8}$	87.879	2.076	0.087	3
$\varphi_{t1 + urban + native}$	88.008	2.205	0.081	4
$\varphi_{t1 + 23-38}$	88.335	2.531	0.069	3
φ_{t1}	88.666	2.862	0.059	2
$\varphi_{t1 + native}$	88.978	3.175	0.050	3
$\varphi_{t1 + year}$	89.027	3.224	0.049	3
$\varphi_{t1 + honey}$	89.519	3.716	0.038	3
$\varphi_{t1 + \geq 38}$	89.541	3.738	0.038	3
$\varphi_{t1 + urban + honey}$	89.701	3.898	0.035	4
$\varphi_{t1 + mass}$	90.514	4.711	0.023	3
$\varphi_{t1 + julian}$	90.786	4.982	0.020	3

Because the second-ranked temporal models for both species were <2 ΔAIC_c from the top-ranked models, we included each as null models in subsequent analyses using the same covariates. However, the results for both species did not differ from the analyses using the top-ranked models.

Habitat use and selection.—Fledgling position in the forest canopy was influenced by the presence of honeysuckle. Average fledgling position (± SE) was 7.4 ± 0.62 m high for flycatchers ($n = 31$) and 4.1 ± 0.37 m high for cardinals ($n = 36$). Fledgling flycatchers found in honeysuckle were 2.7 × lower (2.8 ± 0.34 m, $n = 16$) than those found in other substrates (7.7 ± 0.30 m; $\chi^2 = 15.53$, $P < 0.001$, $n = 287$). Similarly, fledgling cardinals found in honeysuckle were 2.4 × lower (2.1 ± 0.09 m, $n = 152$) than those found in other substrates (5.2 ± 0.20 m; $\chi^2 = 79.0$, $P < 0.001$, $n = 309$). Fledgling age and position were not significantly related for either flycatchers ($\beta = -0.007$, $P = 0.361$, $r = 0.03$) or cardinals ($\beta = 0.001$, $P = 0.687$, $r = 0.00$).
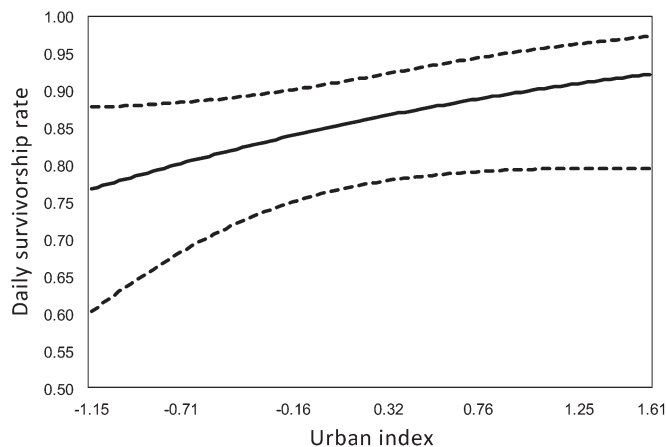

Fig. 2. Daily survivorship rates and 95% confidence interval (dashed lines) for fledgling Northern Cardinals ($n = 42$) during the first 3 days postfledging in relation to the amount of urbanization in the surrounding landscape (urban index) in central Ohio, 2008–2009.
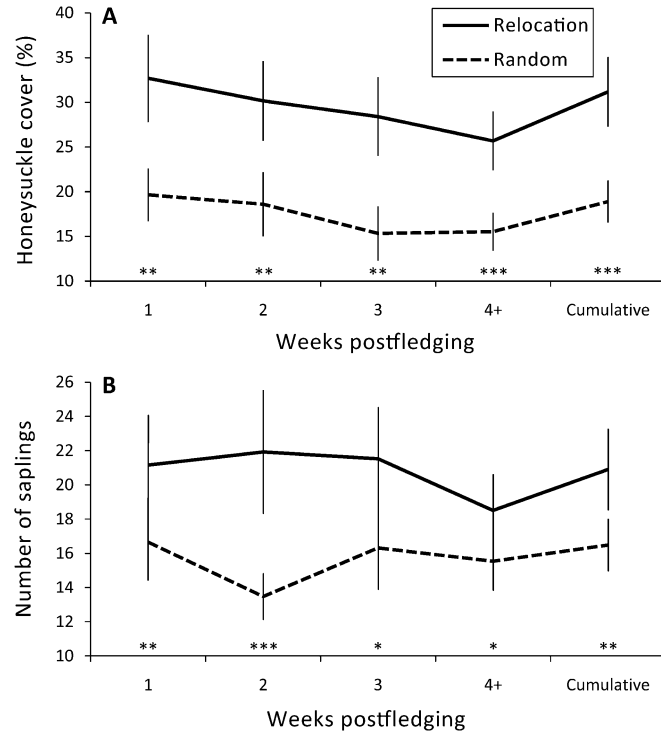

