

Reproductive phenology of the Acadian flycatcher (*Empidonax virescens*), a Neotropical migratory bird species, across an urban to rural gradient in central Ohio, USA

Daniel P. Shustack*

Abstract

The tendency for birds to reproduce earlier in the season has been observed in urban compared to rural populations, but these observations are limited primarily to species that spend all or most of the year in North America (i.e., resident or short-distance migrants). However, the factors that influence the reproductive timing of resident and short-distance migrants are unlikely to have the same influence on Neotropical migrants, a group of birds requiring conservation action due to long-term population declines. To understand the relationship between urbanization and reproductive phenology or timing of a Neotropical migratory bird species I (1) described the pattern of reproductive phenology in Neotropical migratory bird species across an urban to rural gradient, (2) assessed the reproductive consequences of varied breeding phenology, and (3) evaluated the extent to which alternative factors might explain differences in reproductive phenology. Data were collected between 2001 and 2007 on 35 different forests spanning an urban to rural gradient in central Ohio, USA. I used Acadian flycatchers (*Empidonax virescens*) as a model species. Birds were captured, marked, measured, released, and monitored throughout the breeding seasons.

The general pattern of breeding phenology was opposite that found in most resident and

*School of Environment and Natural Resources, The Ohio State University, 210 Kottman Hall, 2021 Coffey Road, Columbus OH 43210, I would like to thank my adviser, Dr. Amanda Rodewald, for her significant contributions to this research. Several anonymous faculty reviewers provided comments during the abstract, manuscript, and presentation review stages of this research. This paper was presented as part of the 22nd annual Hayes Graduate Research Forum at Ohio State University, April 12, 2008.

short-distance migrant birds. Birds arrived later, initiated clutches later, and finished nesting earlier than birds breeding in more urban forests. The combination of delayed clutch initiation and earlier completion of nesting activity resulted in an abbreviated nesting season associated with urbanization. Ultimately, this attenuated nesting season reduced the number of nests attempted and young produced by urban-breeding birds and shifted the timing of fledging, with the first fledglings being produced relatively later in the breeding season. The underlying causes of the phenological differences are less clear. One possibility supported by my data is that urban forests were disproportionately settled by small females, which initiated their first clutches later in the nesting season than larger females. This study provides the first evidence that urbanization is associated with attenuated nesting seasons for Neotropical migratory birds and that this shift in breeding phenology may have reproductive consequences.

Introduction

Populations of native birds may be impacted by urbanization in various ways. Readily obvious and often documented impacts include changes in bird abundance (McKinney 2002). Less easily detected are changes in the reproductive success of individuals nesting in urban areas, and various studies have documented either elevated or depressed nest survival in urban areas (Chace and Walsh 2006). At an even finer and less obvious scale, the timing of reproduction (i.e., phenology) may be mediated by urbanization. Indeed, advanced reproductive phenology has been documented in several species inhabiting urban areas. Yet, these examples typically are of resident or short-distance migrants. The precise causes of altered phenology remain obscure, although several factors have been suggested. Further, the impact of urbanization on reproductive timing in Neotropical migrants is unknown. The factors implicated

in causing advanced reproductive phenology in some species in urban areas focus on ameliorated winter conditions including elevated temperatures (i.e. the urban heat island effect), enhanced food supplies, increased conspecific densities, among others (Erz 1966; Eden 1985; Bowman and Wolfenden 2001; Rollinson and Jones 2002; Antonov and Atanasova 2003; Schoech and Bowman 2003). Because Neotropical migrants do not experience the winter conditions on their breeding grounds, many of the same factors that affect resident species may not be important influences on reproductive timing of Neotropical migrants.

Understanding how urbanization might influence reproductive behavior of Neotropical migrants is critical because this group of birds is of particular conservation interest due to long-term declines in populations (Sauer et al. 2007). My emphasis on seasonal timing of reproduction is especially important in the context of global change and considering that phenology can influence reproductive success and output (Perrins 1970). Therefore I attempted to address the following three questions:

- (1) What is the pattern of reproductive phenology in Neotropical migratory bird species across an urban to rural gradient?
- (2) What are the reproductive consequences of varied breeding phenology?
- (3) Which factors may cause the differences in reproductive phenology?

