



ATTENUATED NESTING SEASON OF THE ACADIAN FLYCATCHER (*EMPIDONAX VIRESCENS*) IN URBAN FORESTS

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ABSTRACT.—Resident or short-distance migrant birds that occupy urban habitats are known to breed earlier than nearby rural populations, but similar data on long-distance tropical migrants are lacking. To understand the relationship between urbanization and reproductive phenology of a tropical migratory bird species, we (1) described variation in patterns and consequences of breeding phenology across an urban-to-rural gradient and (2) assessed underlying reasons why phenology may be related to urbanization. We studied Acadian Flycatchers (*Empidonax virescens*) between 2001 and 2007 in 35 forests spanning an urban-to-rural gradient in central Ohio. The general pattern of breeding phenology was opposite of that described for most resident and short-distance migrant birds. At higher levels of urbanization, site arrival dates and clutch initiations were later and cessation of breeding was earlier than in forests of more rural landscapes. The phenological shifts reduced the length of the nesting season in urban landscapes, with the result that birds in more urban landscapes initiated fewer nests and fledged fewer young than their rural-breeding counterparts. Underlying causes of phenological differences are less clear. One possibility supported by our data is that urban forests are less desirable and selected later by smaller females, which initiated 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 tropical migratory birds and that this shift in breeding phenology may have reproductive consequences. *Received 25 June 2008, accepted 16 October 2009.*

Key words: Acadian Flycatcher, breeding phenology, clutch initiation, *Empidonax virescens*, individual quality, nesting phenology, reproductive timing, urbanization, urban-to-rural gradient.

Temporadas de Cría Atenuadas en Bosques Urbanos en *Empidonax virescens*

RESUMEN.—Se sabe que las aves residentes o migratorias de distancias cortas que ocupan ambientes urbanos se reproducen más temprano que las de las poblaciones rurales cercanas, pero no existen datos similares para aves tropicales que migran a lo largo de grandes distancias. Para comprender la relación entre la urbanización y la fenología reproductiva de una especie de ave tropical migratoria, (1) describimos la variación en los patrones y las consecuencias de la fenología reproductiva en un gradiente urbano-rural y (2) evaluamos las razones por las cuales la fenología podría estar relacionada con la urbanización. Estudiamos poblaciones de *Empidonax virescens* entre 2001 y 2007 en 35 bosques ubicados en un gradiente urbano-rural en el centro de Ohio. El patrón general de fenología reproductiva fue opuesto al descrito para la mayoría de las aves residentes y migratorias de distancias cortas. A mayores niveles de urbanización, las fechas de arribo en los sitios de cría y de inicio de nidadas fueron posteriores y el cese de la reproducción fue más temprano que en los bosques ubicados en paisajes más rurales. Los cambios fenológicos redujeron la extensión de la temporada de anidación en los paisajes urbanos, lo que condujo a que las aves de los paisajes más urbanos iniciaran menos nidos y produjeran menos volantones que las que criaron en ambientes rurales. Una posibilidad apoyada por nuestros datos es que los bosques urbanos son menos deseables y fueron seleccionados más tarde y por hembras más pequeñas, las cuales iniciaron sus primeras nidadas más tarde en la temporada de cría que las hembras más grandes. Este estudio provee la primera evidencia de que la urbanización está asociada con temporadas de anidación atenuadas en aves migratorias tropicales y que este cambio en la fenología de cría podría tener consecuencias reproductivas.

POPULATIONS OF NATIVE birds may be affected by urbanization in various ways. The most obvious and often documented effects 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, Chamberlain et al. 2009). An even less obvious but potentially important consequence of urbanization includes a shift in the seasonal timing of reproduction (i.e., phenology). Advanced seasonal reproduction associated with urbanization has

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been noted in several species (Chamberlain et al. 2009), including Wood Pigeon (*Columba palumbus*; Cramp 1972), Florida Scrub-Jay (*Aphelocoma coerulescens*; Bowman and Woolfenden 2001), Australian Magpie (*Gymnorhina tibicen*; Rollinson and Jones 2002), European Blackbird (*Turdus merula*; Partecke et al. 2005), and Cooper's Hawk (*Accipiter cooperii*; Boal and Mannan 1999). Interestingly, the shifts in breeding phenology can occur over large spatial extents and within adjacent developed and nondeveloped areas. For example, Common Magpies (*Pica pica*) that nested in urban areas of Sofia, Bulgaria, initiated clutches 5 days earlier, on average, than Magpies in rural habitats that were within 1 km (Antonov and Atanasova 2003). In Britain, Perrins (1970) noted that "many species" breed earlier in gardens than in neighboring woodlands.

While many studies have demonstrated that individuals that breed earlier in the year have higher reproductive success than later-breeding individuals (Norris 1993, Verlhurst et al. 1995, Smith and Moore 2005), fitness benefits associated with advanced breeding in urban areas are rarely investigated. Although urban Common Magpies nested before rural ones and produced more fledglings, nest initiation dates were not associated with hatching success or fledging success (Antonov and Atanasova 2003). Suburban Australian Magpies produced no more fledglings than rural Common Magpies despite breeding almost 2 weeks earlier (Rollinson and Jones 2002). On the other hand, nest success for Florida Scrub-Jays tended to be higher earliest in the season, at a time when suburban Florida Scrub-Jays were more likely to initiate nests than later-nesting wildland Florida Scrub-Jays (Bowman and Woolfenden 2001).

