Postfledging Survival of Eastern Bluebirds in an Urbanized Landscape

ALLYSON K. JACKSON,1,2 Department of Biology, Institute for Integrative Bird Behavior Studies, College of William and Mary, Williamsburg, VA 23187, USA
JOSHUA P. FRONEBERGER, Department of Biology, Institute for Integrative Bird Behavior Studies, College of William and Mary, Williamsburg, VA 23187, USA
DANIEL A. CRISTOL, Department of Biology, Institute for Integrative Bird Behavior Studies, College of William and Mary, Williamsburg, VA 23187, USA

ABSTRACT Golf courses ostensibly offer green space in urbanized areas, but it is unclear how suitable these human-modified habitats are for wildlife populations. Golf courses are home to a variety of wildlife, but in particular they have been the focus of research on avian responses to urbanization. Although numerous reproductive and diversity studies have been conducted on birds of golf courses, no research exists on postfledging survival in this created landscape. In 2008 and 2009, we estimated survival of eastern bluebird (Sialia sialis) fledglings using radio telemetry on golf course and other developed sites in Williamsburg, Virginia. We used nest survival models in Program MARK set in an information theoretic framework to assess whether the golf course habitat predicted mortality along with other previously studied variables, such as fledgling age, year, site, body condition, fledging date, and transmitter weight. We found no evidence that inhabiting a golf course increased mortality during the fledgling period, but we did find support for both fledgling age and fledging date as predictors of survival. Mortality decreased for older fledglings and those that fledged later in the season. Cause-specific postfledging survival rates did not differ among sites. Fledgling bluebirds did, however, move into habitat that was significantly more forested and less grassy than their natal habitat. For managers of wildlife on golf courses and other urbanized sites, our study is the first to show that placing nest boxes in manicured habitat may attract birds to areas without suitable habitat for fledglings. © 2011 The Wildlife Society.

KEY WORDS eastern bluebird, golf course, juvenile survival, nest survival model, postfledging, Program MARK, radio telemetry, Sialia sialis, Virginia.

North America is becoming increasingly urbanized, stimulating research on how wildlife populations adapt to changing landscapes. Birds have often been the subjects of such studies, as they are highly visible residents in many suburban and urban environments (Marzluff et al. 2001). We know little about how birds react to novel habitats created by developments such as golf courses and parks. As protected lands cannot provide enough space to conserve all species, potential conservation value must be sought in developed and agricultural property as well. A considerable amount of natural habitat in North America has been set aside for recreation, such as parks, historic areas, golf courses, and trails. Although these areas maintain elements of native habitat, they also introduce new problems for wildlife; for example, golf courses have high levels of direct human disturbance, copious pesticides, and simplified vegetation structure (Cristol and Rodewald 2005).

Received: 7 February 2010; Accepted: 26 November 2010; Published: 25 May 2011

1E-mail: allyson.jackson@briloon.org
2Present Address: BioDiversity Research Institute, 652 Main St., Gorham, ME 04038, USA.

Golf courses have been singled out from other urbanized habitats as the subject of considerable wildlife research. Most such research has focused on birds, examining either nesting success (LeClerc et al. 2005, Rodewald et al. 2005, Smith et al. 2005, Stanback and Seifert 2005), species diversity (Gordon et al. 2003, Jones et al. 2005, LeClerc and Cristol 2005, Merola-Zwartjes and DeLong 2005, White and Main 2005), or pesticide exposure (Rainwater et al. 1995, Burdge 2008). Many results from these studies are contradictory regarding suitability of golf courses for birds. For example, eastern bluebirds (Sialia sialis) nesting on North Carolina golf courses were less productive than those nesting in nearby rural reference sites (Stanback and Seifert 2005), whereas birds on golf courses in Virginia outperformed reference birds (LeClerc et al. 2005). Although results have not been uniform, agreement exists from a variety of sites that the amount of undisturbed habitat (e.g., forest in the eastern U.S.) surrounding a golf course plays a role in the conservation value of the golf course itself (Gordon et al. 2003, Jones et al. 2005, LeClerc and Cristol 2005, Sorace and Visentin 2007).

In most studies of golf courses, researchers have selected reference sites usually based on what habitats would have
been available had the golf course not been built. Using this paradigm, golf courses have been compared to various disparate habitats including native desert vegetation, farmland, or urban centers (Green and Marshall 1987, Merola-Zwartjes and DeLong 2005, Yasuda and Koike 2006). The choice of reference site determines the outcome of the comparison, although little discussion usually occurs regarding the effect of this choice on the results.

We employed a different approach, studying golf courses alongside other human-dominated landscapes with ostensibly similar vegetation structure to identify whether attributes unique to golf courses are detrimental to bird survival. An information theoretic approach allowed us to focus on the hypothesized effect of golf courses on variation in fledgling survival (Burnham and Anderson 2002). The study of survival during the period shortly after leaving the nest is gaining prominence in the ornithological literature because of its potential effect on overall population dynamics (Anders et al. 1997, Schmidt et al. 2008). Although several studies have considered nesting success of birds on golf courses, no study has yet considered the effect of golf courses on fledgling survival. Previous studies have shown that fledgling survival can vary based on many different variables, including year (Yackel Adams et al. 2006), fledging date (Verboven and Visser 1998, Naef-Daenzer et al. 2001, Monró’s et al. 2002), body condition (Kremenz et al. 1989, Yackel Adams et al. 2006, Suedkamp Wells et al. 2007), transmitter weight (Rae et al. 2009), fledging age (Sullivan 1989, Moore et al. 2010), and specific habitat types (King et al. 2006, Berkeley et al. 2007, Rush and Stutchbury 2008).