Methods

Landscape quantification

The percentage of developed land, agricultural land, forest, shrubland, wetland and open water was quantified within a 1-km radius area from the center of each study site using recent (2002–04) digital orthophotos (i.e. similar to aerial photos) available from county auditors (Fig.

1). In addition, I determined the number of buildings in each 1-km buffer based on data available from each county and I corroborated these counts with visual inspection. I used a “landscape” of 1-km radius because this area has been shown to be associated with bird communities in other studies (Tewksbury, Hejl and Martin 1998; Saab 1999; Rodewald and Yahner 2001; Rodewald and Bakermans 2006), is commonly used in conservation efforts and is larger than the average territory size of Acadian flycatchers breeding in the study sites used in this research (Bakermans and Rodewald 2006). A principal components analysis performed on five landscape variables describing development in the landscape produced a first principal component that explained 80% of the variation among sites (eigenvalue = 3.99). I hereafter refer to this first component as the ‘urban index.’ The urban index loaded positively for the number of buildings (0.92), percentage of cover by roads (0.94), pavement (0.90) and lawn (0.88), but loaded negatively for percentage of cover by agriculture (−0.83).



Fig. 1. Digital orthophoto of one of the forested study sites where Acadian flycatchers were monitored between 2001-2007. Different land uses visible in the area surrounding the forest patch include forest, roads, agriculture, and residential development. The large circle represents a 1-km buffer from the center of the site (marked with red dot) and represents the area described as the “landscape” for each site.

Field Methods

Between 2001-2007 a total of 35 mature riparian forests were monitored for Acadian flycatcher activity, although nesting activity was only found on 22 of these sites. The 35 sites were selected to represent a landscape gradient from highly urban to highly rural land uses surrounding each forested site. By sampling forests along this urban to rural gradient I was able to use a regression-based approach in the analyses (see *Data Analysis* below). We used the Acadian flycatcher (Fig. 2a) as a model species for Neotropical migratory bird species because it is a relatively commonly breeder in this study system (Bakermans and Rodewald 2006). The sites were located in central Ohio and range from central Columbus, OH, to ~45 km from the central city, thus these sites extended into highly rural/exurban landscapes. Beginning in early May each year, each site was intensively searched for Acadian flycatchers. Throughout the breeding season, assistants and I attempted to capture and band both male and female Acadian flycatchers. We measured the length of the tarsus (mm) and the wing chord (mm) on each individual. We combined the tarsus and wing length into one variable “body size” by using the first component of a principal components analysis with these two variables. The eigenvalue of the first component was 1.48 and explained 74% of the variation among birds. Each bird was marked with a unique combination of colored plastic bands in order to monitor each individual throughout the breeding season (Fig. 2b).

We attempted to locate and monitor all nesting attempts of every Acadian Flycatcher at each site. Nest searching efforts began 2–3 weeks before nesting began to ensure that the earliest nests were found. Once found, each nest was checked every 2–5 days by directly examining nest contents (e.g. eggs or nestling). If nests were too high to directly observe the contents,

extended observations of parental behaviors indicated whether adults were incubating eggs, feeding young, or tending fledglings.



Fig. 2a, b. Adult Acadian flycatcher, the model species in this study. The Acadian flycatcher breeds in forests through eastern North American and winters in Central America and Northern South America (Whitehead and Taylor 2002). The photo on the right shows the legs of an Acadian flycatcher with a unique combination of colored plastic and metal leg bands. The plastic bands allow for visual identification of each individual bird without recapturing it.

For each bird I determined season-long reproductive activity including number of nesting attempts, nest fates, and number of fledged. Individual birds were intensively monitored but there were some breeding pairs for which nesting attempts were missed. In addition, field teams were able to monitor more breeding pairs than we were able to individually band, however, once settled at a site, breeding birds tend to use the same area for the whole season (D. P. Shustack pers. obs). We were able to use some nesting information from unmarked birds in addition to the individually marked birds. Thus, the sample sizes were different for estimating nest survival (probability that a nest will not be depredated), annual reproductive productivity (number of fledglings produced in one breeding season), and number of nesting attempts per female.