Advancement of breeding date in urban areas has been linked to elevated temperatures (i.e., the urban heat-island effect; Erz 1966, Eden 1985, Rollinson and Jones 2002) that may reduce overwinter energy stress in urban birds (Whyte and Bolen 1984) or promote early development of vegetation and food resources (Eden 1985). Higher spring temperatures also can hasten development of the testicles (Jones 1986) and eggs (Meijer et al. 1999), as might anthropogenic lighting (Bartholomew 1949, Gorski and Kotlarz 1997). Moreover, anthropogenic food sources (e.g., exotic plants, feeders, and refuse) may provide the resources needed for urban birds to achieve breeding condition sooner than rural birds (Cramp 1972, Schoech and Bowman 2003), whereas social facilitation arising from high densities of urban conspecifics might similarly stimulate early reproduction (Jerzak 1995, Silverin and Westin 1995).

Examples of advanced reproduction in urban areas are limited to resident or short-distance migratory species that return to the breeding grounds weeks before they initiate egg laying (Chamberlain et al. 2009). Because long-distance migrants do not experience winter and early spring conditions on their breeding grounds, many of the factors that affect resident species may not influence the reproductive timing of tropical migrants (Ramenofsky and Wingfield 2006). Other factors could be important determinants of reproductive timing. For instance, urban forests might be of lower quality and thus provide fewer resources such as food, nest sites, or building materials. Thus, lower habitat quality in urban areas might constrain reproduction in comparison with higher-quality rural sites. Timing of reproduction can also be influenced by the attributes of the individual bird. One common pattern is that older birds tend to initiate reproduction earlier than younger

individuals, perhaps because of increased experience (Nol and Smith 1987, Martin 1995). As a consequence, earlier breeding could result from a preponderance of older individuals in a particular patch or site. Besides age and experience, certain individuals might be inherently of higher quality than others and, therefore, be able to reproduce sooner (Hochachka 1993, Moyes et al. 2009).

To better understand the effects of urbanization on the reproductive phenology of tropical migratory birds, we studied an Acadian Flycatcher (*Empidonax virens*) population breeding in forest fragments in central Ohio. The Acadian Flycatcher breeds in eastern North America and winters in Central America and South America. We used the Acadian Flycatcher as a model for tropical migratory bird species because it occurs commonly across the urban-to-rural gradient (Bakermans and Rodewald 2006). In our study system, male Acadian flycatchers start to return around the first or second week of May. Females typically arrive 3–10 days after males and begin nesting within 3–7 days of being detected at a site. Females build the nest and incubate the eggs (usually 3, sometimes 2) without male assistance. Males help feed the nestlings and fledglings, especially when males have only 1 mate. Females readily reneest after failure and will regularly double brood. Males are commonly paired with only 1 female, but about 15–20% may mate with 2 or 3 females (Whitehead and Taylor 2002, Rodewald and Shustack 2008).

The purpose of our research was to (1) describe variation in patterns and consequences of breeding phenology in a tropical migratory bird species that nests across an urban-to rural-gradient and (2) assess underlying reasons why phenology may vary with urbanization. Because our previous work in this system suggested that urban forests may provide lower-quality habitat (Bakermans and Rodewald 2006), we expected that Acadian Flycatchers would nest later in the most urban forests and that late-nesting individuals would have lower productivity. We lacked sufficient background information to make precise predictions as to specific causes of the altered reproductive timing, especially as related to the relative contributions of habitat quality and bird quality.

METHODS

Field methods.—From 2001 through 2007, we studied populations of Acadian Flycatchers in 35 mature riparian forest fragments in central Ohio that were embedded along a rural-to-urban gradient (Fig. 1). Acadians Flycatchers nested at 22 of the 35 forest sites. Because of time constraints, we discontinued field efforts at 9 sites that lacked flycatchers between 2001 and 2004 but added 2 new urban sites in 2005. Beginning in early May of each year, sites were intensively searched for Acadian Flycatchers. Starting in 2004, we documented the date of detection of the first singing male at each site, but we were unable to determine arrival dates for each individual. Thus, we used arrival date of the first male as a metric of colonization for the site. Throughout the breeding season, we captured and banded both male and female Acadian Flycatchers with a unique combination of colored plastic bands to monitor individuals throughout the breeding season. For each individual bird, we measured tarsus length (mm) with dial calipers and unflattened wing chord (mm) with a wing ruler (Pyle 1997). We used a Pesola scale to measure body mass to the nearest 0.5 g. We then combined the tarsus length and wing chord into one