Fledgling birds are highly susceptible to predation (Sullivan 1989) and 2 of the defining characteristics of golf course habitat (i.e., pesticide use and lack of structural complexity) affect predation risk in other avian species. Pesticide exposure increased susceptibility to domestic cat predation in bobwhite (Colinus virginianus; Galindo et al. 1985) and the structure of vegetation around the nesting site affected fledgling survival in several passerines (Cohen and Lindell 2004, Berkeley et al. 2007).

Because fledgling birds may require different types of habitat than do adults, developed landscapes that prevent movement or separate habitats into isolated patches may reduce fledgling survival. In many forest-specialist species, fledglings move from the old growth habitat used by nesting adults into denser early-successional habitats (Anders et al. 1998, Marshall et al. 2003, King et al. 2006). Thus, it is generally understood that suitable breeding habitat must also include or be adjacent to suitable fledgling habitat. By attracting birds to nest boxes in areas where they would not usually breed, artificial nest cavities may place fledglings in suboptimal habitat, forcing fledgling dispersal, or reducing fledgling survival.

Our primary objective was to determine whether the golf course environment affects fledgling survival when considered with other covariates thought to affect survival, including year, fledging date, body condition, transmitter weight, fledgling age, and specific habitat types. Because golf courses may cause higher rates of predation than other less manicured habitat, we also documented cause-specific mortality rates between fledglings inhabiting golf courses and other habitats. Our final objective was to, for the first time in a species using artificial nest cavities, examine whether fledglings occupy different habitat than their parents used for nesting.

STUDY AREA

We monitored eastern bluebird reproductive success on 7 sites in Williamsburg, Virginia: 3 golf courses, 1 college campus, and 3 recreational parks (Fig. 1). We picked these sites to represent a range of non-agricultural human-modified landscapes found in southeastern Virginia. Structurally, the golf course sites were similar, with mowed fairways, forested borders, and prominent water features. We verified that each golf course site used either organophosphate or pyrethroid insecticides during the bluebird breeding season by examining maintenance logs, and we confirmed with managers that non-golf sites were not treated with insecticides (Burdge 2008). The non-golf sites were varied, with the college campus dominated by buildings and parking lots, the large state park being primarily forested with heavily used trails, and the 2 smaller municipal parks having disc golf playing fields that resembled golf courses in vegetation structure.

METHODS

Site Characteristics

We digitized aerial photos taken in 2007 (Commonwealth of Virginia, unpublished data) using ArcGIS (Environmental Systems Research Institute [ESRI], Redlands, CA). We classified habitat types into the following 6 categories: 1) unmanaged forest (hereafter forest; continuous canopy with an unmowed forest floor, retaining debris, shrub, and herbaceous layer below the canopy), 2) park-like forest (hereafter park-like; trees with mowed understory, typical of those along golf course fairways), 3) short grass (hereafter grass; grass that is mowed on a regular basis to keep it approximately 0.1 m tall), 4) water and wetlands (hereafter water; includes ponds, creeks, rivers, and tidal marshland), 5) impervious surfaces (hereafter impervious; includes buildings, roads, gravel paths and lots, sand traps, and barren dirt), and 6) mid-level vegetation (hereafter mid-level veg; includes tall and ornamental grasses that are not mowed, crops such as corn and soybeans, and shrubs such as low bushes that provide cover close to the ground). We ground-truthed photographs by visual observations of presence of understory (e.g., difference between forest and park-like forest). We accounted for major changes in habitat (e.g., forest turned into housing) between when the photos were taken in 2007 and our study years of 2008 and 2009 by taking Global Positioning System (GPS) points on the ground at the extent of the landscape change, and altering habitat type accordingly when we digitized the aerial photos. Because these sites were imbedded within a suburban matrix, we defined the boundaries of each site in terms of areas used for nesting by bluebirds, instead of property own-
ership boundaries. We used ArcGIS to create a minimum convex polygon around all the nesting locations (nest boxes) monitored within each site and buffered the resulting polygon by 100 m (approximate bluebird foraging territory; Gowaty and Plissner 1998). This boundary encompassed most of the golf course environment, along with surrounding area that was close to the golf course border (Fig. 2). We also included within the site boundary any obvious golf course habitat excluded from the polygon because no nest boxes were placed there (e.g., driving range at site A). We calculated site area based on the resulting polygon (Table 1).

We calculated site characteristics using FRAGSTATS (McGarigal et al. 2002). We calculated the class metric for edge density for the border between forest or park-like

Figure 1. Eastern bluebird (Sialia sialis) study sites (2008–2009) in southeastern Virginia. Study sites (A–G) are shown in circles. City of Williamsburg (star) is situated between the York River and the James River.

Figure 2. Digitized landcover images of golf course (a–c) and reference sites (d–g) in southeastern Virginia, where eastern bluebird fledglings were radio-tracked in 2008 and 2009.
Jackson et al. • Postfledging Survival in an Urban Landscape

Postfledging Survival in an Urban Landscape

Table 1. Habitat and postfledging survival characteristics for 7 eastern bluebird study sites in Williamsburg, Virginia, USA (2008–2009).