Data Analysis

I determined the date the first egg was laid in each nest by observing the nest during nest building and then again after eggs had been laid. In cases where nests were found after all eggs had been laid, I back-calculated to the date of clutch initiation by estimating a 14 day incubation period and a 14 day nestling period (Whitehead and Taylor 2002). In many cases it was not possible to directly observe nest contents so I used female behavior (i.e. nest building activity and incubation) to indicate when eggs had been laid. I determined the median date of the clutch initiations for each year. The median clutch initiation dates across years varied by only 5 days (day of year 157, 157, 152, 152, 157, 155, 157 for 2001-2007 respectively) however, I standardized the day of year for all years to 2006.

I averaged clutch initiation dates from each year to derive one value per site. I used Proc Genmod (SAS 9.1) to regress dates of clutch initiation, male and female size, on the urban index. I used logistic regression (PROC GENMOD, Distribution=binomial, SAS version 9.1) to assess probability of renesting and probability of males and females returning to a site, both of which have binary outcomes. In order to assess the relationship between the number of fledglings, male and female size, and urbanization I used Poisson regression (PROC GENMOD, Distribution=Poisson, SAS version 9.1). Kolmogorov-Smirnov tests (PROC NPAR1WAY, SAS version 9.1) were used to assess the difference in cumulative probability functions describing the proportion of females nesting over the course of the breeding season and the timing of when fledglings were produced in urban versus rural forests. For the Kolmogorov-Smirnov tests I divided the sites into two groups, urban (>0 on urban index) and rural (<0 on urban index). I used a modified logistic regression call logistic exposure (PROC GENMOD, SAS version 9.1; Shaffer 2004) to estimate nest survival (i.e. whether a nest survives to produce fledglings or not).

The logistic exposure method allows for estimation of nest survival rates as a function of covariates while adjusting for different number of days of observation for each individual nest. Based on these initial investigations I further examined the independent effect of female body size on clutch initiation date by first regressing clutch initiation date of each individual female on the urban index and calculating the residuals. I then regressed the residuals on female body size to determine the independent effects of female body size.

Results

The date of clutch initiation was positively related to the urban index for both the earliest ($X^2=8.21$; $P=0.0042$; $N=22$ sites) and median clutch initiations at a site ($X^2=7.79$; $P=0.0053$; $N=21$ sites; Fig. 3). Both regressions indicate a delay in clutch initiation of about eight days between the most rural and most urban sites. Clutches were initiated later into the summer in more rural forests as well ($X^2=11.26$; $P=0.0008$; $N=22$ sites) with clutches being initiated up to ~20 days later in the most rural sites compared to the most urban sites. When

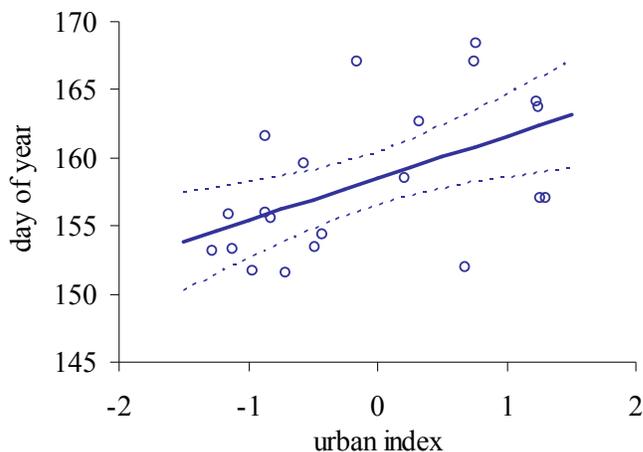


Fig. 3. Relationship between site median clutch initiation date averaged over 2001-2007 and the urban index (where more positive values on index represent more urban landscapes). Bold line is the regression line and dashed lines are 95% confidence intervals. Open circles are the data points for each site.