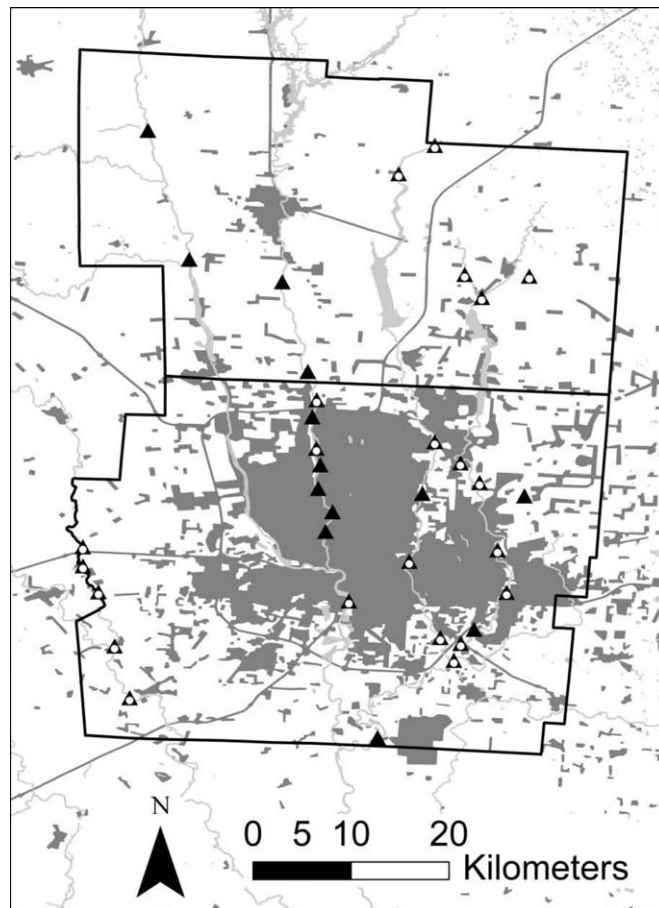


FIG. 1. Location of 35 riparian forest study sites in Ohio monitored for Acadian Flycatchers, 2001–2007. County outlines show Franklin County to the south and Delaware County to the north. Black triangles indicate study sites, and triangles with open circles indicate study sites at which Acadian Flycatchers nested. All 35 sites were used to construct the urban index (see text). Dark gray shading indicates developed land cover, light gray indicates water, and white indicates agriculture or forest.

variable (“body size”) by using the first component of a principal component analysis with these two variables. The eigenvalue of the first component was 1.22 and explained 75% of the variation among individuals. Wing chord and tarsus length loaded equally into the first component (0.71).

We attempted to locate and monitor all nesting attempts of Acadian Flycatchers at each site. Nest searching began 2 to 3 weeks prior to nesting, and each nest was checked every 2 to 5 days by directly examining nest contents (e.g., eggs or nestling). Because of the relatively small size of many of our focal areas, some Acadian Flycatcher territories were on the edge of our defined study areas, and therefore we attempted to find nests and band individuals from territories that were within but also extended beyond the boundaries of our forested study sites. If nest height precluded direct viewing of contents, extended observations of parental behaviors were used to indicate whether adults were incubating eggs, feeding young, or tending fledglings.

For each bird in our focal area, we documented the number of nest attempts, nest fates, and number of young fledged to determine season-long reproductive output. Acadian Flycatchers exhibit high within-season territory fidelity, and therefore we used territory locations to identify unbanded individuals so that we could include their reproductive data. All data were included in analyses except when complete nesting histories were required; in those instances, we excluded cases in which we were not confident that we had located all nesting attempts for a given pair (e.g., when territories were on the edge of our search area or overlapped a river).

Landscape quantification.—The methods and data used to quantify landscape composition are described in detail elsewhere (Rodewald and Shustack 2008). Briefly, within a 1-km-radius area centered on each study site, we calculated proportions of different land-cover types and the number of buildings by inspection of digital orthophotos (2002–2004). We used a 1-km scale because this has previously been shown to be associated with bird communities (Saab 1999, Rodewald and Yahner 2001, Rodewald and Bakermans 2006) and is much larger than the territory size of Acadian Flycatchers (~1 ha; Bakermans and Rodewald 2006). A principal component analysis performed on five variables (percent cover of roads, pavement, lawn, and agriculture and the number of buildings) that described development in the 1-km landscape produced a first principal component that explained 80% of the variation among sites (eigenvalue = 3.99). We hereafter refer to this first component as the “urban index” (i.e., the amount of urbanization in the surrounding landscape; Rodewald and Shustack 2008). The urban index loaded positively for the number of buildings (0.92) and percent cover by roads (0.94), pavement (0.90), and lawn (0.88), but loaded negatively for percentage of cover by agriculture (−0.83). We used the urban index as a continuous variable in regression analyses (see below).

Data analysis.—We estimated the date the first egg was laid in each nest (i.e., clutch initiation date) by observing stage changes in nests. We assumed that Acadian Flycatchers laid 1 egg per day and had a 14-day incubation period and a 14-day nestling period (Whitehead and Taylor 2002). When we observed a nest that transitioned from nest building to laying, laying to incubation, incubation to hatchlings, or hatchlings to fledglings, we backdated to the clutch initiation date. In cases in which direct observation of nest contents was not possible, we used adult behavior (e.g., female sitting on nest, adults feeding nestlings) to indicate change in nest stage and, from this, estimated when eggs had been laid. The median clutch-initiation dates across years varied by only 5 days (Julian days 157, 157, 152, 152, 157, 155, and 157 for 2001–2007, respectively). However, to allow direct comparisons while accounting for annual phase shifts in the distribution of nest initiations, we standardized Julian days for all years to median clutch-initiation date in 2006, which represented the average of the annual medians.