<table>
<thead>
<tr>
<th>Metric</th>
<th>Golf course sites</th>
<th>Reference sites</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>B</td>
</tr>
<tr>
<td>Total area (ha)a</td>
<td>85.67</td>
<td>76.57</td>
</tr>
<tr>
<td>Edge density (m/ha)b</td>
<td>125.30</td>
<td>164.24</td>
</tr>
<tr>
<td>% Forestc</td>
<td>0.374</td>
<td>0.270</td>
</tr>
<tr>
<td>% Park forestc</td>
<td>0.047</td>
<td>0.097</td>
</tr>
<tr>
<td>% Short grassc</td>
<td>0.514</td>
<td>0.461</td>
</tr>
<tr>
<td>% Imperviousc</td>
<td>0.033</td>
<td>0.046</td>
</tr>
<tr>
<td>% Mid-level vegc</td>
<td>0.001</td>
<td>0.059</td>
</tr>
<tr>
<td>% Water and wetlandsc</td>
<td>0.031</td>
<td>0.068</td>
</tr>
<tr>
<td>Sample size (N)d</td>
<td>30</td>
<td>20</td>
</tr>
<tr>
<td>No. mortalitiese</td>
<td>9</td>
<td>5</td>
</tr>
<tr>
<td>DSRf</td>
<td>0.990</td>
<td>0.990</td>
</tr>
<tr>
<td>DSR SEg</td>
<td>0.003</td>
<td>0.005</td>
</tr>
</tbody>
</table>

a Total area of site, where boundary is described as minimum convex polygon that connects all eastern bluebird nest boxes, buffered by 100 m.
b Linear edge (m) of boundary between all forest and grass landcover types per hectare.
c Percentage of each landcover type (digitized from aerial photographs) found within each predefined site boundary.
d No. of radio-tracked birds in 2008 and 2009 combined.
e Number of eastern bluebird fledgling mortalities at each site.
f Daily survival rate of eastern bluebird fledglings at each site, calculated using Program MARK.
g Standard error of daily survival rate for eastern bluebird fledglings at each site, calculated using Program MARK.

Field Procedures

Eastern bluebirds readily nest in man-made nest boxes and generally lay 2 clutches per season (Apr to May and Jun to Jul). We monitored nests throughout the field season across all sites, and tracked individuals from both first and second clutches, to evaluate the effects of fledging date on fledgling survival. We checked nest boxes approximately every 6 days and banded nestlings approximately 14–16 days after hatching. We banded nestlings with a United States Geological Survey (USGS) metal band and a unique combination of 3 plastic color bands (Perler Bead Company, Reading, PA). We also measured nestling unflattened wing chord to the nearest 0.1 cm using dial calipers and recorded mass to the nearest 0.1 g using a digital scale. Using a random numbers table, we selected one nestling from each of 156 broods to receive a transmitter, after excluding any nestlings weighing <26 g to avoid attaching a transmitter exceeding 5% of body weight (14.5% of nestlings excluded). We attached radio transmitters using a figure-8 elastic loop harness over the legs (after Rappole and Tipton 1991) and allowed nestlings to fledge naturally, usually 2–4 days later. In 2008, we made the harness entirely out of elastic beading cord (Hirschberg and Schutz & Co., Inc., Union, NJ) with the outer polyester sheath removed, and attached the harness to the transmitter with ethyl cyanoacrylate (Krazy GlueTM, Columbus, OH). In 2009, we implemented a new harness design that incorporated cotton thread that was intended to degrade and fall off after the study. The new harness had a similar weight to those used in 2008 but included a breakaway link (2 mm long) of 100% cotton locker hooking twine (M.C.G. Textiles, Chino, CA) fused to the elastic cord with ethyl cyanoacrylate.

We used 2 sizes of transmitters, 0.9 g and 1.25 g (Model BD-2, Holohil Systems, Ltd, Carp, Canada), with a battery life of 50 days and 70 days, respectively. With harness, these transmitters weighed approximately 1.0–1.35 g. Because we used 2 transmitter sizes, we were able to analyze the effect of transmitter weight on fledgling survival and included this as a factor in our analysis.

After fledging, we tracked birds using a folding 3-element Yagi antenna (Advanced Telemetry Systems, Isanti, MN) and a handheld receiver (Model R1000, 143–174 MHz, Communication Specialists, Inc., Orange, CA). We searched for each transmitter approximately every other day throughout the season, during daylight hours (between 0600 hours and 1900 hours). Unless we observed fledging directly, we assigned postfledging day 1 (day of fledging) as the day after the last nest check at which the nestling was present (i.e., if a bird was in the box on 1 May, and out of the box on 3 May, we assumed postfledging day 1 to be 2 May). At each search, we recorded each fledgling as dead or alive and took a GPS point of its current location. We attempted to take this point at the first location where we found a bird, even if we did not make a visual confirmation until later, so that we would not chase the birds and change their behavior.

We assumed mortality had occurred only if we recovered the transmitter with signs of predation or with enough of the fledgling’s body to conclude mortality had occurred. Predation occurred by either raptor (feathers, legs, and bands alongside the transmitter) or snake (transmitter recovered inside snake). In other cases we recovered the body intact and still attached to the transmitter.

We started each day’s tracking at the last known location and expanded in a circular pattern, first on foot or golf cart and then, if necessary, by car. For car tracking, we drove on all roads adjacent to the original site, and then expanded into more remote locations for ≥1 hr.