Fig. 3. (A) Average honeysuckle cover and (B) average number of saplings 3-8 cm DBH at fledgling Northern Cardinal ($n = 29$) relocation sites and random plots by week postfledging in central Ohio, 2008–2009. Bars represent standard error of the mean. Significance of univariate F-tests indicated by ***$P < 0.01$, **$P < 0.05$, *$P < 0.10$.

Microhabitats used by cardinal fledglings differed from randomly sampled available microhabitats (Wilks's $\lambda = 0.719$, df = 8 and 49, $P = 0.029$), in that cardinals selected areas with 1.7 × more honeysuckle cover ($F = 6.36$, df = 1 and 56, $P = 0.015$; Fig. 3A) and 1.3 × more saplings ($F = 5.20$, df = 1 and 56, $P = 0.026$; Fig. 3B). Microhabitats selected by flycatchers were not significantly different in structure from random locations (Wilks's $\lambda = 0.819$, df = 8 and 49, $P = 0.242$), although used sites had marginally more saplings ($F = 3.20$, df = 1 and 56, $P = 0.079$).

Less vegetation surrounded nest sites than locations used by fledgling cardinals (Wilks's $\lambda = 0.720$, df = 7 and 50, $P = 0.016$) and flycatchers (Wilks's $\lambda = 0.534$, df = 7 and 48, $P < 0.001$). In particular, fledgling cardinals selected areas with 2.2 × more native shrub cover ($F = 15.16$, df = 1 and 56, $P < 0.001$), whereas fledgling flycatchers selected areas with 3× more honeysuckle cover ($F = 6.26$, df = 1 and 54, $P = 0.015$) and 2.4× more native shrub cover ($F = 26.91$, df = 1 and 54, $P < 0.001$; Fig. 4).

Discussion

Over the entire postfledging period, survivorship was not strongly related to urbanization in either species. However, survival of fledgling cardinals tended to be higher in more urbanized landscapes during the initial 3 days postfledging, when fledgling mortality was greatest. Specifically, cumulative survivorship varied from 0.46 in
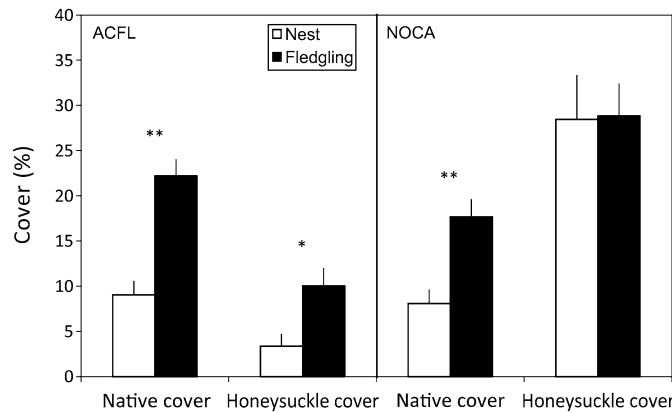
Fig. 4. Average honeysuckle and native shrub cover at nest sites and individual relocations for fledgling Acadian Flycatchers (ACFL; $n = 28$) and Northern Cardinals (NOCA; $n = 29$) in central Ohio, 2008–2009. Bars represent SE. Univariate F statistics are significant where **$P < 0.001$, *$P < 0.05$.

the most rural forests to 0.78 in the most urban forests. At local scales, cardinals and flycatchers were more likely to survive as the structural complexity of forests increased, particularly at understory and midstory layers, respectively.

Because many predators of fledglings are generalist species (Anders et al. 1997, Schmidt et al. 2008, Vitz 2008) that are known to respond positively to urbanization (Prange and Gehrt 2004, Chace and Walsh 2006, Marzluff and Neatherlin 2006, Rodewald 2011), the risk of predation for young birds has been presumed to be high in urban areas (Whittaker and Marzluff 2009). Results from our work and other empirical studies (Whittaker and Marzluff 2009, Jackson 2010, Balogh et al. 2011) have not demonstrated consistent associations between urbanization and fledgling survivorship. In the larger Seattle metropolitan area, juvenile mortality of four songbird species varied inconsistently across different landscapes and spatial scales (Whittaker and Marzluff 2009). Survival rates of fledgling Eastern Bluebirds (*Sialia sialis*) on golf courses and meadows were similar across varying levels of urbanization (Jackson 2010). Conversely, Balogh et al. (2011) found that mortality of juvenile Gray Catbirds (*Dumetella carolinensis*) was highest in urban neighborhoods with high numbers of cats.