Patterns of reproductive phenology.—We used multiple approaches to describe the reproductive phenology of Acadian Flycatchers in relation to urbanization. At a site level, because dates of detection of singing males were non-normal, we used Spearman rank correlation to test for a relationship between the Julian day of detection of the first male at a site and the urban index for each year separately (2004–2007). Using all nests that we found within 1 day of initiation of nest building and for which we had

clutch initiation dates, we calculated the length of time to build a nest and related that to the day of the year and the urban index using multiple regression. Residuals were normalized by performing a natural log transformation on the number of days between initiation of nest building and clutch initiation. We then used the regression equation to estimate clutch initiation dates for nests for which we documented initiation of nest building but were unable to document clutch initiation (likely because of cryptic nest predation; Maddox and Weatherhead 2006), given the high rates of nest predation in our study system (Rodewald and Shustack 2008).

Among sites, we related the date of the absolute first clutch initiation, median clutch initiation, absolute last clutch initiation, and average length of time between the initiation of the first and last clutches to the urban index using multiple regression. The absolute first clutch initiation was the date the first egg was laid at a site in each year. The median clutch initiation was the median date of all first clutches from females at a site. The last clutch initiation was the date the last clutch at a site was initiated in each year. The length of time between the first and last clutches was calculated for each year and averaged for a site to estimate the average length of time (days) between the first and last clutches of all females at a site. To improve normality of variables and residuals, we added 1.28 to the urban index so that all urban index values were positive and then applied a square-root transformation. We used natural log transformations on the absolute first clutch and median clutch initiation dates. Remaining variables satisfied the assumptions for least-squares regression, so we did not transform those data. For first, median, and last clutches, we included year as a class variable. To compare the overall urban versus rural timing of nesting activity, we classified sites as urban (greater than zero on the urban index) or rural (less than zero on the urban index). We then compared the cumulative distributions for the initiation of nesting and the completion of all nesting activity (i.e., initiation of first clutch through completion, failure, or success of final nest) using Kolmogorov-Smirnov tests.

For each nest, we determined whether the female renested after the previous nest either failed (i.e., abandoned, depredated, or fledged a Brown-headed Cowbird [*Molothrus ater*]) or was successful (fledged ≥ 1 host young). We used logistic regression to relate probability of renesting to prior nest fate, the urban index, and the Julian day of the completion of the previous nest. Further, we examined temporal differences in the production of fledglings between urban and rural sites (i.e., using the dichotomous urban-versus-rural approach described above) by testing the cumulative distribution functions of fledging dates with Kolmogorov-Smirnov tests.

Consequences of variation in reproductive phenology.—We described the potential consequences of altered reproductive phenology in four ways. First, we used individual clutch initiation dates from all females from all years to determine whether clutch initiation date was related to the number of fledglings that a female produced over the course of a breeding season and to the urban index using negative binomial regression. Negative binomial regression is appropriate for overdispersed count data (e.g., number of fledglings) like ours (Allison 1999). We included the urban index in this equation to determine whether there was an effect of urbanization after accounting for timing of nest initiation.

Second, we used logistic exposure (Shaffer 2004) to test for a relationship between Julian day and nest survival. Logistic exposure uses maximum likelihood to estimate nest survival probabilities as a function of continuous variables when the number of days between nest checks varies. Third, we related the number of nesting attempts per female to the date of first clutch initiation using Poisson regression. Poisson regression is used to model count data (e.g., number of nesting attempts) that do not suffer from overdispersion (Allison 1999). Fourth, we used logistic regression to test whether clutch initiation date was related to the probability of resighting a female or male in a subsequent breeding season. Resighting a bird in a future year was a binary response variable (e.g., a bird was either resighted or not). Logistic regression is used to relate explanatory variables to a dependent variable with a binary outcome (Allison 1999).

Causes of variation in reproductive phenology.—We considered several possible factors that might influence reproductive phenology. Because advanced age and experience may facilitate earlier reproduction, we compared clutch initiation dates in year t to those in year $t + 1$ for individually marked birds (t -test) to test for an advancement of laying date as birds aged. Given that arrival date limits clutch initiation date, we used multiple regression to examine how the length of time between date of detection of the first singing male and median clutch initiation date was related to the urban index, including year as a factor. Finally, variation in individual quality may be related to reproductive phenology. Because our previous work indicated that flycatchers settling in urban forests were marginally smaller in body size than those that occupied rural forests (Rodewald and Shustack 2008), we further examined the effect of female body size, wing chord, and mass on clutch initiation date. We focused on females because they are likely more important than males in determining clutch initiation. To do this, we included the urban index in multiple regression models with each of the morphometric variables to explain clutch initiation dates. We only used the first year of data from individually marked females.

Analyses were performed in SAS, version 9.1 (SAS Institute, Cary, North Carolina) or R, version 2.8.0 (R Development Core Team 2008). We set statistical significance at $P < 0.05$ and we report nominal P values throughout. Intercepts (β) and slopes (indicated by $\beta_{\text{PARAMETER NAMES}}$) are reported for regression parameters (\pm SE). For Kolmogorov-Smirnov tests, we report D , the test statistic, and associated P value.

RESULTS

Of the 310 pairs of Acadian Flycatchers that we monitored, 185 had one member of the pair banded, 65 had both the male and female banded, and 60 had neither parent banded. Of these, ~60% were located sufficiently within our focal area and monitored adequately to obtain complete nesting histories. The average annual return rate was 46% for males and 32% for females, and over the course of our study, no bird changed territories within a breeding season (similarly, only 1 male and 1 female changed sites between years). We had little evidence that either sex abandoned a site once nesting began, given that there were only seven cases in which a female that nested in May or June disappeared (left or died) before the end of the breeding season. In eight other cases of female

“disappearance,” we had insufficient observations to determine whether females left or remained to breed. In all, these 15 cases represented <5% of all nesting histories. In two cases, banded males left their site (or died) after initial singing in the spring.