Statistical Analysis

We used Kaplan–Meier survival estimation to plot survival to 40 days postfledging for all tracked fledglings. Because we
relocated fledglings every other day, we assumed that the mortality had occurred on the day that we recovered the bird dead. We estimated daily survival rates (DSR) for tracked fledglings using nest survival models in Program MARK, which allow for uncertainty in the date of mortality. We coded each fledgling’s encounter history to include the date of fledging, the last day the bird was seen alive, the last day that the bird was looked for, the bird’s fate, and 8 covariates. The variables we evaluated were either discrete (Year and Site) or continuous (Age, Condition, Landcover, Fledge, Golf, and Trans). Because we wanted to evaluate whether certain variables had greater effects on fledgling survival using Akaike’s Information Criterion corrected for small sample sizes (AICc), we included Age and Year in all models (as these are known to affect fledgling survival) and we included the other covariates based on our hypotheses.

We included 2 covariates (i.e., Year and Age) in all models, as these 2 factors have been shown in many studies to affect fledgling survival. The covariate Year accounts for the inter-annual variation common in all biological systems (Monróes et al. 2002, Yackel Adams et al. 2006, Schmidt et al. 2008), whereas Age affects survival in almost every study of passerine fledging survival, with younger birds being more susceptible to mortality (Sullivan 1989, Anders et al. 1997, Kershner et al. 2004, Berkeley et al. 2007, Moore et al. 2010).

To account for variability between years in terms of fledging dates, we calculated ordinal dates of fledging with respect to the first clutch initiation date of the season (Fledge). Clutch initiation (ordinal day 1) occurred on 31 March 2008 and 7 April 2009. Fledging dates of tracked fledglings ranged from days 38 to 137. The variable Fledge accounts for seasonal differences in food availability and predation pressure and the use of ordinal dates corrects for inter-annual differences in onset of spring.

We created an index of prefledging body condition to indicate how heavy each bird was for its size using size-corrected mass (Condition). Using all nestlings measured at the 7 sites (n = 922 nestlings), we regressed mass on wing chord for each year separately. We stored and used the residuals from the overall regression for each year as the individual condition score for each tracked fledgling. Because we also used different sizes of transmitters, we included the weight of the transmitter (Trans) as a body condition-independent measure.

Because our sites were so variable, we wanted to determine if site could be a good predictor of fledgling survival, so we included individual sites as predictors (Site). We estimated golf exposure (Golf) by classifying each fledgling GPS location as either on or off of a golf course, based on the site boundaries described above. We divided the number of points on the golf course for each bird by the total number of locations for that bird to estimate the bird’s golf exposure score. Thus, a bird that fledged on a golf course but immediately moved off into surrounding habitat would have a low exposure score, whereas a bird spending its entire first 40 days on a golf course would have the maximum exposure score.

We used FRAGSTATSBATCH (Mitchell 2008) to calculate the percentage of each habitat type within a 300-m buffer around each nest box (Landcover). There were 6 different landcover types—forest, park-like forest, short grass, mid-level vegetation, impervious surface, and water. We always ran these 6 covariates together in models that included Landcover.

We created 18 nest survival models in Program MARK with different combinations of these variables. We used AICc to evaluate competing models; we considered the model with the lowest AICc score to be the best fit of the models we evaluated (Burnham and Anderson 2002). We interpret scaled AICc scores (∆AICc) and Akaïke weights (wi). Because there were multiple models that ranked highly, we also model-averaged the beta estimates for each variable. We then used intercept-only nest survival models in Program MARK to calculate average DSR for 2 fledgling groups, those that died because of predation (either snake or hawk) and those that died because of some other cause. Because we only classified birds as mortalities if we recovered the transmitter with some indication of cause of death, all birds included were either predated or not predated.

We used ArcGIS to analyze movements of all birds that survived to the end of the study (i.e., 40 days postfledging). In addition, each point where we located a bird was circumscribed by a circle with a radius of 30 m, and we calculated the habitat types found within the circle using FRAGSTATSBATCH. We then calculated the habitat types around the nest box using the same method and calculated the difference scores between what the fledglings used and what we found around their nest box. We binned these differences over 5-day intervals to better visualize whether fledgling habitat preferences changed as birds aged. We compared difference scores for each age group using an analysis of variance (ANOVA).

RESULTS

Golf course sites had more short grass than did reference sites (Table 1; Mann–Whitney U, Z = −2.12, P = 0.03). Golf course sites had higher edge density than non-golf sites, as expected because of their layout with forest-bordered fairways, but this difference was not significant (golf = 123.8, reference = 67.5, Mann–Whitney U, Z = −1.41, P = 0.16). Golf sites also averaged less forest, but this trend, too, was not significant (golf = 0.39, reference = 0.62, Mann–Whitney U, Z = −1.41, P = 0.16).

Over the 2 yr of our study, we tracked 156 bluebird fledglings (2008: n = 70, 2009: n = 86). Overall survival rate to 40 days postfledging was 65.4% (Fig. 3). The highest-ranked model in Program MARK included Age, Year, and Fledge. The top 5 models all contained fledging date as a factor and together accounted for 96% of the weights (Table 2). Because many top models potentially fit the data well, we model-averaged the beta estimates from this analysis so as to determine which variables best explained the variance in fledgling survival.