considering the nesting histories of individual females, there was a significant relationship between the window of time for egg laying (calculated as the number of days between their first clutch initiation and last clutch initiation of each female) and the urban index ($X^2=10.83$; $P=0.001$; $N=178$ female nesting histories) with females at the most rural sites having ~28 days between first and last clutches and the most urban sites having ~13 days (i.e. a shorter window of time for egg laying in more urban forests). The attenuated nesting season was also evident through the lower probability of renesting as the season progressed and as a result of urbanization (urban index $X^2=5.6$; $P=0.018$; day of year $X^2=94.41$; $P<0.0001$; $N=365$ possible renesting opportunities; Fig. 4). Further, the overall shorter length of nesting activity (i.e., including time spent attending to eggs and nestlings) by females ($N=147$ rural female nesting histories; $N=37$ urban female nesting histories) decreased both at the beginning of the breeding season ($D=0.301, P=0.0093$) and at the end ($D=0.240, P=0.066$).

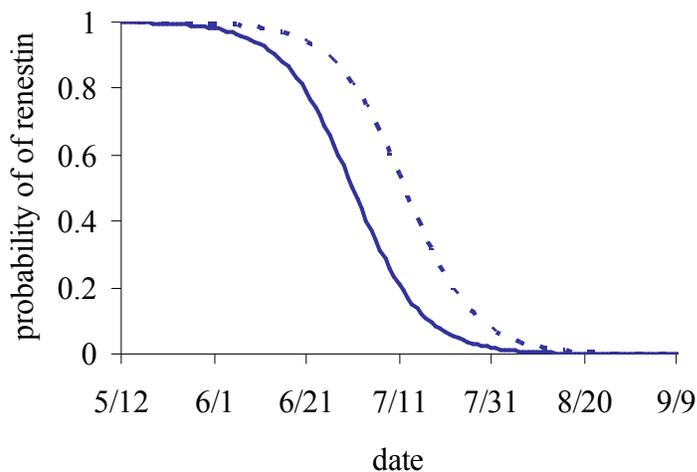


Fig. 4. Probability of renesting (making a new nest and laying another clutch of eggs after the prior nest either failed or successfully fledged young) based on a logistic regression model with day of the year and urban index as predictor variables. The dashed line reflects the probability of renesting for the most rural site and the bold line represents the probability of renesting at the most urban site in our study. Notice that the urban line drops off much sooner than the rural line indicating a shortened nesting season at urban sites.

As females began nesting later in the season, the number of fledglings they produced decreased ($X^2=11.0$; $P=0.0009$; $N=226$ season long productivity values), which corresponded to a decrease of ~ 0.7 fledglings for a three week delay in clutch initiation (Fig. 5). Further, the number of fledglings was also related to the urban index ($X^2=5.26$; $P=0.022$; $N=226$ season long productivity values) which corresponds to a decrease of ~ 0.6 fledglings from the most rural to the most urban sites. Fledglings were produced over a shorter time frame in urban versus rural sites, although this difference was not significant ($D=0.148$; $P=0.258$; $N=273$ rural fledglings, $N=56$ urban fledglings). As females initiated nesting later in the season, they made fewer nesting attempts ($X^2=16.72$; $P<0.0001$; $N=184$ female nesting histories) with a decrease in ~ 1.2 total nesting attempts over the first three weeks of the season.