Patterns of reproductive phenology.—In 3 of 4 years for which we have site arrival dates, the date of detection of the first singing male was positively related to the urban index (2004: $\rho = 0.660$, $P < 0.001$, $n = 23$; 2005: $\rho = 0.305$, $P = 0.180$, $n = 21$; 2006: $\rho = 0.546$, $P = 0.006$, $n = 24$; 2007: $\rho = 0.490$, $P = 0.009$, $n = 27$). The length of time between initiation of nest building and clutch initiation was not related to the urban index but was strongly related to the Julian day that nest building was initiated ($F = 37.16$, $df = 2$ and 167 , $P < 0.0001$; $\beta = 3.61 \pm 0.22$; $\beta_{\text{LN(JULIAN DAY)}} = -0.011 \pm 0.0013$, $t = -8.52$, $P < 0.0001$; $\beta_{\text{URBAN INDEX}} = -0.031 \pm 0.031$, $t = -1.03$, $P = 0.305$). As the season progressed, the length of time between the initiation of nest building and the first egg laid in the nest decreased from an average of ~8 days on 20 May to ~4 days on 20 July. We used this regression equation to estimate clutch initiation dates for 37 nests.

The date of the first clutch initiated at a site (using only actually observed laying dates) was positively related to the urban index ($\beta_{\text{SQRT(URBAN INDEX)}} = 0.045 \pm 0.012$, $t = 3.77$, $P < 0.001$, $n = 96$), and this did not vary among years (all $P > 0.12$), with the exception of 2003 ($\beta_{2003} = 0.067 \pm 0.024$, $t = 2.86$, $P = 0.005$). Similarly, median clutch initiation dates (natural log transformed) were later in more urban forests ($\beta_{\text{SQRT(URBAN INDEX)}} = 0.034 \pm 0.010$, $t = 3.37$, $P = 0.001$, $n = 85$), and there was no significant year effect (all $P > 0.18$). The last nests at a site were initiated later in the breeding season in more rural forests ($\beta_{\text{URBAN INDEX}} = -7.344 \pm 1.65$, $t = -4.45$, $P < 0.001$, $n = 96$) with some significant differences among years (2004, 2005, and 2006: all $P < 0.05$). Breeding-season length was shorter in more urban landscapes: the average length of time between the initiation of a female's first clutch and last clutch decreased with the index of urbanization ($\beta_{\text{URBAN INDEX}} = -6.717 \pm 1.73$, $t = -3.881$, $P = 0.001$, $n = 19$). Urban females tended to initiate first clutches later than rural females (rural: $n = 147$ females; urban: $n = 37$ females; $D = 0.302$, $P = 0.009$; Fig. 2); on average, urban females also completed nesting activity sooner than rural females, although

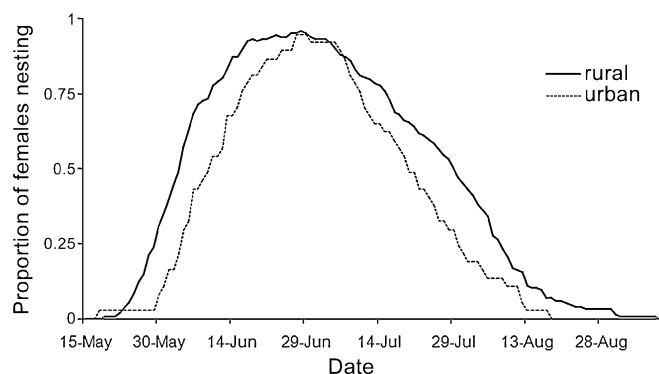


FIG. 2. Proportion of females nesting in rural (urban index < 0) and urban (urban index > 0) forests in central Ohio, 2001–2007. Notice that the urban females tended to initiate nesting later (rural: $n = 147$ females; urban: $n = 37$ females, $D = 0.302$, $P = 0.009$) but that the timing of completion of nesting did not significantly differ between urban and rural females ($D = 0.226$, $P = 0.097$).

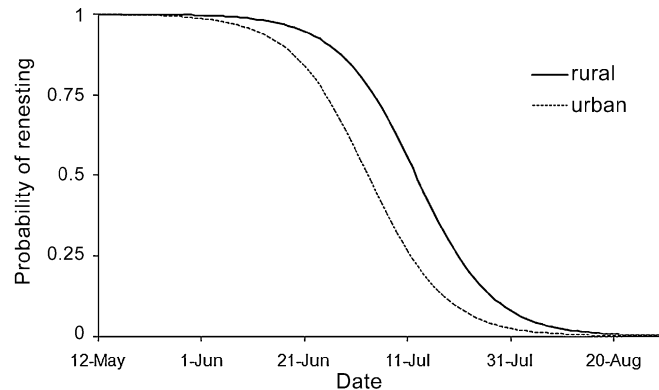


FIG. 3. Probability of reneating by Acadian Flycatchers over the course of the breeding season, for the most rural site (lowest value on urban index) and most urban site (highest value on the urban index) on which the species was detected. The logistic regression equation used to fit these data included the fate of the previous nest as an explanatory variable. The fate of previous nests was nonsignificant (see text), and the figure shows expected reneating probabilities when the previous nest was successful (e.g., fledged young). Notice that the probability of reneating declines sooner in the most urban sites.