There were 2 significant beta estimates when considering fledgling survival: Age and Fledge (Table 3). Predictably, as fledglings got older, daily survival increased (β = 0.039, CI = 0.012–0.066). Setting other parameters equal to aver-
age values, this translates into a 1.3% increase in DSR between postfledging day 1 and postfledging day 40. Unexpectedly, as fledge date increased (i.e., later in the season), fledgling survival also increased ($\beta = 0.017$, CI = 0.004–0.030), indicating a 1.18% increase in DSR between the first and last fledge dates of the year. If we were to assume fledgling survival did not vary based on any other parameters, birds that fledged on the last day of the season would be 60% more likely to survive to 40 days postfledging than those that fledged on the first day. We found slight differences between the 2 years of the study, with fledglings in 2009 having lower survival than fledglings in 2008 ($\beta = -0.387$, CI = -0.961–0.187). The other variables, including exposure to golf courses (Golf), did not appear to influence fledgling survival.

We documented 54 mortalities over the 2 years of our study. Cause-specific daily fledgling survival rates did not vary significantly among sites (Fig. 4). Although raptors caused most predation events, snakes also killed fledglings at 5 geographically different sites, indicating that this was not specific to one snake or site. Similarly, we detected hawk predation (Buteo spp. or Accipiter spp.) at all sites, indicating hawks were ubiquitous enough in the study area that all fledglings were at risk. Non-predated birds were those we

Figure 3. Kaplan–Meier cumulative percent survival based on age postfledging for all eastern bluebird fledglings ($n = 156$) tracked in Williamsburg, Virginia, USA (2008 and 2009). Error bars indicate standard error.

Table 2. Akaike’s Information Criterion (AIC) ranking of Program MARK nest survival models used to estimate survival of eastern bluebird fledglings in Williamsburg, Virginia, USA (2008–2009).

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>$\Delta$AIC</th>
<th>$w_0$</th>
<th>K</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age + Year + Fledge</td>
<td>498.99</td>
<td>0.00</td>
<td>0.36</td>
<td>4</td>
</tr>
<tr>
<td>Age + Year + Fledge + Landcover</td>
<td>500.04</td>
<td>1.05</td>
<td>0.21</td>
<td>9</td>
</tr>
<tr>
<td>Age + Year + Fledge + Cond</td>
<td>500.36</td>
<td>1.36</td>
<td>0.18</td>
<td>5</td>
</tr>
<tr>
<td>Age + Year + Fledge + Golf</td>
<td>500.80</td>
<td>1.81</td>
<td>0.15</td>
<td>5</td>
</tr>
<tr>
<td>Age + Year + Fledge + Site</td>
<td>502.68</td>
<td>3.68</td>
<td>0.06</td>
<td>10</td>
</tr>
<tr>
<td>Age + Year</td>
<td>506.71</td>
<td>7.72</td>
<td>0.01</td>
<td>3</td>
</tr>
<tr>
<td>Age + Year + Trans</td>
<td>507.21</td>
<td>8.21</td>
<td>0.01</td>
<td>4</td>
</tr>
<tr>
<td>Age + Year + Cond</td>
<td>507.65</td>
<td>8.66</td>
<td>0.00</td>
<td>4</td>
</tr>
<tr>
<td>Age + Year + Golf</td>
<td>508.02</td>
<td>9.02</td>
<td>0.00</td>
<td>4</td>
</tr>
<tr>
<td>Age + Year + Site + Cond</td>
<td>508.21</td>
<td>9.22</td>
<td>0.00</td>
<td>4</td>
</tr>
<tr>
<td>Age + Year + Landcover + Site + Fledge + Cond + Trans + Golf</td>
<td>508.59</td>
<td>9.60</td>
<td>0.00</td>
<td>18</td>
</tr>
<tr>
<td>Age + Year + Landcover</td>
<td>508.85</td>
<td>9.86</td>
<td>0.00</td>
<td>8</td>
</tr>
<tr>
<td>Age + Year + Site + Golf</td>
<td>508.88</td>
<td>9.89</td>
<td>0.00</td>
<td>10</td>
</tr>
<tr>
<td>Age + Year + Cond + Golf</td>
<td>509.22</td>
<td>10.22</td>
<td>0.00</td>
<td>5</td>
</tr>
<tr>
<td>Age + Year + Landcover + Cond</td>
<td>509.27</td>
<td>10.28</td>
<td>0.00</td>
<td>9</td>
</tr>
<tr>
<td>Age + Year + Site</td>
<td>509.40</td>
<td>10.41</td>
<td>0.00</td>
<td>9</td>
</tr>
<tr>
<td>Age + Year + Landcover + Golf</td>
<td>510.81</td>
<td>11.81</td>
<td>0.00</td>
<td>9</td>
</tr>
<tr>
<td>Age + Year + Landcover + Site</td>
<td>513.40</td>
<td>14.41</td>
<td>0.00</td>
<td>14</td>
</tr>
</tbody>
</table>

$^a$ Akaike’s Information Criteria corrected for small sample size.
$^b$ Scaled AIC; $\Delta$AIC = 0.00 is interpreted as the best fit to the data among all models.
$^c$ Weight of evidence interpreted as a proportion. Weights across all models sum to 1.00.
$^d$ No. of parameters.
recovered still intact and attached to their transmitters, with no obvious signs of predation. With the exception of 2 in this category that collided with windows, we assumed these birds died of starvation or disease, but without necropsy their exact cause of death is unknown.