The fact that urbanization had no apparent strong effect on flycatcher fledgling survival and a potentially positive effect on cardinal fledgling survival is paradoxical given that numbers of predators were positively related to urbanization in our study system (Rodewald 2011, Rodewald et al. 2011). Recent lines of evidence suggest, however, that anthropogenic resource subsidies (e.g., outdoor pet food, refuse, birdfeeders) can weaken the link between predator numbers and avian demographic parameters. For example, in our same study system, relative numbers of predators and rates of nest predation were uncoupled in urban landscapes, though they were positively related in more rural landscapes (Rodewald et al. 2011). Similarly, species known to be important nest predators in rural landscapes seldom depredated nests in cities, despite occupying cities in high numbers (Chiron and Julliard 2007, Weidinger 2009). Functional responses might be especially likely in generalist predators (e.g., Raccoon, Virginia

Opossum [*Didelphis virginiana*], Striped Skunk [*Mephitis mephitis*], and corvids) that can adjust foraging behavior in response to prey abundance (Schmidt and Whelan 1999b). Moreover, because predictable sources of anthropogenically derived food can spatially aggregate certain predators (e.g., Raccoons; Prange et al. 2004), predators may be less likely to encounter fledgling birds, which are likely taken on an incidental basis rather than through detection by specialized search strategies (Vickery et al. 1992, Vigallon and Marzluff 2005). Raptors, in particular, may be less likely to prey on fledglings within urban landscapes because of the availability of easily captured alternative prey (Adamczewska-Andrzejewska et al. 1988, Mannan and Boal 2000, Chernousova 2010). Changes in resource and prey distribution can alter predator movements such that their effect varies even over relatively small spatial scales. Although Domestic Cats can be important predators of juvenile birds within the urban matrix (Balogh et al. 2011), they may preferentially select matrix habitat over vegetation fragments, which could result in less pronounced predation by Domestic Cats within fragments (van Heezik et al. 2010).

Our study provides evidence that habitat characteristics selected by juveniles promoted survival. Cardinals and, to a lesser extent, flycatchers selected microhabitats with complex understory structure—a behavior that was associated with improved survivorship. Preference for thick vegetation by fledglings has been reported for a variety of forest and grassland birds, including Ovenbirds (*Seiurus aurocapilla*; King et al. 2006, Vitz 2008), Worm-eating Warblers (*Helmitheros vermivorum*; Vitz 2008), Hooded Warblers (*Wilsonia citrina*; Rush and Stutchbury 2008), Swainson's Thrushes (*Catharus ustulatus*; White et al. 2005), White-throated Thrushes (*Turdus assimilis*; Cohen and Lindell 2004), Dickcissels (*Spiza americana*; Berkeley et al. 2007), and Botteri's Sparrows (*Aimophila botterii*; Jones and Bock 2005). However, few studies have explicitly linked survivorship with habitat selection. Vitz (2008) found that surviving Ovenbirds and Worm-eating Warblers in southern Ohio used microhabitats with 20% more woody stems than those used by nonsurvivors. Likewise, vertical vegetation structure was positively associated with Ovenbird survival in New Hampshire (King et al. 2006). Although we cannot determine the extent to which parents influenced the habitat-use patterns of fledglings, our results are consistent with the general idea that habitat selection influences survivorship of fledglings.

The link between fledging survivorship and structural complexity may partly explain the positive relationship that we detected between cardinal survivorship and urbanization. In our system, as landscapes surrounding forests urbanized, the forest understory increased in density and was dominated by the exotic and invasive Amur Honeysuckle (Borgmann and Rodewald 2005, Rodewald 2011). Although flycatchers seldom used honeysuckle or shrubs, cardinals were usually found in microhabitats rich with honeysuckle, which resulted not only in greater cover surrounding birds, but lower perching height. Despite our initial predictions that lower perch heights would result in increased predation by mammals, honeysuckle was not negatively associated with survivorship. In contrast to the risk that exotic shrubs pose for nests (Schmidt and Whelan 1999a, Borgmann and Rodewald 2004, Rodewald et al. 2010), the dense vegetation provided by exotics might prove beneficial to young birds by drawing them into areas with more protective cover.