the difference was not statistically significant ($D = 0.226$, $P = 0.097$; Fig. 2). Three additional patterns also emerged from the data: (1) as the season progressed, birds were significantly less likely to reneat ($\beta_{\text{JULIAN DAY OF COMPLETION OF PRIOR NEST}} = 0.132 \pm 0.014$, $\chi^2 = 89.53$, $P < 0.001$, $n = 365$ reneating opportunities), (2) birds were less likely to reneat in more urban forests ($\beta_{\text{URBAN INDEX}} = 0.478 \pm 0.20$, $\chi^2 = 5.48$, $P = 0.019$, $n = 365$ reneating opportunities), and (3) prior nest fate was not significantly related to reneating probability ($\beta_{\text{PRIOR FATE}} = 0.1175 \pm 0.35$, $\chi^2 = 0.11$, $P = 0.738$, $n = 365$ reneating opportunities; Fig. 3). There was no significant difference in the timing of fledging between urban (29 fledged nests) and rural sites (143 fledged nests, $D = 0.141$, $P = 0.725$; Fig. 4).

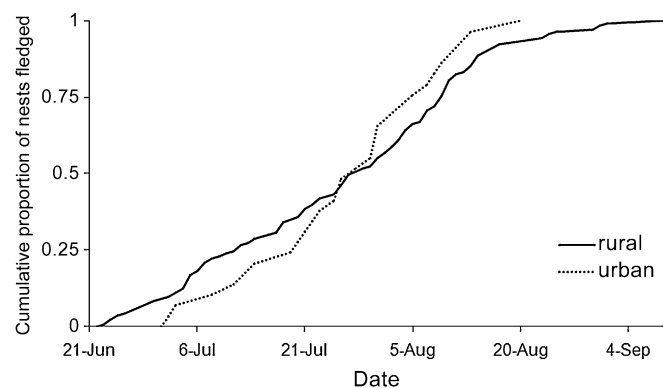


FIG. 4. Proportion of successful nests produced over the course of the breeding season (all years combined) in rural (urban index < 0) and urban (urban index > 0) forests. Difference in timing is nonsignificant, but note the pattern of urban fledglings being produced over a narrower period of time than rural fledglings.

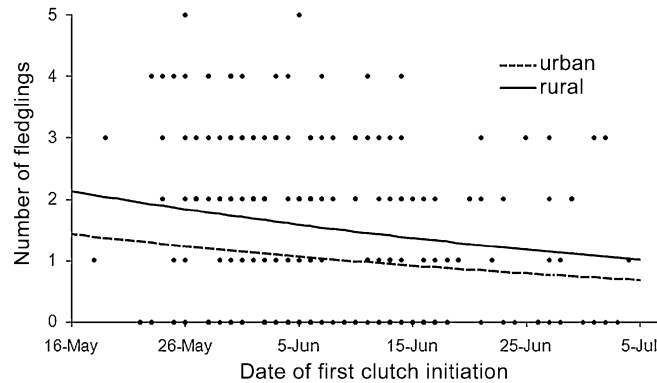


FIG. 5. Number of fledglings produced by Acadian Flycatchers over the breeding season, based on the date that each female initiated its first clutch of the season. Fit lines are based on negative binomial regression. Urban index (see text) was fit as a continuous variable; for purposes of illustration, the expected numbers of fledglings in the most rural site (solid line) and the most urban site (dashed lines) are shown. Note that the expected number of fledglings declined over the season ($\beta_{\text{CLUTCH INITIATION DATE}} = -0.0147$, $t = 7.62$, $P = 0.037$) and that for any given date of clutch initiation, there was a nonsignificant trend for urban birds to fledge ~0.5 fewer fledglings ($\beta_{\text{URBAN INDEX}} = -0.114$, $t = -1.202$, $P = 0.229$, $n = 224$).

Consequences of variation in reproductive phenology.—Birds that initiated clutches earlier in the spring produced more fledglings over the season ($\beta = 2.560 \pm 1.12$, $\beta_{\text{CLUTCH INITIATION DATE}} = -0.0147 \pm 0.0071$, $t = 7.62$, $P = 0.037$), but the additional effect of urbanization did not significantly reduce the number of fledglings, although the trend was toward fewer fledglings in the more urban sites ($\beta_{\text{URBAN INDEX}} = -0.114 \pm 0.095$, $t = -1.202$, $P = 0.229$, $n = 224$; Fig. 5). Nest success was lowest early in the season (~30% nest success as calculated for a 28-day nest cycle) and rose to ~55% in early August ($\beta_{\text{JULIAN DAY}} = 0.0072 \pm 0.003$, $t = 2.089$, $P = 0.037$, $n = 469$ nests, $n = 2,633$ nest check intervals, effective sample size = 8,526 [see Rotella et al. 2004]; Fig. 6). Females that initiated nests later in the season