We lost approximately 10% of tracked fledglings (golf = 8, reference = 8) before their transmitter battery should have failed and censored these birds from the analysis at their last known age. Because we followed an extensive searching protocol whenever we lost a bird, and most disappeared near the end of their expected transmitter battery life, we believe that nearly all of these birds were lost because of transmitter failure. Although it is possible that these 16 individuals were killed by predators (and the transmitter damaged or carried off), we opted to censor them instead of assuming their fate.

Of the 156 tracked fledglings, 85 survived the 40-day observation period without suffering mortality or transmitter failure. As fledglings aged, they moved farther away from their natal nest box (Fig. 5). The difference scores calculated by comparing nest box habitat with habitat used during 5-day periods indicate that young fledglings used different landcover than their parents had for nesting; specifically, fledglings moved into more forested areas (Fig. 6a) and out of open short grass (Fig. 6b). These landcover differences

Table 3. Model-averaged beta estimates for each covariate used to explain variation in eastern bluebird fledgling survival in Williamsburg, Virginia, USA (2008–2009).

<table>
<thead>
<tr>
<th>Covariate</th>
<th>( \beta^a )</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>3.251</td>
<td>-406.618</td>
<td>413.120</td>
</tr>
<tr>
<td>Age</td>
<td>0.039</td>
<td>0.012</td>
<td>0.066</td>
</tr>
<tr>
<td>Year</td>
<td>-0.387</td>
<td>-0.961</td>
<td>0.187</td>
</tr>
<tr>
<td>Fledge</td>
<td>0.017</td>
<td>0.004</td>
<td>0.030</td>
</tr>
<tr>
<td>Trans</td>
<td>-0.005</td>
<td>-0.338</td>
<td>0.329</td>
</tr>
<tr>
<td>Condition</td>
<td>-0.013</td>
<td>-0.095</td>
<td>0.070</td>
</tr>
<tr>
<td>Golf</td>
<td>-0.026</td>
<td>-0.389</td>
<td>0.338</td>
</tr>
<tr>
<td>Landcover</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forest</td>
<td>-0.305</td>
<td>-410.173</td>
<td>409.562</td>
</tr>
<tr>
<td>Park</td>
<td>1.530</td>
<td>-408.387</td>
<td>411.446</td>
</tr>
<tr>
<td>Short</td>
<td>-0.590</td>
<td>-410.461</td>
<td>409.282</td>
</tr>
<tr>
<td>Imperv</td>
<td>-0.956</td>
<td>-410.840</td>
<td>408.929</td>
</tr>
<tr>
<td>Mid-level</td>
<td>1.492</td>
<td>-408.432</td>
<td>411.417</td>
</tr>
<tr>
<td>Water</td>
<td>-0.363</td>
<td>-410.230</td>
<td>409.505</td>
</tr>
<tr>
<td>Site(^b)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>-0.005</td>
<td>-0.329</td>
<td>0.319</td>
</tr>
<tr>
<td>B</td>
<td>-0.015</td>
<td>-0.404</td>
<td>0.374</td>
</tr>
<tr>
<td>C</td>
<td>-0.006</td>
<td>-0.344</td>
<td>0.332</td>
</tr>
<tr>
<td>D</td>
<td>-0.016</td>
<td>-0.372</td>
<td>0.340</td>
</tr>
<tr>
<td>E</td>
<td>-0.011</td>
<td>-0.291</td>
<td>0.268</td>
</tr>
<tr>
<td>F</td>
<td>-0.025</td>
<td>-0.455</td>
<td>0.405</td>
</tr>
</tbody>
</table>

\(^a\) Model-averaged beta estimate for daily survival, calculated using the equations in Burnham and Anderson (2002). 
\(^b\) Beta estimate compared to Site G.

Figure 4. Cause-specific mortality for eastern bluebird fledglings on each study site (A–G) in Williamsburg, Virginia, USA (2008–2009). Daily survival rate (DSR) is separated into mortality due to predation (including hawk and snake) and mortality due to causes other than predation (body recovered intact). Error bars indicate 95% confidence interval.
scores approached zero as the fledglings aged, though fledglings generally continued to move farther away from their nest box (Fig. 5). Fledglings did not appear to select other landcover types (park-like forest, impervious surface, mid-level vegetation, water) in any different proportion than the nesting habitat (Fig. 6c–f). Birds initially moved into habitat that was more forested and less grassy than their natal habitat (paired samples \( t \)-test \([n = 85], \text{forest: } T = 4.319, P < 0.001, \text{grass: } T = -3.184, P < 0.002\)).

**DISCUSSION**

By using an information theoretic approach, we determined that fledging survival was best predicted by fledgling age and fledging date and was not affected by time spent on golf course sites. Cause-specific mortality rates also did not differ within different urbanized sites, but we did find that fledging eastern bluebirds moved away from the types of habitat used by their parents for nesting (i.e., grass edges) into more forested areas immediately after fledging. It appears that golf courses should not be considered differently than other urban recreational land in terms of their conservation value. Although our modeling results did not indicate that Site was a significant predictor of fledging survival, we did note that the least developed site in our study, a large state park, had the highest overall fledging survival. This may indicate that all our urbanized sites have lower fledging survival than would be expected in natural habitats, however, our study is not able to address this hypothesis directly.