Our estimates of cumulative postfledging survivorship for Northern Cardinals and Acadian Flycatchers represent among the highest (0.72 for flycatchers; weeks 1–3) and lowest (0.44 for cardinals; weeks 1–9) estimates of survivorship in the literature (Ausprey 2010). The dramatic difference in survivorship between the two species is likely tied to different fledging strategies that mediate exposure to predators. Flycatchers in our system fledged as much as 6 days later than cardinals and, consequently, were behaviorally more advanced. For example, flycatchers move into the forest canopy immediately after fledging (Mumford 1964), but cardinals have limited flight ability and remain in shrubs near the nest (Laskey 1944, Halkin and Linville 1999). On many occasions during the first week postfledging, fledgling cardinals were also observed begging within 1–2 m of the ground (I. Ausprey pers. obs.), a conspicuous behavior that could have attracted mammalian predators (Martin and Briskie 2009). The ratio of average transmitter mass to body mass was also slightly smaller for flycatchers than for cardinals, and this may have contributed to differences in cumulative survivorship.

In our system, predation was the primary source of mortality for fledglings, and risk of mortality for cardinals and flycatchers was greatest during the first few days after fledging. Likewise, daily survivorship was lowest during the first 5 days postfledging for Rose-breasted Grosbeaks (Moore et al. 2010), Worm-eating Warblers (Vitz 2008), Ovenbirds (Vitz 2008), Hooded Warblers (Rush and Stutchbury 2008), White-throated Thrushes (Cohen and Lindell 2004), and Great Tits (*Parus major*) and Coal Tits (*Periparus ater*) (Naef-Daenzer et al. 2001). Eighty percent of flycatcher and 93% of cardinal fledgling mortality occurred during the first week postfledging (Fig. 1), which is similar to the 70% mortality rate King et al. (2006) reported for Ovenbirds during the initial 5 days. Temporal shifts in survivorship have been attributed anecdotally to behavioral development (Anders et al. 1997, Rivera et al. 1998) and the propensity of fledglings to spend their first days on the ground (Cohen and Lindell 2004, White et al. 2005), especially when young fledge from ground nests (Vitz 2008). Additionally, some species experience a second peak in mortality when juveniles disperse from the natal area and attain independence (Sullivan 1989, Anders et al. 1997, Davies and Restani 2006). However, survivorship of cardinals did not change 5–7 weeks postfledging when the majority of individuals that survived to independence dispersed from natal areas (Ausprey 2010).

Our results suggest that forests within urban landscapes or those heavily invaded by exotic shrubs do not necessarily expose fledglings to greater mortality risk, but there are two important caveats to our findings. First, differences in avian density among sites prevented us from obtaining a balanced sample across the urban index, reducing the precision of our survivorship models at sites where sample sizes were smaller. Second, our 2-year study is unlikely to sufficiently capture potential seasonal or annual variation in survival rates. Because our sample was dominated by individuals that fledged in late spring and early summer, we may not have detected elevated mortality rates for individuals that fledged later in the breeding season (Vitz 2008).

During the 2 years of our study, survivorship of fledgling cardinals and flycatchers was not strongly related to the extent of urbanization in the surrounding landscape or to honeysuckle cover. Across the rural-to-urban landscape gradient, survivorship of both species was highest in microhabitats that were structurally more complex than those that surrounded nest sites, signifying the importance

that complex forest structure has in supporting birds throughout the breeding season. Given the influence of fledgling survivorship in population viability (Anders and Marshall 2005) and source–sink status of breeding sites (Anders et al. 1997, Rush and Stutchbury 2008, Moore et al. 2010), rates of fledgling mortality must not soar if urban forests are to support bird populations. The fact that urbanization did not seem to depress flycatcher fledging survivorship and slightly promoted cardinal survival suggests that the urban forests in our system have the potential to contribute to avian conservation. Furthermore, at least 29% of the cardinals that survived to independence made postfledging dispersal movements to areas within the surrounding landscape matrix (Ausprey 2010). Their future breeding locations are unknown, but such movements suggest that urban forests may act as sources for cardinal populations in the urban matrix, where predation pressures can be more severe (Balogh et al. 2011). The ability of urban forests to provide habitat for songbirds during the highly sensitive postfledging stage supports the assertion that conserving open space in urbanizing landscapes should remain a conservation priority (Dearborn and Kark 2010).

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