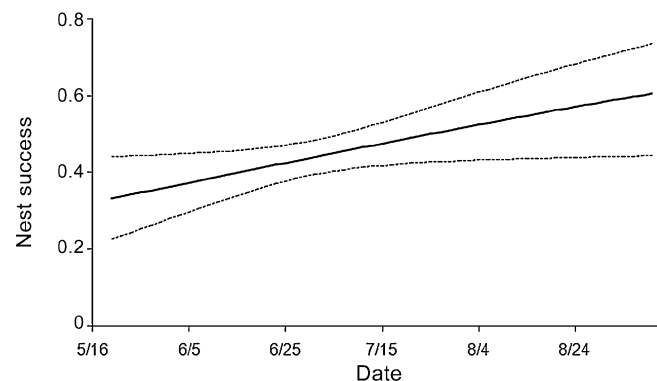


FIG. 6. Nest success (daily survival probability to the 28th power) increased over the breeding season for Acadian Flycatchers in central Ohio from 2001 to 2007. Estimates were based on a logistic exposure model (Shaffer 2004) from 469 nests and 2,633 nest-check intervals.

made fewer nesting attempts ($\beta_{\text{CLUTCH INITIATION DATE}} = -0.027 \pm 0.0062$, $t = -4.32$, $P < 0.001$, $n = 184$). However, the probability of resighting a male ($\beta_{\text{MATE'S CLUTCH INITIATION DATE}} = -0.0143 \pm 0.016$, $t = -0.887$, $P = 0.375$, $n = 132$) or female ($\beta_{\text{CLUTCH INITIATION DATE}} = -0.026 \pm 0.034$, $t = -0.773$, $P = 0.440$, $n = 54$) in a subsequent breeding season was not related to when they initiated their first nest in the previous year.

Causes of variation in reproductive phenology.—We examined three factors as potential causes of variation in reproductive phenology: age and experience, timing of arrival at a site, and individual variation in morphology. We confirmed clutch initiation dates in two years for 17 females. On average, returning females initiated clutches ~3 days earlier than in the previous year; however, the 95% confidence interval (CI) overlapped zero (7.7 days earlier to 1.4 days later in subsequent year). For males, we confirmed 64 instances of clutch initiations in years t and $t + 1$ for the male's mate. Average clutch initiation dates were similar (0.7 days later) among years, and the 95% confidence interval included zero (2.2 days earlier to 3.6 days later in subsequent year). The average length of time between detection of the first singing male and the median clutch-initiation date was 22.2 days (95% CI: 20.1–24.2 days). The length of time between the detection of the first singing male at a site and the median first clutch-initiation date at the site was not related to the urban index ($\beta_{\text{URBAN INDEX}} = -1.595 \pm 1.09$, $t = -1.459$, $P = 0.150$, $n = 66$) with a significant year effect in 2006 ($P = 0.023$). Females with shorter wing chords ($\beta_{\text{WING}} = -1.775 \pm 0.60$, $t = -2.98$, $P = 0.005$, $n = 47$), lower body mass ($\beta_{\text{MASS}} = -1.615 \pm 0.72$, $t = -2.23$, $P = 0.031$, $n = 46$), and smaller body sizes ($\beta_{\text{BODY SIZE}} = -2.830 \pm 1.387$, $t = -2.041$, $P = 0.047$, $n = 46$) initiated first clutches later.

DISCUSSION

Unlike other studies of reproductive phenology, most of which have demonstrated an advancement of breeding date of resident and short-distance migrants in urban areas (Erz 1966, Eden 1985, Bowman and Woolfenden 2001, Rollinson and Jones 2002, Antonov and Atanasova 2003, Schoech and Bowman 2003; reviewed in Chamberlain et al. 2009), we found that breeding was delayed in a tropical migratory bird as our index of urbanization increased. Our 7-year study showed that Acadian Flycatchers also ceased nesting earlier in forests that were surrounded by greater amounts of urban development. Thus, urbanization does not appear to influence the timing of reproduction identically in all bird species.

We found evidence of several reproductive consequences of delayed reproduction in our study population of Acadian Flycatchers that occurred independently of the effects of urbanization. Most striking was that the earliest-nesting females (e.g., mid-May) produced twice as many fledglings as females that initiated a clutch 5 weeks later (i.e., 2 rather than 1 fledgling for the entire breeding season). This pattern is consistent with work on other species (Norris 1993, Verhulst et al. 1995). The greater number of fledglings produced by earlier versus later breeders can arise in several ways. First, clutches laid earlier in the spring tend to be larger than later clutches (Klomp 1970, Perrins 1970). Second, the average number of young fledged per egg laid or the mass of nestlings is often higher earlier than later in the season (Arnold et al. 2006; but see Schwagmeyer and Mock 2008). Third, compared with late-season nests, nesting early allows more time for renesting after a successful or failed nest (Barba et al. 1995, Ortega et al. 2006, Murray and

Nolan 2007). In our system, birds that began nesting later in the season made fewer nesting attempts (i.e., one fewer nest attempt for each 2.5-week delay in nest initiation), with the Julian day being the most important predictor of renesting probability.