It is important to note that the lack of effect of exposure to golf courses may have been a function of our location and choice of golf courses. Anecdotally, we observed that there were many small pockets of complex vegetation on each course where birds found cover, which may not be the case on more manicured golf courses in other regions. Additionally, a previous study on nestling bluebirds in this area documented little exposure to organophosphate pesti-

We found that nestlings that fledged later in the season survived better than those that fledged from early clutches. Although not the norm, an increase in fledging survival later in the season has been documented at least once before; great tits (Parus major) showed year-to-year variation in whether it was beneficial to fledge early or late in the season (Monró et al. 2002). More commonly, studies document no seasonal differences in fledging survival (Anders et al. 1997) or a decrease in fledging survival later in the season (Verboven and Visser 1998, Naef-Daenzer et al. 2001, Gruebler and Naef-Daenzer 2008). The proximate cause for later birds surviving better is probably some combination of factors including: decreased predation, decreased brood size, longer parental investment, increased egg size, and weather-related mortality.

Because most of the early-season mortality was due to predators, seasonal variation in fledging survival may have been linked to behavior of predators, especially hawks. Raptors we commonly observed at the study sites were Cooper’s (Accipiter cooperii), red-shouldered (Buteo lineatus), and red-tailed (Buteo jamaicensis) hawks. Generally, accipiters are considered primarily predators of birds, whereas the Buteo hawks prey on mammals, reptiles, and amphibians more often than on birds (Curtis et al. 2006, Dykstra et al. 2008, Preston and Beane 2009). We observed Cooper’s hawks chasing songbirds at our sites; we believe this species was responsible for most fledgling deaths. Cooper’s hawks initiate clutches between early and late April and their nesting period would fall sometime between 1 May and 1 July (Curtis et al. 2006). Thus, the time period when Cooper’s hawks provision their young corresponds with the time of highest hawk predation on bluebird fledglings. Although we did not detect Cooper’s hawks provisioning their young with bluebird fledglings, it is reasonable to expect that fledglings provided easy sources of prey for nesting hawks early in the season.

Weather differences can also potentially explain the differences in fledging survival we documented between 2008 and 2009. The breeding season of 2008 was hotter, whereas the breeding season of 2009 was wetter. The average monthly high temperature was higher in 2008 by 3.4° C in June and 1.8° C in July. From May to August 2009, the study area received an average of 2.1 times the amount of rain than during that month in 2008 (Keck Lab Weather 2009). The increase in precipitation may have been a cause of the increased mortality in 2009, as birds, especially perch and dive hunters such as bluebirds, cannot hunt in rainy weather. Further, rain may affect the fledgling’s ability to thermoregulate efficiently, making it more susceptible to predation. The combination of low foraging opportunity and lowered body temperature could have reduced fledging survival in 2009.

**Figure 5.** Average distance fledgling eastern bluebirds in Williamsburg, Virginia moved away from the natal nest box, based on age postfledging (2008–2009). \(N\) is the number of locations used for average, with some birds showing >1 location within an interval.
Figure 6. Eastern bluebird fledgling landcover use across all sites in Williamsburg, Virginia, USA (2008–2009). Points are average percent difference score (from the habitat around the fledgling's natal nest box) and error bars represent 95% confidence interval of the mean. Difference scores are compared using an analysis of variance (ANOVA) for a) forest (ANOVA, $F_{(8,1817)} = 3.730, P < 0.001$), b) short grass (ANOVA, $F_{(8,1817)} = 3.350, P = 0.001$), c) mid-level vegetation (ANOVA, $F_{(8,1817)} = 2.025, P = 0.040$), d) park-like forest (ANOVA, $F_{(8,1817)} = 1.060, P = 0.389$), e) impervious (ANOVA, $F_{(8,1817)} = 0.519, P = 0.843$), and f) water (ANOVA, $F_{(8,1817)} = 0.622, P = 0.760$). Asterisk represents scores that are significantly different from zero (i.e., different than natal nest box habitat). Letters represent differences in habitat use between intervals for landcover categories with significant ANOVA results ($P < 0.05$), based on post hoc Bonferroni test.
Body condition had little effect on fledgling survival to 40 days postfledging, even though fledgling birds must use a large amount of energy to avoid predators and build up flight muscles. It is possible that the lack of effect was the result of poor correspondence between the condition measure and actual health, vigor, and long-term growth trajectories of fledglings. Other postfledging survival studies have shown a similar lack of correlation between body condition and fledgling survival (Anders et al. 1997, Berkeley et al. 2007). Although the common assumption is that heavier nestlings survive better (Krementz et al. 1989, Yackel Adams et al. 2006), in the presence of hawk predation, stabilizing selection for intermediate fledgling mass may occur because a heavier mass may make it harder for birds to maneuver and escape from predators (Adriaensen et al. 1998). Further research on this question is warranted, possibly with a more reliable body condition measurement than mass-corrected wing chord. Although we chose this commonly used method for its ease of use in the field, wing length and mass are not always reliable predictors of body condition (Green 2001). Additionally, because we measured birds between 14 days and 16 days posthatch, there may be age-related variability that we did not account for.

We did not detect an effect of transmitter weight on mortality. Because we used transmitters that ranged 2.9–5.2% of preflighting nestling body mass, we are able to compare transmitters close to the 3% cutoff cited most recently by the USGS Bird Banding Lab (North American Bird Banding Manual 2010) to those approximating the widely used 5% cutoff for small passerines suggested from an experimental study (Caccamise and Hedin 1985). Although we have no information on birds without transmitters, we observed no difference in fledgling survival between birds with transmitters corresponding to the older or newer set of guidelines, indicating that all birds were either unaffected or handicapped equally.