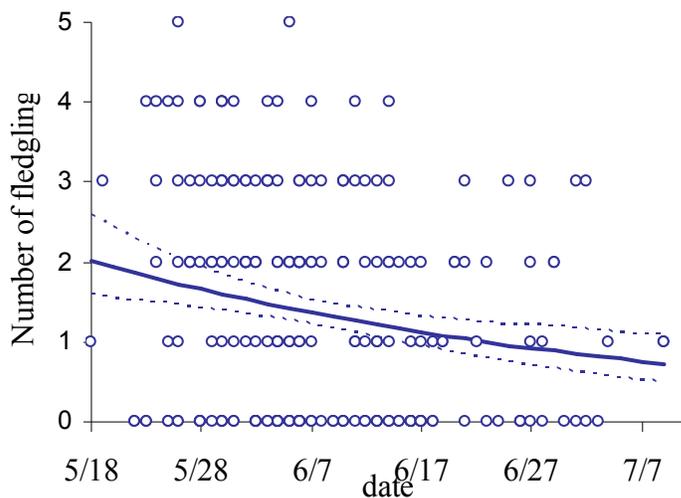


Fig. 5. Number of fledglings produced by a female as a function of when she first initiated her clutch for the season. The x axis represents the date that a given female initiated her first clutch and the y axis is how many fledglings were produced over the course of the whole breeding season. The bold line is the fit Poisson regression line and the dashed lines are the 95% confidence intervals. Notice that as a female initiates her first clutch later in the season she ultimately produces fewer fledglings for the year.

Smaller females initiated nesting later ($X^2=7.67$; $P=0.006$; $N=64$ females nesting histories) which corresponds to a 12 day difference over the range of female sizes observed. The relationship was almost significant for males ($X^2=3.71$; $P=0.054$; $N=153$ nesting histories) and in the same direction as for females. Females tended to be smaller in more urban forests ($X^2=4.78$; $P=0.029$; $N=48$ females) but there was not a significant pattern for males ($X^2=1.47$; $P=0.226$; $N=93$ males). Probability of nest survival increased over the season ($X^2=4.35$; $P=0.037$; $N=2633$ nest check intervals) with 30% success rate earliest in the season increasing to 55% in early August (Fig. 6).

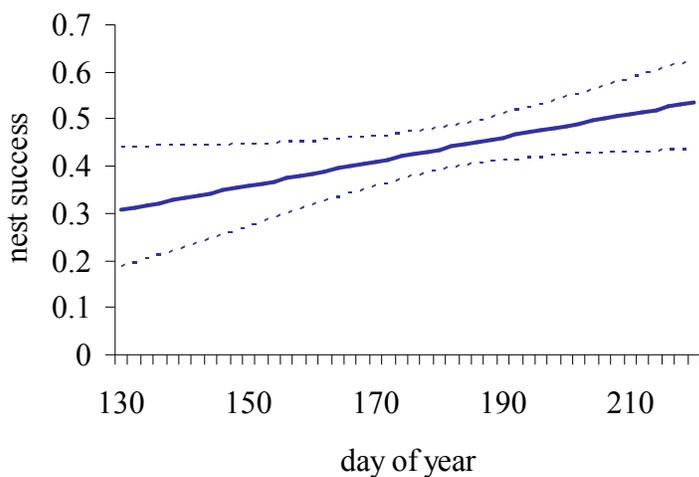


Fig. 6. Probability of nest success over the course of the breeding season as estimated by a logistic exposure model (Shaffer 2004). Notice that nest success is lowest earliest in the season.

However, nest success was not related to the urban index ($X^2=0.85$; $P=0.358$; $N=2633$ nest check intervals). Nest success was negatively related to female size ($X^2=3.92$; $P=0.048$; $N=760$ nest check intervals) but there was not a significant relationship for males ($X^2=0.31$; $P=0.578$; $N=1846$ nest check intervals). Smaller females tended to have more fledglings per successful individual nesting attempt ($X^2=4.71$; $P=0.030$; $N=136$ nest attempts) but there was no pattern with male size ($X^2=0.00$; $P=0.968$; $N=326$ nest attempts). Over the course of the whole season,

there was not a pattern between female size ($X^2=1.44$; $P=0.231$; $N=66$ season long productivity values) or male size ($X^2=1.71$; $P=0.191$; $N=165$ season long productivity values) and the total number of fledglings. The probability of either females or males returning to the study site in subsequent years was not related to body size, urban index or when they initiated nesting (all $P_s > 0.39$; $N=54$ female return opportunities; $N=134$ male return opportunities). After controlling for the effect of urbanization, there was still an effect of female body size on timing of nest initiation with smaller females starting later ($X^2=5.06$; $P=0.025$; $N=64$ female nesting histories).