There are other possible benefits to early breeding besides a greater number of fledglings. The quality of fledglings from early nests may be higher because those fledglings have more time to gain experience, improve body condition, and prepare for migration than young from later nests. We found that the earliest fledglings in our study were from rural sites, though the overall timing of fledging did not significantly differ between urban and rural landscapes. There was no significant effect of urbanization on the timing of when fledglings were produced. We did not measure fledgling survival, but other studies have documented higher survival rates among birds hatched early than those hatched late in the season (Perrins 1970, Norris 1993, Barba et al. 1995, Møller et al. 2006, Vitz 2008). Adults that initiate and complete nesting earlier may also benefit from having more time or energy to devote to molt (Morales et al. 2007, Gardner et al. 2008) and prepare for winter or migration (Nilsson and Svensson 1996), which may ultimately promote higher winter survival (Wiggins et al. 1998). Because we detected no relationship between clutch initiation date and return rates the following year, we have no evidence to support the idea that early breeding and survival were related.

Paradoxically, given the potential benefits of early breeding, we found that nest success was lowest early in the season—a pattern that likely dampened the effect sizes that we detected. Interestingly, despite the fact that early nests tended to be less successful, early-breeding pairs still derived some benefits (e.g., more nesting attempts and greater number of fledglings) from initiating nests earlier in the season. The pattern of increasing nest survival over the course of a season is not ubiquitous among species, and many conflicting temporal patterns of nest survival have been observed (see references in Wilson et al. 2007). In this same study system, we have also found that nest success of Northern Cardinals (*Cardinalis cardinalis*) increases over the season (Rodewald et al. 2010). Although the underlying causes are unclear, we have evidence that nest sites are relatively limited and not very diverse early in the season before full leaf-out. This homogeneity in nest placement may increase vulnerability to nest predation by promoting density-dependent functional responses of predators (i.e., cause predators to specialize on nests when nests are more abundant within certain strata) or facilitate predators' search efforts early in the season (Martin 1993a, b). However, Acadian Flycatchers initiate breeding 6–8 weeks later than Northern Cardinals, choose very different nest sites, and seem less dependent on foliage concealment (i.e., their nests are often highly visible near the ends of branches; D. Shustack pers. obs.). Because forest foliage density between late May and July increases noticeably, the possibility remains that vegetation phenology affects the ability of nest predators to find Acadian Flycatcher nests.

What accounts for the pattern of shortened nesting activity in urban forests? We consider several possible explanations. First, settlement biases may have driven the pattern. Initiation of nesting was constrained by arrival time, and the first singing males were detected later in more urban forests. Because we lacked arrival dates for individual birds, we could not determine the length of time between arrival at a site and nest initiation on an individual level for

either rural or urban birds. However, our site-level arrival data did not suggest that the time between site arrival and clutch initiation varied with the degree of urban development. Second, the quality of habitat that a bird encountered at a site may have delayed reproduction. For instance, although we found no association between the length of the nest-building period and urbanization, it is possible that females in more urban forests took longer to find a suitable nest site or lay clutches. Third, breeding seasons could end sooner in urban sites if more first nesting attempts by urban birds were successful and those birds did not attempt to double brood. Although we found that urban birds were less likely to renest (Fig. 3), this was not related to whether or not previous nests were successful.

A fourth factor that might constrain nesting seasons in urban forests is individual quality of birds. For instance, if birds that settled in urban forests returned from their wintering grounds later or in poorer condition than birds that settled in rural forests, differences in individual quality may underlie the abbreviated nesting season in urban forests. Differences in individual quality that influence the timing of migration, arrival date, and the quality of the breeding territory may be related to winter territory quality (Marra et al. 1998). We found evidence that heterogeneity among individuals was related to reproductive phenology, and we have previously shown that smaller males and females tended to be found in more urban forests (Rodewald and Shustack 2008). Moving beyond our previous findings, here we show that smaller females also tended to initiate first clutches later. In this way, the smaller size of females that occupied urban forests contributed an additional delay to nest initiation, even after we accounted for the possible effect of urbanization. Although initially our finding would seem to suggest that smaller females are of lower quality, surprisingly, they surpassed larger females in terms of nest survival (Shustack 2008). Information on the relationship between body size and quality in species like Acadian Flycatchers is sparse in the literature, but Murphy (2007) found a negative relationship between female size and lifetime reproductive success in Eastern Kingbirds (*Tyrannus tyrannus*). This pattern may indicate that large females outcompete (e.g., through despotic interactions, *sensu* Fretwell and Lucas's [1970] "ideal despotic habitat selection" model) small females for the best nesting areas, perhaps by earlier arrival after migration (Francis and Cooke 1986, Bowlin 2007) or through direct interactions over mates or territories (Jonart et al. 2007). Competitive interactions might force smaller females into less desirable habitats (i.e., urban forests) and lead to delayed reproductive timing because of the additional time needed to find a territory and a mate (Alatalo et al. 1985). However, once a breeding area is secured, smaller females may have other advantages to breeding, such as securing food for their young (Bowlin and Winkler 2004), increased clutch sizes (Murphy 2007), or possibly nest defense.

Our results demonstrate that the effects of urbanization cannot easily be generalized across species that have different migratory strategies. Although many studies have described advanced breeding phenologies and extended breeding seasons associated with urbanization, we found that the breeding season was truncated for a tropical migratory species because initial clutch laying dates were delayed and because breeding tended to end sooner in the later part of the season. Delayed reproduction was also associated with fewer fledglings. We suggest that delayed reproduction by Acadian Flycatchers in urban forests is indirectly caused

by the quality of urban versus rural forests because it appears that smaller (i.e., lower-quality) birds either select or are relegated to urban forests. This study adds to the growing literature showing that urbanization can elicit complex, and sometimes unpredictable, behavioral and demographic responses by animals.

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