We reinforce the findings of Sullivan (1989) that fledglings tend to suffer the highest level of predation shortly after fledging and later succumb to other forms of mortality. Because we conducted no necropsies, we cannot conclusively determine cause of death in instances where we found the fledgling’s body intact; starvation or disease seem likely explanations. Types of mortality did not appear to vary among sites, suggesting that predation and mortality rates were similar in the various types of modified habitats we explored.

Hawks were the most frequent predator, as found in other studies of fledgling survival (Anders et al. 1997, Naef-Daenzer et al. 2001, Cohen and Lindell 2004, Yackel Adams et al. 2006, Whittaker and Marzluff 2009). Hawks preyed on fledglings less frequently as bluebirds aged, probably because bluebirds fledge while still weak flyers and are therefore most vulnerable to predators before they have mastered flight. Snakes (eastern black rat snake [Pantherophis alleghaniensis], black racer [Coluber constrictor]) killed fledglings of different ages (range 2–42 days postfledging) 5 times, both early and late in the season. Both species are common in Virginia forests (Pinder and Mitchell 2007). Although cats killing birds have a major effect on fledgling survival in other urban areas (Dauphiné and Cooper 2010), we did not find any instances of domestic cat predation. Many of our study sites were adjacent to residential neighborhoods, but we rarely saw cats in the study area. Perhaps nest sites were far enough away from homes that fledglings did not encounter cats until they were older and more proficient at flying.

Our study is the first, to our knowledge, documenting habitat use of fledglings from artificial nest boxes. We found that fledglings moved into areas with more forest and less grass immediately after fledging and, as they aged, back into habitat much like their parents used for nesting (Fig. 6). As fledglings aged, they also moved farther away from their nest box (Fig. 5), so it does not appear that fledglings moved back into their parents’ territories but instead found other suitable habitat away from their parents.

Other studies have shown that fledglings prefer different habitat than their parents (Anders et al. 1998, Marshall et al. 2003, King et al. 2006), but it is especially notable within the framework of artificial nest boxes in urbanized landscapes. Few natural cavities exist in these manicured habitats, so bluebirds were attracted by nest box placement in areas where those birds would not, under natural circumstances, be able to nest. Wildlife managers typically view attraction of adult birds to nest boxes in previously unoccupied habitat as a completed conservation success story, but our results indicate that nest box placement in extremely manicured settings may make it difficult for fledging birds to find suitable habitat.

To understand how the urbanized environment is affecting all bird species, a comprehensive study of nest and fledgling survival on developed sites is needed for species other than the edge-specializing eastern bluebird. Although bluebirds readily nest in this environment, and thus make a convenient study organism, they do not fully represent the requirements of many declining bird species that are losing habitat because of urbanization. When we consider the undeveloped land that many of these human-modified habitats are replacing, it is important to consider if all the birds that once nested in that habitat can now find suitable nesting locations. Because we found variation between the 2 years of our study, we recommend that any researcher following survival in urbanized habitats conduct multiple field seasons.

**MANAGEMENT IMPLICATIONS**

The amount of time spent on golf courses did not appear to affect fledgling survival to 40 days in fledgling eastern bluebirds, a finding that has never been reported. Thus, programs that attract wildlife to golf courses, such as erection of nest boxes, are likely to promote successful reproduction and fledgling survival despite human disturbance, habitat fragmentation, and intensive use of pesticides typical of these sites. Although people frequently attract eastern bluebirds to nest boxes in areas where those birds would not naturally find a cavity (e.g., in fields with no trees), our results indicate that bluebirds require more forest habitat in the weeks immediately following fledging than they do as nesting adults. Bluebirds may be adapted to select nesting locations based solely on presence of a suitable cavity and nearby grassy areas.
in which to forage, which historically would have encouraged birds to place their nests at forest clearings and edges with suitable cover for fledglings. For golf course and other land managers trying to provide adequate habitat for birds, postfledging survival must be considered. Programs, such as Audubon International’s Cooperative Sanctuary Program (Audubon International 2010), that certify golf courses for conservation value, as well as agencies that promote nest box use, should consider suitability of the surrounding habitat for offspring survival.

**ACKNOWLEDGMENTS**

We thank the golf course and park managers for unlimited access to their sites and golf carts. Funding was provided by the National Fish and Wildlife Foundation Wildlife Links Grant (funded by the United States Golf Association), the College of William and Mary Biology Department, the Association of Field Ornithologists E. Alexander Bergstrom Memorial Award, Sigma Xi Grants-in-Aid of Research grant, Coastal Virginia Wildlife Observatory Joy Archer Student Research Grant, Williamsburg Bird Club Student Research Grant, and W&M Arts and Sciences Graduate Research Grant. K.C. Duerr, G.W. Gilchrist, and J.P. Swaddle provided helpful statistical consultation. The model averaging spreadsheet was provided online by B.R. Mitchell, S.A. Ware, R.M. Chambers, and the W&M Keck Environmental Field Lab provided meteorological data. T.M. Russell and S.E. Hamilton helped with ArcGIS analyses. Field assistants were funded by a National Science Foundation Undergraduate BioMath grant (0436318). We are grateful for the help of the BioMath interns from Thomas Nelson Community College M. Cagle, C. Carter, E. Davila-Reyes, and A. Sale and 2 anonymous reviewers for their helpful comments.

**LITERATURE CITED**


Associate Editor: David King.