Discussion

This study expands our current understanding of how urbanization influences bird populations. Specifically, these results demonstrate that the effects of urbanization on the timing of bird breeding are not consistent across species. I showed that one Neotropical migratory species, the Acadian Flycatcher, experienced delayed clutch initiation as the amount of urban development in the landscape increased. In contrast, previous studies of avian breeding phenology in urban areas have showed that birds in urban areas, specifically resident and short-distance migrant species, tend to advance their breeding phenology (i.e., nest earlier) compared to rural populations (Erz 1966, Eden 1985, Bowman and Wolfenden 2001, Rollinson and Jones 2002, Antonov and Atanasova 2003, Schoech and Bowman 2003). Our study provides the first example of the effects of urbanization on the breeding phenology of a Neotropical migratory bird species.

Some fitness consequences of delayed reproduction were evident in this population. Delayed initiation of nesting was associated with fewer fledglings being produced over the season. A female that initiated nesting in the earliest parts of the season (e.g. mid-May) would

on average expect twice as many fledglings as a female initiating clutches five or six weeks later (i.e. two versus one fledgling for the entire breeding season). The benefits of initiating nesting early in the spring can arise in at least four ways. First, clutches laid earlier in the spring tend to contain a greater number of eggs than later clutches (Perrins 1970), which maximizes the potential number of fledglings. However, I do not have data on clutch size because contents of many high nests could not be viewed. Second, by nesting earlier in the spring there is more opportunity to initiate a second nest following either a successful or failed first nesting attempt (Barba et al. 1995). Indeed, birds nesting in the first part of the season attempted on average one or more nests than birds which initiated first clutches three or more weeks later. Third, early nesting allows fledglings from early nests more time to gain experience, improve body condition, and prepare for migration in the following autumn. The difference can be quite striking, as fledglings coming out of a nest in late June would have two additional months to prepare for migration than fledglings in late August. Although fledging of young started earliest at rural sites, there was not an overall significant pattern to the timing of when fledglings were produced. Other studies have documented higher survival rates among birds born early versus late in the season (Perrins 1970, Barba 1995, Moller et al 2006, Vitz 2008). A fourth benefit to early breeding is conferred to adults which successfully breed early can complete their nesting earlier and leave more time post-breeding to molt and prepare for migration. I did not find any patterns in timing or likelihood of return relative to breeding phenology.

Given these potential benefits of early breeding attempts, I found that nest success paradoxically was lowest early in the season – a pattern that likely dampened the effect sizes that I detected. Interestingly, despite early nests having the lowest success rates of the season, early-breeding pairs still derived some benefits from their early attempts.

What accounts for the pattern of delayed initiation of nesting in urban forests? The main driver of this pattern seems to be that a greater proportion of small females select urban forests for nesting and that smaller females tend to initiate nesting later. The effect of female size persisted even after controlling for amount of urbanization. Thus, not only did urbanization delay nest initiation, but smaller females initiated nesting later than larger females even at the same degree of urbanization. While conceptually attractive, the assumption that smaller females are lower quality birds has mixed support in the literature. Murphy (2007) found that female size was negatively related to lifetime reproductive success in Eastern Kingbirds (*Tyrannus tyrannus*). In my study system, smaller females initiated nesting significantly later, but smaller females were actually more successful breeders than larger females in terms of nest success and number of fledglings per attempt. This pattern suggests that large females out compete small females for nesting areas (perhaps by earlier arrival after migration or through direct interactions) and thereby force smaller females into less desirable habitats (i.e. more urban forests) leading to delayed reproductive timing through increase time to find a territory and a mate. Perhaps once a breeding area is secured smaller females have other advantages such as securing food for their young or increased agility in nest defense. However, these positive aspects of smaller females may be at least partially counterbalanced by the reduced probability of re-nesting and the lower productivity of birds in urban forests. Elucidating the mechanisms of these fine-level interactions and effects will require further study.

Clearly the effects of urbanization on bird populations are complex. These results demonstrate that the effects of urbanization can not necessarily be generalized across species with different migratory strategies. In this research I demonstrated that reproductive timing is delayed in urban areas and that delayed nest initiation has fitness consequences in terms of the

number of offspring produced. The cause of this pattern of urbanization appears to be related to individual variation within the species coupled with variation in habitat quality between urban and rural forests.

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